Plant invaders open opportunities for novel ecosystems under climate stress

Dissertation

zur Erlangung des akademischen Grades einer
Doktorin der Naturwissenschaften (Dr. rer. nat.)
an der Fakultät für Biologie, Chemie und Geowissenschaften
der Universität Bayreuth

vorgelegt von

Vanessa Maria Sabrina Vetter-König

aus Ludwigsburg, Baden-Württemberg

Bayreuth, 2019

Die vorliegende Arbeit wurde in der Zeit von August 2015 bis Januar 2017 in Landau am Lehrstuhl Geoökologie/Physische Geographie der Universität Landau unter Betreuung von Frau Dr. Constanze Buhk, sowie von Februar 2017 bis August 2019 in Bayreuth am Lehrstuhl Störungsökologie unter der Betreuung von Frau Professor Dr. Anke Jentsch (Professur für Störungsökologie, Universität Bayreuth) angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erlangung des akademischen Grades einer Doktorin der Naturwissenschaften (Dr. rer. Nat.).

Dissertation eingereicht am: 05.09.2019

Zulassung durch die Promotionskommission: 10.09.2019

Wissenschaftliches Kolloquium: 29.05.2020

Amtierender Dekan: Prof. Dr. Matthias Breuning

Prüfungsausschuss:

Prof. Dr. Anke Jentsch	(Gutachterin)
Prof. Dr. Vicky Temperton	(Gutachterin)
Prof. Dr. Thomas Köllner	(Vorsitz)
Prof. Dr. Bettina Engelbrecht	

Weiterer Gutachter: Prof. Dr. Steven Higgins

“Nature is ever at work building and pulling down, creating and destroying, keeping everything whirling and flowing, allowing no rest but in rhythmical motion, chasing everything in endless song out of one beautiful form into another.” – John Muir

“None of Nature’s landscapes are ugly so long as they are wild.” – John Muir

TABLE OF CONTENTS

1 SUMMARY

1.1 Summary

The ecological novelty phenomenon (*sensu* Kueffer 2014) is driven by the human-induced rapid environmental changes of the Anthropocene and comprises novel organisms (e.g. non-native species; *sensu* Jeschke et al. 2013) as well as the emergence of novel ecosystems (*sensu* Hobbs et al. 2009). Novel ecosystems are systems with a new combination of species that differ in their composition, function, and/or appearance from present and historic systems (*sensu* Landres et al. 1999). Global change drivers like climate change and the invasion by non-native species may negatively affect native ecosystem stability and functioning and thus, either lead to severe degradations of ecosystems or to the enhanced emergence of novel ecosystems. Both is of scientific and conservation concern as this process is often accompanied by a reduction in ecosystem services and biodiversity, which in turn negatively affects society.

With the five manuscripts presented in this thesis, I contribute to the understanding of the drivers of novel ecosystems: i) the performance of invasive plants under various environmental conditions, ii) their interaction with extreme weather events, iii) their impact on native plant communities, iv) the estimation of their likely spread under climate change conditions, and v) the interaction of invasive plants and extreme weather events on the diversity-stability relationship of native plant communities. Thus, this thesis contributes to the understanding of invasion processes, disturbance ecology and implicitly community assembly. I use a versatile approach that combines experiments with data recording in the field as well as species distribution modelling.

Plant invaders, ecosystem engineers (such as *Lupinus polyphyllus* and *Lupinus nootkatensis)* and non-native species which have not previously been labeled as ecosystem engineers (such as *Senecio inaequidens* and *Verbascum thapsus*), will certainly open opportunities for the emergence of novel ecosystems under climate stress. Invaders are able to germinate under a broad range of climatic conditions (manuscript 1), enabling the species to successfully establish themselves even under an uncertain range of future climate conditions. Seeds from different source regions (proveniences, ecotypes) cover a broader range of climatic conditions in native ranges and could therefore increase invasiveness in target regions. Invaders show a relatively better performance under combined drought and competition effects than common native grassland species of Europe (manuscript 2, 4). Especially invaders from warm origins (like *Senecio inaequidens*) may profit from a drier future climate in Europe. Habitat suitability for the two legume ecosystem engineers is projected to increase under future climate change scenarios (manuscript 3, 5). Consequently, the spreading of invaders into the impacted native communities of adjacent ecosystems may be facilitated by the disturbance caused due to extreme drought events. Therefore, the transformation of natural into novel ecosystems could progress faster and without direct human intervention under future climate warming. Both invader types are able to influence the recovery of native species communities and thus, further promote the formation of novel ecosystems under climate stress in addition to their sheer presence. The invasive legumes are able to change species richness and composition as well as the nutrient pool of the invaded habitats (manuscript 5), two effects that very likely lead to the formation of novel ecosystems.

The emergence of novel ecosystems due to invader presence can have very different implications reaching from loss of biodiversity (*Lupinus nootkatensis* in species-rich heathland-ecosystems of Iceland; manuscript 5) and a deterioration of the diversity-stability relationship (*Lupinus polyphyllus* in semi-natural biodiversity-rich European grasslands; manuscript 4) to the increase of biodiversity in highly degraded ecosystems (*Lupinus nootkatensis* in Iceland; manuscript 5). Invasive legume ecosystem engineers impact and change native ecosystem services (e.g. productivity, habitat provisioning, fodder), but also provide new ecosystem services (e.g. stabilization and improvement of soils). Whether those services are perceived “positive” or “negative” depends on the affected habitat. The novel ecosystems considered in this thesis show a reduction in biodiversity compared to native ecosystems of the same successional stage (manuscript 5), and thus, may contribute to global homogenization and species loss. Summing up, this thesis confirms that invasive species and extreme climatic events will work as catalysts for the emergence of novel ecosystems, individually but especially when global change drivers act in synchrony.

Based on the result of this thesis, I suggest the design for a new global experiment (chapter 6) which tests the formation of novel ecosystems under the combined pressures of invasive species and extreme drought events. These globally distributed invader case studies provide new insights into invader impact, susceptibility of native communities (to invasive species and extreme drought events), community assembly rules, spatial and temporal resistance and recovery trajectories of grasslands. The data and results collected in this experiment will inform science/ecology and conservation as well as may be further used to model and project species distributions and ecosystem regime shifts.

1.2 Zusammenfassung

Das Phänomen der ökologischen Neuheiten (*sensu* Kueffer et al. 2014) wird durch die vom Menschen verursachten raschen Umweltveränderungen des Anthropozän vorangetrieben und umfasst sowohl neuartige Organismen (z.B. nicht-heimische Arten; *sensu* Jeschke et al. 2013) als auch die Entstehung von neuen Ökosystemen (*sensu* Hobbs et al. 2009). Neuartige Ökosysteme sind Systeme mit einer neuen Kombination von Arten, die sich in ihrer Zusammensetzung, Funktion und / oder Erscheinungsform von gegenwärtigen und historischen Systemen unterscheiden (*sensu* Landres et al. 1999). Der globale Wandel mit Triebfedern wie dem Klimawandel und der Invasion nicht-heimischer Arten kann die Stabilität und Funktionsweise heimischer Ökosysteme negativ beeinflussen und somit entweder zu einer Veränderung der Ökosysteme oder zur verstärkten Entstehung neuer Ökosysteme führen. Beides ist von wissenschaftlicher und naturschutzfachlicher Bedeutung, da dieser Prozess häufig mit einer Verringerung der Ökosystemdienstleistungen sowie der biologischen Vielfalt einhergeht, was sich wiederum negativ auf die Gesellschaft auswirken könnte.

Mit den fünf in dieser Arbeit vorgestellten Manuskripten trage ich zum Verständnis der ursächlichen Entstehung neuartiger Ökosysteme bei: i) der Leistung invasiver Pflanzen unter verschiedenen Umweltbedingungen, ii) ihrer Interaktion mit extremen Wetterereignissen, iii) ihrer Auswirkung auf einheimische Pflanzengemeinschaften , iv) die Abschätzung ihrer wahrscheinlichen Ausbreitung unter zukünftigen Klimabedingungen sowie v) das Zusammenwirken invasiver Pflanzen und extremer Wetterereignisse auf die Diversitäts-Stabilitäts-Beziehung einheimischer Pflanzengemeinschaften. Somit trägt diese Arbeit zum Verständnis von Invasionsprozessen, der Störungsökologie sowie implizit der Zusammensetzung von Pflanzengemeinschaften bei. Ich verwende hierzu einen vielfältigen Ansatz aus Experimenten, Erhebung von Felddaten und Modellierung.

Invasive Pflanzenarten, Ökosystemingenieure (wie *Lupinus polyphyllus* und *Lupinus nootkatensis*) und nicht-einheimische Arten, die zuvor nicht als Ökosystemingenieure eingestuft wurden (wie *Senecio inaequidens* und *Verbascum thapsus*), werden sehr wahrscheinlich zur Entstehung neuartiger Ökosysteme unter Klimastress führen. Die Invasoren waren in der Lage unter den verschiedensten klimatischen Bedingungen zu keimen und können sich dadurch vermutlich auch unter ungewissen zukünftigen Klimabedingungen erfolgreich etablieren (Manuskript 1). Da Samen aus verschiedenen Herkunftsgebieten (Provenienzen, Ökotypen) eine größere Klimabandbreite abdecken und dadurch zu einer höheren Invasivität führen können, sollte deren Einfuhr vermieden werden. Zudem zeigten die untersuchten invasiven Arten unter kombinierten Dürre- und Konkurrenzbedingungen eine relativ bessere Leistung als die einheimischen Grünlandarten (Manuskript 2, 4). Insbesondere invasive Arten aus warmen Herkunftsgebieten (wie *Senecio inaequidens*) können von den zunehmend trockeneren klimatischen Bedingungen in Zentraleuropa profitieren. Darüber hinaus wird davon ausgegangen, dass

die Lebensraumeignung der beiden in dieser Arbeit untersuchten Leguminosen-Ökosystemingenieure unter zukünftigen Klima-Szenarien zunimmt (Manuskript 3, 5). Die Ausbreitung invasiver Arten in benachbarte Ökosysteme wird aufgrund der Störung der einheimischen Gemeinschaften durch extreme Dürreereignisse in Zukunft wohl erleichtert. Daher könnte die Umwandlung von natürlichen in neue Ökosysteme aufgrund der Klimaerwärmung in Zukunft schneller und ohne direkten menschlichen Eingriff vonstatten gehen. Beide Invasorentypen sind in der Lage, die Erholung einheimischer Artengemeinschaften zu beeinflussen und somit die Bildung neuer Ökosysteme unter Klimastress zusätzlich zu ihrer bloßen Präsenz zu fördern. Die invasiven Leguminosen sind in der Lage, Artenreichtum und Artenzusammensetzung sowie den Nährstoffhaushalt der betroffenen Lebensräume zu verändern (Manuskript 5). Aufgrund dieser beiden Faktoren wird die Ansiedlung dieser Arten höchstwahrscheinlich zur Bildung neuer Ökosysteme führen.

Die Entstehung neuer Ökosysteme aufgrund der Anwesenheit von invasiven Pflanzenarten kann sehr unterschiedliche Auswirkungen auf die betroffenen Systeme haben, die vom Verlust der biologischen Vielfalt (z.B. *Lupinus nootkatensis* in artenreichen Heidelandschaften Islands; Manuskript 5) über eine die Verschlechterung der Diversitäts-Stabilitäts-Beziehung (z.B. *Lupinus polyphyllus* in artenreichem halbnatürlichem Grünland in Europa; Manuskript 4) bis hin zur Zunahme der biologischen Vielfalt (hier Artenreichtum) in stark degradierten Ökosystemen (z.B. *Lupinus nootkatensis* in Island; Manuskript 5) reichen. Invasive Ökosystemingenieure, hier die Lupinen, beeinflussen und verändern native Ökosystemdienstleistungen einheimischer Systeme (z.B. Produktivität, Bereitstellung von Lebensräumen, Futter), führen aber gleichzeitig auch zur Entstehung neuer Dienstleistungen (z.B. Stabilisierung und Verbesserung von Böden). Ob diese Dienstleistungen als „positiv“ oder „negativ“ wahrgenommen werden, hängt vom betroffenen Lebensraum ab. Die in dieser Arbeit betrachteten neuartigen Ökosysteme zeigen eine Verringerung der Artenvielfalt im Vergleich zu einheimischen Ökosystemen im selben Sukzessionsstadium (Manuskript 5) und können somit zur globalen Homogenisierung und zum Artenverlust beitragen. Zusammenfassend bestätigt meine Doktorarbeit, dass invasive Arten und extreme Klimaereignisse als Katalysatoren für die Entstehung neuer Ökosysteme fungieren, insbesondere, wenn beide Treiber des globalen Wandels synchron agieren.

Basierend auf den Ergebnissen dieser Doktorarbeit, schlage ich den Entwurf eines neuen globalen Experiments vor (Kapitel 6), welches die Entstehung neuartiger Ökosysteme im Zusammenspiel von invasiven Arten und extremen Dürreereignissen untersucht. Basierend auf global verteilten Fallstudien können neue Erkenntnisse zu den Auswirkungen invasiver Arten, der Anfälligkeit einheimischer Pflanzengemeinschaften gegenüber invasiven Arten und Extremwetterereignissen, der Zusammensetzung von Pflanzengemeinschaften, sowie den räumlichen und zeitlichen Verlauf der Resistenz und Erholung von Grünland gewonnen werden. Die in diesem Experiment erhobenen Daten und Ergebnisse werden die Wissenschaft / Ökologie und den Naturschutz beeinflussen und können verwendet werden, um Artenverbreitungen sowie Zustandsänderungen von Ökosystemen zu modellieren und zu projizieren.

2 GLOSSARY

Box 1: Glossary

Abiotic change: All sorts of changes that affect species, communities, and ecosystems but are not initiated by living organisms; e.g. climate change, land use change, pollution, urbanization, nitrogen deposition, nutrient enrichment.

Biodiversity: Diversity of all forms of life at all levels of organization (species, ecosystems, genes), as well as the species and communities and the processes that connect them to each other and their abiotic environment.

Biotic change: All sorts of change that are initiated by the presence or absence of living organisms; e.g. decline or loss of species, invasion of non-native species.

Chronic drought: Chronic deprivation of part of the natural precipitation (e.g. 50% or 80% rainfall reduction), usually over longer periods of time (e.g. months or years). Simulated by the usage of rain-out stripes above the experimental plots.

Climatic extreme: Period of statistical climate extremity. Defined either by 1) exceeding the statistical frequency of defined values in a certain period (extreme event of 100 or 1000 year recurrence; extreme value theory) or by 2) exceeding a defined absolute limit. See pulse drought. (IPCC, 2013)

Combined change: Combination of abiotic and biotic changes; see ecosystem engineer.

Disturbance: External stresses and shocks. A temporary change in the abiotic conditions of an ecosystem or the intrinsic processes defining an ecosystem, usually resulting in long-term changes/effects on ecosystem characteristics and functioning.

Ecosystem engineer: Organisms (plants/animals) that are able to change the biotic interactions as well as the biogeochemical cycling of the affected habitat. (Invasive) ecosystem engineers have the potential to change the existing species composition as well as the prevailing abiotic conditions by changing the physical properties of the affected habitat (e.g. nutrient availability, microclimate).

Fundamental niche: N-dimensional hypervolume. The full range of abiotic environmental conditions within which a certain species is able to survive and reproduce without the interference of other species.

HIREC: **H**uman **i**nduced **r**apid **e**nvironmental **c**hange. Emphasis to anthropogenically driven and occurrence at a historically rapid pace. They can be either abiotic or biotic in nature or a combination of both (invasive ecosystem engineers). HIRECs impact natural ecosystems or the biosphere (Robertson et al., 2013; Sih et al., 2011).

Hybrid system: Ecosystem in-between a novel and a historic ecosystem. These ecosystems still retain some of the characteristics of the historic system, while other characteristics already lie outside the historic range of variability (Hobbs et al. 2009).

Invasion window: Time lag between the beginning of the recovery of an invasive species and the native species. Occurs as soon as the abiotic conditions (e.g. after a pulse drought event) return to favor the intruder and ends when the indigenous species' recovery reaches a point where they are again competitive (biotic threshold) (Diez et al., 2012).

Invasiveness: Invasion potential. Capacity of an non-native species, once introduced to a new range, to establish, survive and finally reproduce and spread.

Non-engineering invasive: Non-native species without the characteristics of an ecosystem engineer.

Novel ecosystem/ecological novelty: Ecosystems resulting from HIREC that differ in composition, function, and/or appearance from historic as well as present natural ecosystems. Novel ecosystems show three characteristics: 1) consist of native and non-native organisms, 2) persistent without human intervention, 3) restoration to historical conditions is not possible. (Higgs, 2017; Hobbs et al., 2009; Robertson et al., 2013)

Pulse drought: For a short, defined period of time (days to weeks), the natural precipitate of a system is completely withdrawn. Pulse drought events in this thesis were simulated by covering the experimental plots with rain-out shelters for a defined amount of days. Gumble I distributions were fitted to the reference period of 1961-1990 to calculate the amount of days for an extreme pulse drought event with a recurrence rate of 1000 years.

Realized niche: Part of the fundamental niche. Narrowed (e.g. by competition) or extended range (e.g. by facilitation) of abiotic environmental conditions occupied by a species due to interactions with other species.

Resilience: Includes the (a) resistance, (b) recovery and (c) adaptability of a system. (a) The amount of stress/disturbance a system can absorb without deviating significantly from its initial state, (b) the degree to which a system is able to return to pre-disturbance levels induced by self-organization (c) the degree to which a system is able to adapt to new conditions (Folke et al., 2002)

Resistance: Resistance is defined as the degree of change of an ecosystem property in response to a disturbance event; no change would indicate complete resistance.

Recovery: Recovery is defined as the degree to which an ecosystem property returns to control levels after the cessation of the disturbance event.

Vulnerability: Antonym of resistance, recovery and resilience. Likelihood of exposure to disturbance events, sensitivity of the systems to those events as well as the capability of the system to tolerate/resist and recover from disturbance events due to adaptive measures (Folke et al., 2002).

3 INTRODUCTION

3.1 Ecological novelty

We live in the Anthropocene, an epoch that is named after its predominant forming force: us humans (Lewis and Maslin 2015; Clement and Standish 2018). We live in a time in which human-induced rapid environmental change (HIREC; e.g. climate change, invasive species; see Glossary) is occurring at an unprecedented speed and scale (Sih et al. 2011; Robertson et al. 2013). And, we live in a time when humanity is pushing, more or less, all living beings, that are unable to keep pace with the rapid changes we cause, to the edge of existence (Barnosky et al. 2017; Diaz et al. 2019).

The environmental changes of the Anthropocene can be summarized under the term ‘ecological novelty’ (Kueffer 2014). Human-induced rapid environmental change (HIREC) leads to the formation of novel ecosystems, a phenomenon we are increasingly confronted with and a phenomenon that has not only an ecological but also a social component (socio-ecological novelty) (Folke et al. 2002; Hobbs et al. 2006; Robertson et al. 2013; Collier and Devitt 2016), as novel ecosystems likely impact ecosystem services and biodiversity which in turn directly or indirectly benefit society (Collier, 2014; Evers et al., 2018; Figure 1). Novel ecosystems are either designed or are self-assembling (Higgs 2017; Evers et al. 2018), while the latter emerge either due to degradation or invasion of wild/semi-natural ecosystems or due to the abandonment of intensively managed systems (Hobbs et al., 2006; Figure 1). Thus, they are self-organizing, persistent systems (but induced by human-caused changes) with a new combination of species that differ not only in their composition, function, and/or appearance from present and historic systems, but may also show novel disturbance regimes or novel rules of interaction and selection pressures that have not occurred previously within a given biome (Hobbs et al. 2009; Robertson et al. 2013; Morse et al. 2014; Higgs 2017; Evers et al. 2018). This new set or combination of species that form novel ecosystems often comprises novel organisms, which can be either non-native species, synthetic organisms (e.g. genetically modified organisms) or pathogens that have evolved towards the use of novel hosts (Jeschke et al. 2013).

The disturbances and changes which induce novel ecosystems may affect any variable that can be used to characterize an ecosystem or habitat (Grimm and Wissel, 1997; Higgs, 2017; Figure 1). Those disturbances may be induced by primarily biotic changes (extinction and/or invasion), primarily abiotic changes (e.g. land use or climate change) or a combination of abiotic and biotic changes (Hobbs et al. 2009). And the reaction of the recipient habitat will depend on the strength, frequency, spatial and temporal pattern, and regularity of the respective disturbance (Grimm and Wissel 1997). However, whether climate change on its own qualifies as a driver of novel ecosystems or not is discussed controversially and thus, depends on the respective definition on the emergence of novel ecosystem (Hobbs et al. 2009; Morse et al. 2014; Truitt et al. 2015; Higgs 2017). According to Morse et al. (2014), ecosystems arising only by indirect anthropogenic stressors, e.g. climate change, do not qualify as novel ecosystems, because those large scale stressors affect all ecosystems and thus may not serve as a qualifier to distinguish between degraded, impacted and novel ecosystems. While in other definitions, climate change plays an explicit and important role in the emergence of novel ecosystems (e.g. Williams and Jackson 2007; Hobbs et al. 2014). In this thesis, however, the focus lies on the combined effects of climate change (abiotic change) and species invasions (biotic change), which together definitely have the potential to create novel ecosystems (Doney et al. 2012).

The changes induced by HIREC are comprehensive as many factors, e.g. physical, chemical and biological factors, change in parallels (Kueffer 2014; Hobbs et al. 2014). The speed and scale of change as well as the interconnectedness of its factors, creates a high level of uncertainty (scientifically, social, conservational, ecological) and this may not only destabilize ecological, but also social structures at various levels (Kueffer 2014; Collier and Devitt 2016; Clement and Standish 2018). Owing to the interactions and synergies among the multiple factors, a given change can result in very different or even opposing ecological effects in different places (Bridgewater et al. 2011; Kueffer et al. 2013). However, there is still an ongoing discussion if ecological novelty, and consequently novel ecosystems, only emerge through human action or lack thereof (Evers et al. 2018).

There are three possible responses of HIREC-affected systems: 1) the system is able to remain in, or near, its historical state (*sensu* resistance/stability); changes only occur within the historical range of variability of the ecosystem, 2) the system becomes altered into a hybrid system with some new features (e.g. new species or new abiotic conditions) but also still holding some of its old features, 3) with ongoing pressure, the system experiences such a degree of change that it may be considered as a novel ecosystem with nearly completely new features (abiotic and biotic) (Hobbs et al. 2009). Novel ecosystems may represent an alternative stable state of a system, which got pushed over the tipping point by HIREC (Collier and Devitt 2016; Higgs 2017). Hence, they are potentially irreversibly changed (Hobbs et al. 2009). Restoration is only feasible if either abiotic conditions or the biotic composition remain near the historical state of the ecosystem. If one factor is altered, restoration in terms of ecosystem structure and function is feasible, but if both abiotic conditions and biotic composition are altered simultaneously, a novel ecosystem emerge and restoration is difficult or and/or impossible (Figure 1b, Hobbs et al. 2009).

However, to date it is not clear if the genesis of a novel ecosystem is necessarily preceded by a tipping point, by which one alternative stable state of a system is separated from another. Multiple equilibria may be possible, all with presumably different characteristics and formed by different pressures or attractors (Scheffer and Carpenter 2003). Tipping points may be seen as catalysts of change, because when crossed they usually induce a big change (Scheffer and Carpenter 2003). Additionally, not all novel ecosystems may be stable against further changes or are able to provide crucial ecosystem services (e.g. habitat, food/resources for other species) (Hobbs et al. 2009). Therefore, conservation should aim for the provision of ecosystem services, biodiversity conservation, and ecological integrity of novel ecosystems (Kueffer and Kaiser-Bunbury 2014; Evers et al. 2018; Clement and Standish 2018), as a return to a historic state of a system is – owing to the serious changes – difficult to achieve, very expensive or impossible and often not desirable (Folke et al. 2002; Bridgewater et al. 2011; Larson et al. 2013; Collier and Devitt 2016; Higgs 2017, see Figure 1d). Currently, there is only little guidance available on the management of novel ecosystems (Higgs 2017) and the observed effects on biodiversity and provisioning of ecosystem functions range from tradeoffs and disservices to protection against further degradation (Kueffer et al. 2010; Evers et al. 2018).

The fact that ecologists are not able to predict ecosystem shifts in advance, but to understand them retrospectively (Folke et al. 2004; Russell et al. 2012) and only recently new methods are developed to predict catastrophic regime shifts (e.g. Weissmann and Shnerb 2015), illustrates the need for further research, especially on the topics of catalysts, effects and limitations of the ecological novelty phenomena.

This thesis contributes to the understanding of the role of invasive species (biotic HIREC) and extreme weather events (abiotic HIREC) on the emergence of novel ecosystems in European semi-natural grasslands.

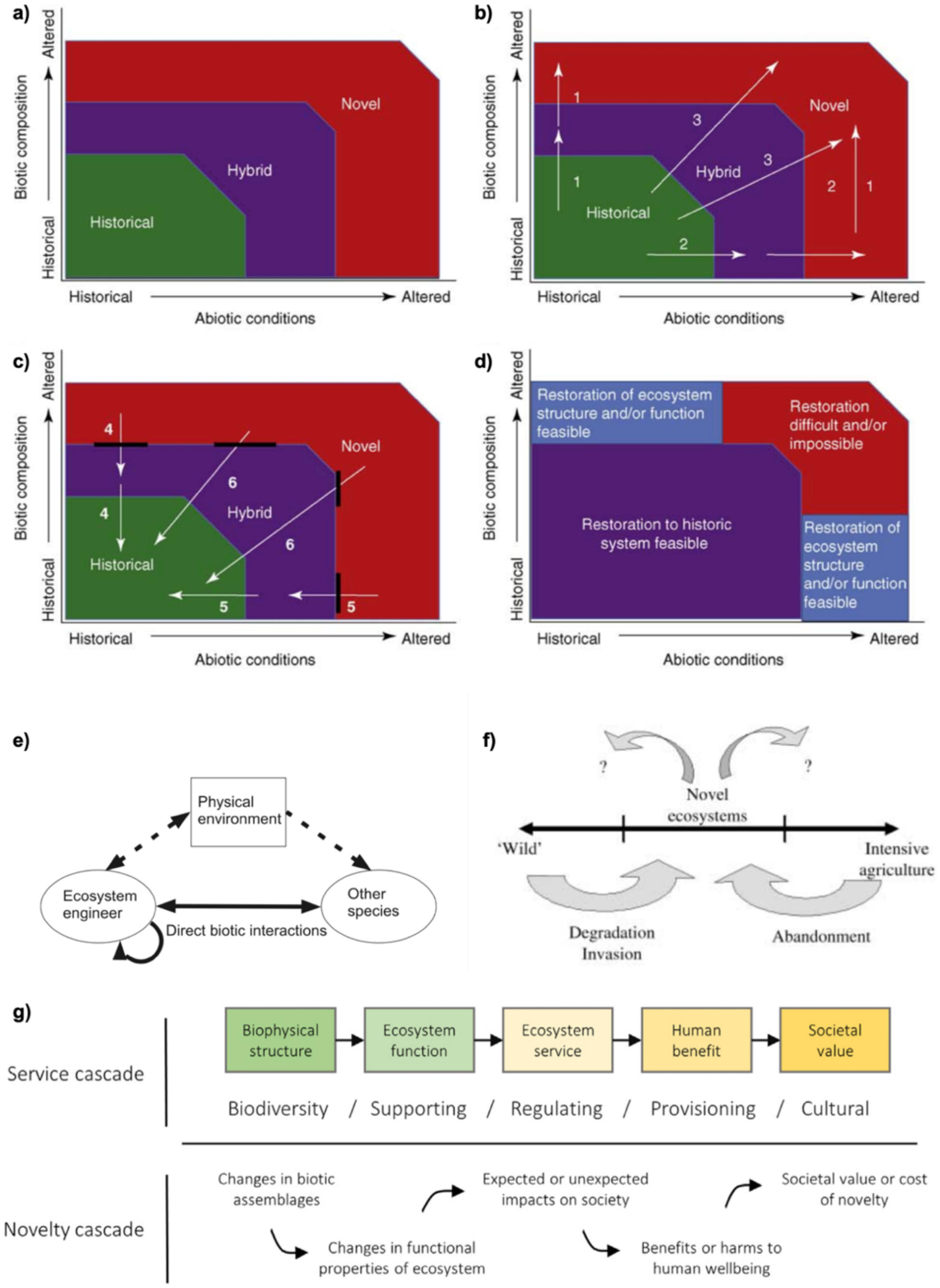


Figure 1: Genesis and management of novel ecosystems (a-d), impact of ecosystem engineers (e), human-induced rapid environmental changes (f), service and novelty cascade (g). **(a)** The three main types of ecosystem state. Stages merge from one to another by changing abiotic and biotic conditions. **(b)** Potential pathways of development from historic to novel ecosystems, depending on the main causes of change: biotic (pathway 1) or abiotic (pathway 2) or a combination of both (pathway 3). **(c)** Possible conservation measures reversing the pathways of development depending on the former predominant forming force: e.g. pathway 4 removal of invasive species; pathway 5 amelioration of altered environmental conditions; pathway 6 a combination of both. Restoration thresholds (black lines) separate novel ecosystems from less altered hybrid and historical systems. They might only be crossed, and thus, the system might only be returned to a former state, by significant restoration effort. **(d)** Feasibility of different management and restoration strategies. **(e)** Ecosystem engineers interact with other species (and themselves) either direct or by changing the physical environment in which they and other species live. **(f)** Novel ecosystems are formed by human-induced rapid environmental change and emerge either due to the degradation or invasion of wild systems or due to the abandonment of agricultural systems. The question if and to which extent these changes are reversible remains to be solved. **(g)** Service and novelty cascade: illustrates how novel ecosystems may differ from the structure and functioning of historic ecosystems and how this interferes with the services society derives from ecosystem. Figure 1 is based on figures modified from Hobbs et al. (2006, 2009) (a-d,f), Hastings et al. (2007) (e) and Evers et al. (2018) (g).

3.2 Climate change and extreme weather events

Climate change (IPCC 2013) is one of the most prominent and obvious human-induced abiotic changes (abiotic HIREC) that leads, already today but certainly even more in the future, to the formation of novel ecosystems (*sensu* Hobbs et al., 2009), as it may pave the way for further change, e.g. species invasions.

Climate change will lead to a change in so-called trends and events (Jentsch et al. 2007; Ummenhofer and Meehl 2017), while both effects will likely result in the emergence of novel ecosystems, the main difference between them may be seen in the speed and intensity at which abiotic change occurs. Climate trends are long-term developments of climate parameters. One example for climate trends are the changes in average conditions, e.g. the rise of the global average temperature, and the increase in CO_2, but we also observe increasing trends in climatic extreme events (Seneviratne et al. 2012; IPCC 2014). The frequency and magnitude of extreme weather events e.g. drought, heat waves, heavy rainfall and storms, is also projected to increase due to global climate change (Seneviratne et al. 2012; Tippett et al. 2016; Lehner et al. 2017; Bathiany et al. 2018). As the global average temperature rises, the percentage probability of the occurrence of heat waves increases. Owing to the warmer atmosphere, the overall evaporation increases. In addition, the rise of the global average temperature increases the percentage of water vapor which can be stored in the atmosphere (Bathiany et al. 2018). This favors the occurrence of droughts in some regions (Lehner et al. 2017; Cook et al. 2018) and the occurrence of heavy rainfall events in others (King and Karoly 2017). The probability of occurrence of storms is also likely to increase, because due to the raised water vapor in the atmosphere more latent energy is available. Summing up, the overall variability of the climate increases (IPCC 2013; Bathiany et al. 2018).

In Europe, climate change will likely lead to a rise of the mean air temperature, as well as a shift of precipitation, e.g. lack of precipitation in summer for Central Europe, increase of extreme precipitation for Northern Europe especially in winter, decrease of precipitation in Southern Europe (IPCC 2014). For Europe, the rise in winter temperature is projected to be more rapidly than in summer (Andrade et al. 2012; Vautard et al. 2014), and is accompanied by a decrease in number of frost days and snow cover days (Jylhä et al. 2008). The frequency and magnitude of extreme climatic events, such as drought (Dai 2013), are also predicted to increase in Europe as a result of climate change (Seneviratne et al. 2012; Lehner et al. 2017).

Minimum winter temperatures are currently the limiting factor for many invasive species originating from warmer regions (Kreyling 2010). Consequently, the rise of winter temperatures and reduced frosts in temperate systems due climate change may lead to an increase of invasion processes into these systems, as the distribution limits are gradually reduced and a more suitable habitat is provided (Thuiller et al. 2007; Kreyling and Henry 2011; Sheppard et al. 2014, 2016). Hence, invasive species from native ranges warmer than the introduced ranges, may benefit from climate change as their mortality due to cold temperatures decreases and they are potentially well adapted to warm and dry future climates (Vilà et al. 2007). In this thesis, I evaluate the impact of extreme drought events on the resistance and recovery of both native as well as on invasive species originating from warm (such as *Senecio inaequidens*) and cool climates (such as *Lupinus polyphyllus* and *Lupinus nootkatensis*) and thus, contribute to the risk assessment of these two invader types (performance, impact on native species, spreading ability) under a future higher climate variability.

Altered drought regimes in semi-natural grasslands may lead to plant mortality, shifts in species composition, degradation and desertification, and erosion (Craine et al., 2012; Reichstein et al., 2013; Wang et al., 2011). Altered droughts can cause lasting effects on community composition by selecting for drought tolerant species, resulting in dominance shifts and/or local extinction of drought intolerant species (Reichstein et al. 2013; Alba et al. 2017; Török et al. 2018). Such drought-induced changes in the plant community structure of grasslands may subsequently affect plant productivity as well as ecosystem functioning and the delivery of ecosystem services (Cantarel et al. 2013; Reichstein et al. 2013; Caldeira et al. 2015), e.g. water flow regulation, nutrient cycling, successional trajectory, conservation value (Dengler and Tischew 2018; Török et al. 2018). However, some European grasslands have proven high resistance towards extreme drought events (Jentsch et al. 2011).

Invasive species (biotic HIREC) and climate change (abiotic HIREC) may simultaneously affect biodiversity and thus ecosystem functioning and stability (Kreyling et al. 2008; Wardle et al. 2011; Vilà et al. 2011; Reichstein et al. 2013; Murphy and Romanuk 2014; Hautier et al. 2018). It is unclear if the diversity-stability-relationship is maintained in the presence of an invader (see e.g. Pinto and Ortega, 2016). Disturbances, such as extreme drought events, which may cause productivity losses and species community shifts in grasslands, may enhance the invasion risk (Hautier et al., 2018; Török et al., 2018; Figure 2). Extreme drought events likely make native communities more prone to invasion by opening canopy gaps and increasing the availability of unused resources (e.g. nutrients, light) and at the same time reinforce the impact invaders have on native species (Diez et al. 2012; Pinto and Ortega 2016; Alba et al. 2017; Hautier et al. 2018). Additionally, extreme drought events may facilitate invasion processes by opening windows of opportunity for invasion during these phases of reduced community stability (Jentsch et al. 2007; Kreyling et al. 2008; Diez et al. 2012), or via pulsed resource changes (Davis et al. 2000; Pearson et al. 2018), both being mutually dependent on each other. Thus, increased invasion risk in European semi-natural grasslands due to climate change is a likely scenario.

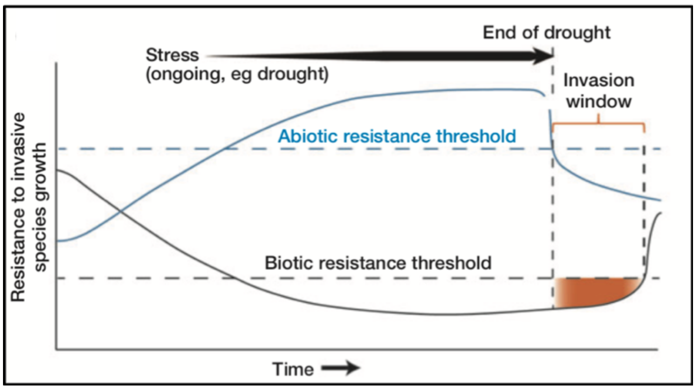


Figure 2: Emergence of invasion windows after disturbance or stress events. Stress events, e.g. droughts, can lead to the emergence of an 'invasion window' if the time lag between when environmental conditions become suitable for the invader and the onset of the recovery of native species is large enough. With increasing level of stress due to the abiotic conditions (e.g. extreme drought event) the abiotic resistance threshold to invasion rises (blue line), while the biotic resistance threshold (black line), the ability of the native community to withstand invasion, decreases. The invasion window opens as soon as the abiotic stress subsides (e.g. due to rain which ends the drought) and returns to an invader compatible value but while abiotic conditions are still stressful for the native vegetation (Diez et al. 2012). Figure 2, as well as the figure caption, were taken and adapted based on a figure from Diez et al. (2012).

3.3 European semi-natural grasslands

In most of the manuscripts of this thesis, I evaluate the impact of the global change drivers ‘invasion’ and ‘climate change’, as well as the formation of ‘novel ecosystems’ upon European semi-natural grasslands. The (following) special features make European semi-natural grasslands a globally unique case study and a well suited study system.

Unlike most other grasslands, the extensive semi-natural grasslands of Europe originate from millennia of low-intensity human land use on sites that would naturally support forests (Vrahnakis et al. 2013; Török et al. 2018; Bahn et al. 2019). Therefore, they are a unique feature of Europe’s cultural landscape and essential for agricultural production, mainly meat and dairy products, but also high quality hay production for horses (Dengler et al. 2014; Bengtsson et al. 2019). In 2015, the economic value of grasslands of Western- and Northern Europe summed up to 71.0 billion EUR (82.7 billion US $), this is 0.7% of the Gross Domestic production of the EU (Dengler and Tischew 2018). The comparably high economic value of the European semi-natural grasslands is complimented by an high ecological value, as they play an extraordinarily important role for biodiversity conservation in Europe (Wilson et al. 2012; Sutcliffe et al. 2015), but also on a global scale (Habel et al. 2013). European semi-natural grasslands harbor 18% of the endemic vascular plants of Europe (Habel et al. 2013), are habitat for 88% of Europe’s butterfly species and are particularly important habitats for birds and reptiles (Nagy 2009; WallisDeVries and van Swaay 2009; Dengler et al. 2014). European grasslands are global plant diversity hotspots at small spatial scales, e.g. world record holder of vascular plant species richness at grain sizes of 1 m^2, and between 0.0001 m^2 to 0.001 m^2 (Löbel et al. 2006; Wilson et al. 2012; Dengler et al. 2016).

In Europe, species invasions show a stable rate of increase (Butchart et al. 2010; Vilà et al. 2011; Diez et al. 2012; Caldeira et al. 2015) which may lead to large scale homogenization and reduced ecosystem (multi-)functioning (Dornelas et al., 2014; Hautier et al., 2018; Vellend et al., 2013) depending on the affected habitat. Generally, European grasslands seem to be rather resistant against plant invasions, they belong to the least invaded habitat types in Europe (Chytrý et al. 2009; Pyšek et al. 2010). However, locally extreme invasions, especially of tall forbs, occur and the reasons are not fully understood (Dengler and Tischew 2018). Neophytes like *Lupinus polyphyllus* tend to form dominance stands in former semi-natural grasslands (Volz and Otte 2001; Dassonville et al. 2008), changing the vegetation structure and species diversity in a drastic manner (Thiele et al. 2010). Those changes will very likely also affect biotic interactions, abiotic processes and consequently ecosystem functioning of the invaded habitats (Kreyling et al. 2008; Sousa et al. 2011; Strayer 2012), possibly leading to the formation of lupine-dominated novel ecosystems.

This thesis contributes to the conservation of semi-natural grasslands in Europe by testing the impact of the global change drivers, invasive species, extreme weather events and native species loss against the stability (in terms of resistance and recovery) of native grassland species.

3.4 The role of biodiversity and stability of plant communities against invasions under climate change conditions

For more than a decade, humans, e.g. scientists and conservation managers, try to attribute monetary value to biodiversity in order to justify its conservation or to apply market-driven instruments to environmental goods in the hope that these will prevent the overuse of ecosystems (McCauley 2006; Costanza et al. 2017; Mace 2019). Biodiversity should be conserved for its own sake and just because of the intrinsic value every species and every living being has (McCauley 2006; Batavia and Nelson 2017). Following the Evolutionary-Ecological Land Ethic founded by Aldo Leopold (1886 - 1948) we should learn to value every species (including us humans) as a part of the ecosystem, as a component of the whole, without attaching their value to the services they provide for us and other living beings (Hunter Jr. and Gibbs 2007; Meine 2017). We are a part of nature and therefore we have both, the right and the responsibility to use and manage nature in a way that acknowledges the intrinsic value of other species and whole ecosystems (Meine 2017; Tinch et al. 2019). Due to the global changes that are currently taking place, it gets increasingly difficult to manage and maintain ecosystems for stability, functioning and biodiversity (Clement and Standish 2018).

Consequently, one of the major goals of ecological research is to find out if a respective ecosystem is sustainable and which factors drive stability in the face of rapidly ongoing environmental changes. However, when it comes to novel ecosystems and stability, there are no historical references to rely on (Hobbs et al. 2014). So, how do we test if a novel ecosystem is sustainable and able to provide crucial ecosystem services without reference values? In an era of global change, stability should be perceived as preserving functionality, ecological integrity and protection against further changes (resilience aka resistance/recovery), changes that might lead to the malfunction of HIREC-affected ecosystems, as well as preserving as much biodiversity as possible (Hobbs et al. 2009; Evers et al. 2018).

Ecologists use a lot of different concepts to describe ecosystem stability (see Grimm and Wissel, 1997), but in this thesis I focus on the terms resistance (Pimm 1984) and recovery (Hodgson et al. 2015). Resistance is defined as the degree of change of an ecosystem property in response to a disturbance event; no change would indicate complete resistance (Kreyling et al. 2017b; Jentsch and White 2019). ‘Resistance’ allows us to test how much stress/disturbance an ecosystem is able to tolerate before its properties/functions begin to change. Recovery is defined as the degree to which an ecosystem property returns to control levels after the cessation of the disturbance event (Hodgson et al. 2015;

Bahn and Ingrisch 2018). ‘Recovery’ allows us to test if and to which degree the ecosystem permanently loses its property/function due to a disturbance event. Resistance and recovery can be affected differently by biodiversity (Isbell et al. 2015; De Boeck et al. 2018; Craven et al. 2018).

There is a broad scientific consensus that biodiversity infers stability in times of ongoing environmental changes (i.e. climate change, invasions) and unclear future conditions (i.e. extreme weather events). But how does biodiversity infer stability? There are four reasons why species-rich ecosystems are likely more stable: **1)** more redundancy: if there are more species the relative likelihood of having more species with a similar (or equal) ecological role is higher (*sensu* redundancy hypothesis: Naeem, 1998); **2)** species rich ecosystems are said to be more invasion-resistant: due to the different traits of the species, all niches are occupied, and all the space and resources of the ecosystem are used-up by the inhabitants, thus there is no vacant niche space left for non-native species to establish (*sensu* niche complementarity: Hooper et al., 2005); **3)** the more species the less is the relative density per species, and the less is the susceptibility for diseases; **4)** sampling effect: the more species the greater the likelihood that one or a few of those species show resistance / tolerance to a respective stressor (e.g., drought) (Huston 1997). Therefore, a more diverse (plant) community leads to an overall more stable community functioning under a wider range of conditions when species react in asynchrony due to compensatory responses (*sensu* insurance hypothesis: Yachi & Loreau, 1999; de Mazancourt et al., 2013; Loreau & de Mazancourt, 2013; Tilman et al., 2014). Increased stability maintains community productivity while the availability of free resources declines (Gross et al., 2014; Tilman, Reich, & Isbell, 2012).

Invasion ecology holds a lot of theories explaining how propagule pressure, the abiotic characteristics of an habitat, and/or the biotic characteristics of an affected community influence the invasiveness of a non-native species or the invasibility of communities. They can be summarized in the PAB framework: Where sufficient propagule pressure (P) meets suitable abiotic conditions of the environment (A) an invasion occurs, unless the biotic conditions (B) of the affected habitat hinder the establishment of the non-native species (Catford et al. 2009). Thus, biotic interactions play a key role in invasion ecology and many theories exist seeking to explain why some communities are more prone to invasion (Richardson and Pyšek 2006) or why some non-native species are more effective invaders than others (van Kleunen et al. 2015; Divíšek et al. 2018). Theories associated with the four points of the diversity-stability relationship mentioned above are, for example, the limiting similarity hypothesis and the empty niche hypothesis (Macarthur and Levins 1967; MacArthur 1970; Hierro et al. 2005) as well as the disturbance hypothesis (Colautti et al. 2006) and the increased resource availability hypothesis (Richardson and Pyšek 2006). The biotic resistance hypothesis (Parker and Hay 2005) and the diversity-invasibility theory (Elton 1958) can be seen as an analogue to the diversity-stability relationship in invasion theory (Jeschke 2014). However, several of those theories are currently under debate

(Jeschke et al. 2018) and the biotic resistance hypothesis, for example, might only be valid at small spatial scales (Fridley et al. 2007; Jeschke 2014).

Nevertheless, biodiversity is one of the major determinants of community and ecosystem dynamics and functioning (Tilman et al. 2014). While loss of biodiversity (Butchart et al., 2010; Tilman, Reich, & Isbell, 2012) itself, but especially accelerated by climate change (IPCC 2014) and invasion of non-native species will most certainly negatively affect ecosystem stability and functioning (Cardinale et al. 2012; Reichstein et al. 2013; Pinto and Ortega 2016). The role of biodiversity for the stability of ecosystem functioning in the face of global change (in terms of this thesis: extreme climatic events and invasion) is therefore of utmost importance. Global change drivers lead to exogenous changes in resource availability and the introduction of non-native species, leading to uncertainty as to whether the diversity-stability relationship persists in the face of extreme climatic events (De Boeck et al. 2018) and invasion (Pinto and Ortega 2016). Climate extremes may impact all of the mechanisms conferring ecosystem stability (Cardinale et al. 2012; De Boeck et al. 2018), thus, enabling the establishment of non-native species in the first place (Wardle et al. 2011; Török et al. 2018; Hautier et al. 2018). Invasive species may be able to compromise the diversity-stability relationship by weakening the ability of communities to resist to and/or recover from an extreme event. A highly competitive invader or an invader, that tolerates abiotic stress more effectively than the native species, may be able to outcompete natives before or during an extreme event respectively (Diez et al. 2012). This could diminish the resistance of an ecosystem (e.g. to biomass fluctuations) by additionally increasing the competitive pressure on native species. The same accounts for recovery: if the invader recovers more quickly from harsh climatic conditions, then it might impede the partitioning of resources after stress release as the invader instead captures the majority of available resources (Diez et al. 2012; De Boeck et al. 2018).

This thesis contributes to the biodiversity-stability concept by testing how the global change drivers, invasive species, occurrence of extreme drought and native species loss interact to affect the stability of plant communities.

3.5 Invasive ecosystem engineers

Ecosystem engineers (*sensu* Jones et al., 1994) are part of the primarily biotic changes that may induce novel ecosystems (Hobbs et al. 2009; Vetter et al. 2018).

> "Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats." (Jones et al. 1994)

However, ecosystem engineers not only modify biotic interactions, but also biogeochemical cycles of the recipient habitat (Wright and Jones 2006; Figure 1). They have a direct impact upon the physical space in which they and other species live (Hastings et al. 2007) and modify the availability of resources for other species either direct via competition and/or facilitation effects or indirect through changes in the physical space (Jones et al., 1994; Figure 1). However, due to their characteristics, ecosystem engineers are able to change both, the abiotic and biotic conditions of the recipient habitat, and thus are likely to show a pronounced impact upon the recipient ecosystems. Their far-reaching consequences may be further intensified through habitat feedback and changes in the rate of dissemination (Cuddington and Hastings 2004; Wright and Jones 2006).

The ability of invasive ecosystem engineers to bring profound and lasting changes to the ecosystem they inhabit (Jones et al. 1994) may be a curse and a blessing at the same time, it depends on the affected ecosystem. If they inhabit an ecosystem we want to preserve, the change to a novel ecosystem with (completely) new characteristics to the historic system is a curse. On the other hand, if they inhabit (or are introduced in) degraded ecosystems, they might ensure or enable important ecosystem processes and stabilize the newly created ecosystem against further changes. However, usage of invasive species to restore degraded ecosystems may come along with some undesired effects (Schlaepfer et al. 2011).

(Non-native) ecosystem engineers are often intentionally introduced to new environments by humans e.g. for soil and water conservation, soil improvement or to restore degraded ecosystems (Lazzaro et al. 2014; Ayanu et al. 2015; Vetter et al. 2018). They generally possess traits that can positively influence soil stability, nutrient and hydrological cycling, and light infiltration (Ayanu et al. 2015) and show protective characteristics, e.g. reduced erosion (Fei et al. 2014; Vetter et al. 2018). But if they become invasive, those positive traits of the respective non-native ecosystem engineer can have negative and long-lasting effects on native communities and ecosystem properties (Richardson et al. 2000; Catford et al. 2012; Fei et al. 2014) that often extend far beyond its life span and/or presence (Ehrenfeld 2003, 2010; Jones et al. 2010). Ecosystem engineers that have become invasive, are called 'transformer species' as they transform the infected habitats to novel ecosystems (Richardson et al.

2000). Invaders that are introduced for management purposes, such as the ecosystem engineers, are usually widely and deliberately applied by humans and are thus able to spread into large areas right at the beginning of the invasion process with many starting points for the invasion. However, sometimes invasive ecosystem engineers are also accidently released such as the European earthworms in e.g. North America. These soil invertebrates have colonized terrestrial ecosystems alongside the European settlers and changed the hydrological flow, the density of other soil invertebrates and plant diversity of the affected ecosystems (Hendrix et al. 2008; Klein et al. 2017) and thus created novel ecosystems at a large spatial scale (Truitt et al. 2015). Ecosystem engineers – native and invasive ones – exist in the plant and animal kingdom and show very different modes of action. Some prominent examples of invasive ecosystem engineers, besides the one of the European earthworms in North America are 1) the North American beaver (*Castor canadensis*) in Chile, 2) invasion of the water hyacinth (*Eichhornia crassipes*) in Lake Victoria, and 3) the invasion of blue gum (*Eucalyptus globulus*) (Box 2).

Box 2: Examples of invasive ecosystem engineers

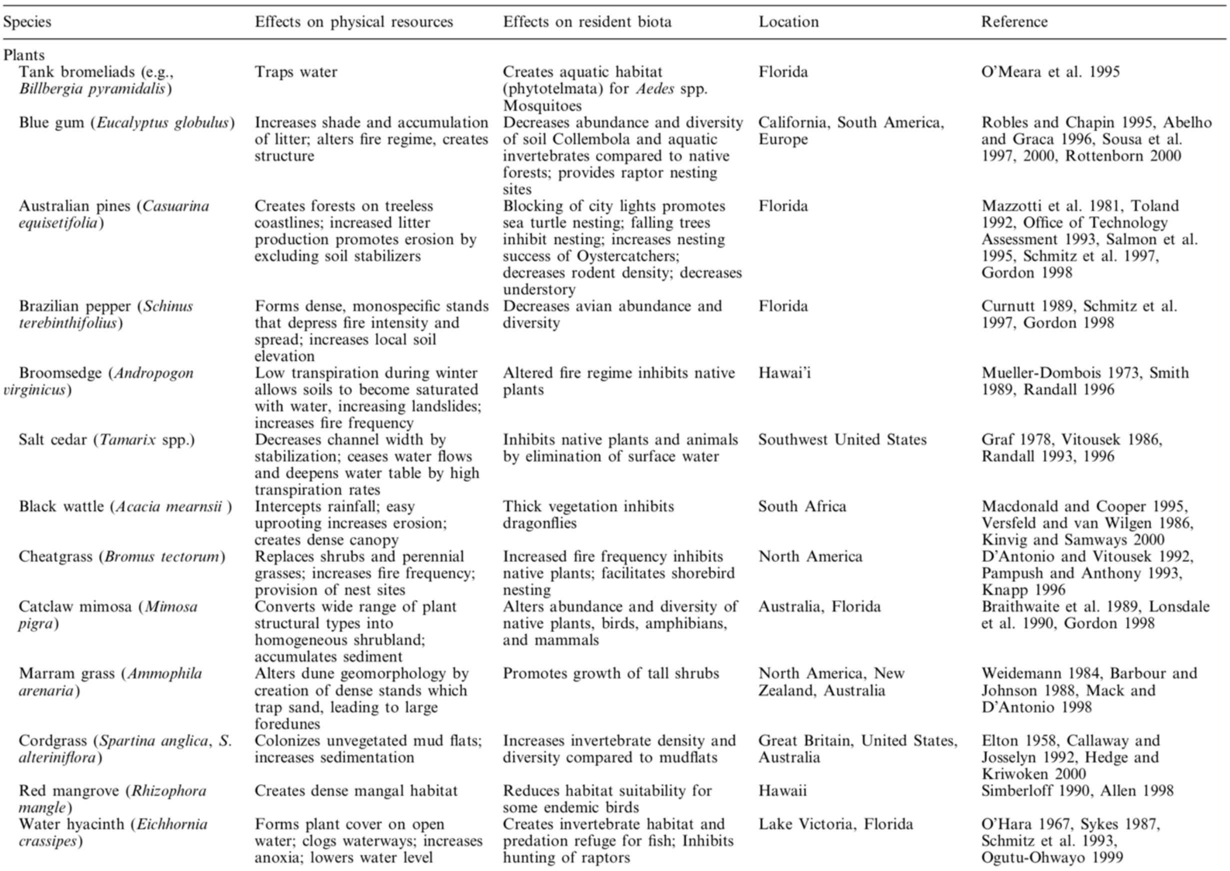
1) Beavers are a classic example of an ecosystem engineer, as they significantly alter their environment by cutting trees and building damns in which they live. Beavers clear forests, dam rivers to ponds and wetlands or change their course thereby creating new habitat also for species other than themselves. The set of species inhabiting an area modified by ecosystem engineers differs from the original set of ecosystem inhabitants (Cuddington and Hastings 2004; Rilov et al. 2012). Beavers are allogenic ecosystem engineers, as they actively change the physical state of living and non-living materials/structures/landscapes of the environment in which they live (Hastings et al. 2007). *Castor canadensis* is invasive in the *Nothofagus* forests of Tierra Del Fuego Chile, a very pristine wilderness area and home of the southernmost forests of our planet. It was introduced for fur production and hunting (Anderson et al. 2009). The absence of predators and the availability of abundant habitat have led to an exponential population increase of *C. canadensis* since its first introduction in 1946 to the Argentine portion of the Tierra del Fuego (Anderson et al. 2009). Although their engineering does not significantly differ from that in their home range, they are accounted as the largest disturbance agent to these forest since the last ice age (Anderson et al. 2009; Papier et al. 2019). Their impact comprises dramatic changes of the carbon and methane cycle of the affected habitat and landcover alterations, thus leading to major ecosystem level changes (Papier et al. 2019).

Plants are usually autogenic ecosystem engineers as they passively modify their environment due to their own physical form, which is part of the emerging new ecosystem, and at the same time the habitat changes with the growing and evolving engineer (Rilov et al. 2012). **2) *Eichhornia crassipes***, the world's worst aquatic weed, originates from the Amazon basin in Brazil and was initially spread by gardeners as ornamental plant (Koutika and Rainey 2015). The water hyacinth forms dense plant cover on open water, as in 1995 when it covered 80% of the shores of Lake Victoria in Uganda. As a result, it clogs waterways, increases anoxia and lowers the water level. However, it also creates invertebrate habitat and provides refuge against predation for fish (Crooks 2002).

3) Eucalyptus globulus originates from the Australian continent and was introduced to Europe, South America and California for reforestation, afforestation and timber production (Wolf and DiTomaso 2016). Blue gum shows effects upon the physical resources of the invaded habitats (abiotic impact) as well as on the resident biota (biotic impact) (Crooks 2002). The abiotic changes include: alteration of the fire regime (old leaves are highly flammable; production of highly ignitable oily resins), accumulation of litter (more fuel for wildfires), allelopathic effects, hydrological effects (decrease in water availability up to depths of 14 m and distances of 30 m around the trunk), changes in nutrient cycles (slow litter decomposition) and light availability (increase of shading) (Wolf and DiTomaso 2016). The biotic changes include: changes in plant community dynamics (outcompetes native vegetation, forms monotypic stands, increases succession of grasslands), unpalatability for cattle and sheep, decrease of aquatic invertebrates, decrease of terrestrial vertebrates, decrease in abundance and diversity of soil Collembola, increases raptor nesting sites and abundance of California slender salamander (Crooks 2002; Wolf and DiTomaso 2016). By this, *Eucalyptus globulus* decreases competition and passively increases habitat suitability for itself.

While the general threat imposed by non-native species may be seen controversial (Goodenough 2010; Boltovskoy et al. 2018), it is highly likely that invasive ecosystem engineers will cause shifts in the ecosystem functions of the recipient habitat and thus, may subsequently lead to biodiversity loss, large scale homogenization and reduced ecosystem functioning of the historic ecosystem (Wardle et al. 2011; Simberloff et al. 2013). Invasive species have recently been identified as drivers of extinctions (see e.g. Bellard et al., 2016) and ecosystem engineers may be among those non-native species with the largest ecological impacts (Crooks 2002; Cuddington and Hastings 2004; Wright and Jones 2006; Reynolds et al. 2017).

Table 1: Invasive pant ecosystem engineers and their effects. Table taken from Crooks (2002).



Species	Effects on physical resources	Effects on resident biota	Location	Reference
Plants				
Tank bromeliads (e.g., *Billbergia pyramidalis*)	Traps water	Creates aquatic habitat (phytotelmata) for *Aedes* spp. Mosquitoes	Florida	O'Meara et al. 1995
Blue gum (*Eucalyptus globulus*)	Increases shade and accumulation of litter; alters fire regime, creates structure	Decreases abundance and diversity of soil Collembola and aquatic invertebrates compared to native forests; provides raptor nesting sites	California, South America, Europe	Robles and Chapin 1995, Abelho and Graca 1996, Sousa et al. 1997, 2000, Rottenborn 2000
Australian pines (*Casuarina equisetifolia*)	Creates forests on treeless coastlines; increased litter production promotes erosion by excluding soil stabilizers	Blocking of city lights promotes sea turtle nesting; falling trees inhibit nesting; increases nesting success of Oystercatchers; decreases rodent density; decreases understory	Florida	Mazzotti et al. 1981, Toland 1992, Office of Technology Assessment 1993, Salmon et al. 1995, Schmitz et al. 1997, Gordon 1998
Brazilian pepper (*Schinus terebinthifolius*)	Forms dense, monospecific stands that depress fire intensity and spread; increases local soil elevation	Decreases avian abundance and diversity	Florida	Curnutt 1989, Schmitz et al. 1997, Gordon 1998
Broomsedge (*Andropogon virginicus*)	Low transpiration during winter allows soils to become saturated with water, increasing landslides; increases fire frequency	Altered fire regime inhibits native plants	Hawai'i	Mueller-Dombois 1973, Smith 1989, Randall 1996
Salt cedar (*Tamarix* spp.)	Decreases channel width by stabilization; ceases water flows and deepens water table by high transpiration rates	Inhibits native plants and animals by elimination of surface water	Southwest United States	Graf 1978, Vitousek 1986, Randall 1993, 1996
Black wattle (*Acacia mearnsii*)	Intercepts rainfall; easy uprooting increases erosion; creates dense canopy	Thick vegetation inhibits dragonflies	South Africa	Macdonald and Cooper 1995, Versfeld and van Wilgen 1986, Kinvig and Samways 2000
Cheatgrass (*Bromus tectorum*)	Replaces shrubs and perennial grasses; increases fire frequency; provision of nest sites	Increased fire frequency inhibits native plants; facilitates shorebird nesting	North America	D'Antonio and Vitousek 1992, Pampush and Anthony 1993, Knapp 1996
Catclaw mimosa (*Mimosa pigra*)	Converts wide range of plant structural types into homogeneous shrubland; accumulates sediment	Alters abundance and diversity of native plants, birds, amphibians, and mammals	Australia, Florida	Braithwaite et al. 1989, Lonsdale et al. 1990, Gordon 1998
Marram grass (*Ammophila arenaria*)	Alters dune geomorphology by creation of dense stands which trap sand, leading to large foredunes	Promotes growth of tall shrubs	North America, New Zealand, Australia	Weidemann 1984, Barbour and Johnson 1988, Mack and D'Antonio 1998
Cordgrass (*Spartina anglica*, *S. alteriniflora*)	Colonizes unvegetated mud flats; increases sedimentation	Increases invertebrate density and diversity compared to mudflats	Great Britain, United States, Australia	Elton 1958, Callaway and Josselyn 1992, Hedge and Kriwoken 2000
Red mangrove (*Rhizophora mangle*)	Creates dense mangal habitat	Reduces habitat suitability for some endemic birds	Hawaii	Simberloff 1990, Allen 1998
Water hyacinth (*Eichhornia crassipes*)	Forms plant cover on open water; clogs waterways; increases anoxia; lowers water level	Creates invertebrate habitat and predation refuge for fish; Inhibits hunting of raptors	Lake Victoria, Florida	O'Hara 1967, Sykes 1987, Schmitz et al. 1993, Ogutu-Ohwayo 1999

In invasion biology there are many examples of invasive plant ecosystem engineers with very different effects and modes of action (some examples can be found in Table 1), reaching from changes in the resource availability and disturbance regimes, as well as induction of succession to direct habitat provision/facilitation (Vitousek and Walker 1989; Crooks 2002). Lupines are a globally invasive genus of ecosystem engineers, which are able to change both, abiotic (e.g. nutrient cycling, micro-climate within the vegetation) and biotic conditions (e.g. competition, plant-pollinator interactions, induction of succession by introduction of tall herb vegetation layers into open habitats), of the recipient habitat (Volz 2003; Thiele et al. 2010; Lauterbach and Nehring 2013; Jakobsson et al. 2015) and thus likely form novel ecosystems right from the start of their introduction. Consequently, it is highly likely that lupines will show a pronounced impact upon the invaded ecosystems. In this thesis, I concentrate on *Lupinus polyphyllus* (LINDL.) in Germany/Europe and *Lupinus nootkatensis* (DONN EX SIMS) in Iceland as model ecosystem engineers and test their performance against the invasive performance of other habitat changing invasives [*Senecio inaequidens* (DC.) and *Verbascum thapsus* (L.)], which have not previously been labeled as ecosystem engineers. Lupine invasion in Germany, as well as in Iceland, is the result of human-induced landscape changes as the nitrogen fixers were intentionally sown, e.g. to improve soil quality or to promote soil formation (Fremstad 2010; Magnusson 2010). *Lupinus polyphyllus* and *L. nootkatensis* are both legumes which are able to change soil chemistry due to the nitrogen fixing bacteria living in the nodules of the lupine roots, which are able to convert the free nitrogen of the atmosphere into plant and animal available soil compounds (Fremstad 2010; Vuijk 2016). Both lupine species, *L. polyphyllus* and *L. nootkatensis*, pursue niche construction (Fei et al. 2014) and induce succession (facilitation of nitrophilous species/other invasives, changed community assembly) (Volz and Otte 2001; Thiele et al. 2010; Vetter et al. 2018) making them a prime example of invasive ecosystem engineers (Hastings et al. 2007). However, they both show pronounced effects in terms of species loss as well as changes in population structure, including wildlife, on the habitats they invade (Otte and Maul 2005; Thiele et al. 2010; Ramula and Pihlaja 2012; Wasowicz et al. 2013; Ramula and Sorvari 2017; Vetter et al. 2018).

3.6 Thesis objective

In this thesis, I observe whether there are increasing levels of synergism among two drivers of ecosystem change: invasion and climate change. The conclusions of this thesis are based on several case studies of four invasive species, two of them being typical ecosystem engineers (*Lupinus polyphyllus* and *Lupinus nootkatensis*) and two showing less pronounced characteristics of an ecosystem engineer (*Senecio inaequidens* and *Verbascum thapsus*) and their behavior under climate change scenarios, here extreme drought events. Due to ecological novelty, it is of high scientific relevance to combine experimental research on climate change and invasion with biodiversity research and conservation across larger landscape areas. I use a versatile approach combining experiments with data recording in the field as well as modelling. In doing so, I am adding to answer the following questions within my PhD thesis:

1. Do plant invaders engineer novel and hybrid ecosystems under climate stress?
2. To what extent is the invasive potential of non-native species controlled by their pre-adaption to the recipient climate?
3. Will there be changes of biotic interactions due to climatic changes and how will these affect the spread of invasive species or the future invasiveness of communities?
4. How do plant invaders affect native species and the biodiversity-stability relationship?
5. How do invasive ecosystem engineers create novel and hybrid ecosystems?
6. Does the occurrence of novel and hybrid ecosystems necessarily correlate with the degradation of the affected habitat, or with the loss of biodiversity?
7. Does the stability concept stand in contrast to ecological novelty? / Are novel and hybrid ecosystems sustainable, that are created by ecosystem engineers?
8. At which point do hybrid ecosystems turn into novel ecosystems?
9. Can we use/engineer novel and hybrid ecosystems to solve environmental problems?

4 MOST IMPORTANT FINDINGS OF MANUSCRIPTS PRESENTED IN THIS THESIS

In this section, I will shortly summarize all the manuscripts presented in this thesis, highlight their most important findings, and I will outline how each of them contributes to the overall storyline of the thesis.

Manuscript 1 Crucial first steps

Arfin-Khan et al. (2018): Factors influencing seedling emergence of three global invaders in greenhouses representing major eco-regions of the world. Plant Biology, 20, p. 610-618.

Successful germination and seedling emergence in a new environment are crucial first steps in the life history of non-native species.

Manuscript 1 tests the success of germination and seedling emergence of three global plant invaders (*Lupinus polyphyllus*, *Senecio inaequidens*, *Verbascum thapsus*) across a global gradient of seven ecoregions, because both features play a key role in the process of range expansion. Additionally, it was tested if the seed source region (native versus invasive) has an impact on the species performance (phenotypic plasticity). All three invader species were able to germinate under all climate conditions (warm, semi-arid and humid climates), besides the cold (humid sub-arctic) and the hot deserts (arid sub-tropical). While the adaptation of the species to the climate of its seed source region shaped the germination success of the respective species under the prevailing climate conditions, not its status as being invasive or native.

This experiment was conducted using seeds in petri dishes which were placed in greenhouses and climate chambers representing seven ecoregions of the world.

Manuscript 2 Stress tolerance of the invader – (where) can they prevail after germination?

Vetter et al. (2019): Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters. Plant Biology, 21, p. 832-843.

After successful germination, the non-native species must be able to prevail under multiple stressors. Successful plant invasion is influenced by both climate change/extreme events and plant-plant interactions.

Manuscript 2 tests the abiotic stress tolerance of the global legume invader *Lupinus polyphyllus* to an extreme drought event, its performance in competition but under ambient climate conditions, as well as its performance under combined abiotic and biotic stress. The invader gained an advantage under drought conditions by having a smaller reduction in performance relative to its native competitors, while it showed competitive inferiority under control conditions. This very likely allows *L. polyphyllus* to use arising ‘invasion windows’ during phases of increased abiotic stress and reduced community performance. Drier future climate conditions could possibly lead to a slowing of the *L. polyphyllus'* invasion process at the dispersal and establishment stage, while simultaneously providing advantages for extant populations relative to their native neighbors.

Abiotic stress test: field experiment; biotic stress test: pot experiment in climatic chambers, combined abiotic and biotic stress test: field experiment in the ecological botanical gardens of the University of Bayreuth.

Manuscript 3 Niche shift and propagation limits – how far will they come?

Vetter et al. (in prep. for resubmission): Niche conservatism or niche shift? Implications for the management of a legume invader.

Estimating range expansion means estimating invader impact, as the maximum amount of suitable habitat under different climate conditions also estimates the maximum area at risk of transformation by an invader.

Manuscript 3 tests the niche dynamics of *L. polyphyllus* in its native (Northern America) versus its invasive range (Europe). Based on those niche calculations the limits of range expansion of *L. polyphyllus* in both ranges under current and future climate conditions were projected to observe possible divergent effects between the behavior of the invader on the two continents. *Lupinus polyphyllus* experiences a niche shift, in terms of a niche expansion in its invasive range, the European continent. The amount of suitable habitat is projected to increase under future climate conditions in both ranges (though this effect is more pronounced in the invasive range), however, the overall habitat suitability will decrease in both ranges, but especially in the invasive range. Thus, for invader control, management measures might be combined with the occurrence of extreme weather events.

A species distribution model (ensemble modelling approach, BIOMOD2) along with species occurrence data from the Global Biodiversity Information Facility (gbif.org) were used to project the current and future habitat suitability.

Manuscript 4 Impact of invader presence on the biodiversity-stability relationship

Vetter et al. (2020)*:* Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought. Global Change Biology, 26, p. 3539-3551.

Per definition, an invader is an non-native species which has a negative impact upon the native communities/ecosystems and/or human society.

Manuscript 4 addresses the resilience of European semi-natural grasslands in the face of invasion and extreme drought events. Understanding how global change drivers interact to affect plant community stability is critical for our ability to predict future ecosystem functioning and services. Manuscript 4 is a multisite invader x biodiversity x drought manipulation experiment that examines resistance and recovery at three semi-natural grassland sites across Europe (Germany, Belgium, Bulgaria). Biodiversity stabilizes community productivity by increasing the ability of native species to recover from extreme drought. Invader presence disturbs this stabilizing relationship and can even turn it into a negative relationship, depending on the invader. The negative invader impact is independent of the invaders own performance under increased stress.

This experiment used buried field mesocosms (varying in species richness, composition and functional group richness) and was implemented across three European countries.

Manuscript 5 Another legume invader – impact and succession of an ecosystem engineer in a cold biome

Vetter et al. (2018): Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity. Frontiers in Plant Science, 9 (715), p. 1-12.

Invasive ecosystem engineers can strongly influence native ecosystems by altering energy, water and/or nutrient fluxes, which consequently leads to altered ecosystem-level properties.

Manuscript 5 uses *Lupinus nootkatensis* as an example species to estimate and project the hazardous potential of nitrogen fixing herbaceous plants in a sub-polar oceanic climate. Invader presence leads to loss of species diversity and richness, as well as changes in the community composition. Climate change significantly increases the amount of suitable habitat for *Lupinus nootkatensis*. Due to the invader's ability to pursue niche construction and to speed up succession, as well as the additive effects of climate change, significantly enlarging the amount of suitable habitat of *L. nootkatensis*, an acceleration of ecological change across large parts of Iceland under future climate conditions is very likely.

In a local field survey, the impact of *L. nootkatensis* on the native plant community in three different habitats (heathland, woodland, grassland) was observed and afterwards scaled up to the landscape level, using a species distribution model.

5 DISCUSSION OF MAIN RESULTS AND CONCLUSION

This section summarizes and discusses the results of all five manuscripts presented in this thesis. I start this section with a conceptual figure which illustrates the thesis results and puts them into a larger framework. Thus, I am able to illustrate how plant invaders engineer novel ecosystems under climate stress. Based on the research questions I have presented in the introduction, I will outline how the establishment of invaders, their stress tolerance & ability to spread and their expected impact will work together to form novel ecosystems. This chapter ends with some reflections on nature conservation and a short description of possible management measures against those effects induced by highly invasive species.

5.1 Conceptual context – invasion, climate change and biodiversity in novel ecosystems

In my dissertation, I dealt with the interaction of invasive plants, climate change and biodiversity. In detail, I observed the performance of invasive plants with and without extreme weather events, their impact on native plant communities, the estimation of their likely spread under climate change conditions, and the interaction of invasive plants and extreme weather events on the diversity-stability relationship of native plant communities. Figure 3 illustrates how those factors contribute to the emergence of novel ecosystems.

Humans impact biodiversity either through direct intervention, e.g. (un-)intentional spread of invasive species (Figure 3a), or indirect e.g. by human induced climate change (Figure 3b). According to the definition of Morse et al. (2014) indirect human impact, like climate change or nitrogen deposition, does not necessarily lead to the emergence of novel ecosystems, however, it may set the common ground for other disturbances (Morse et al. 2014). In Figure 3 climate change shifts natural ecosystems to impacted ecosystems, thus making it likely easier for invasive species to spread, as well as reducing the buffer capacity of biodiversity, such as resilience towards invasion (**manuscripts 2, 4**). The better the system is buffered, the higher the functional resilience, the later change occurs (Isbell et al. 2015) or the better able the ecosystem is to return to its original state (**manuscript 4**; Kreyling et al., 2017), and the later it might be pushed to or over the tipping point (Jentsch and White 2019).

I do not completely agree with the definition of Morse et al. (2014) excluding indirect anthropogenic stressors as drivers of novel ecosystems. Particularly future climate change will lead to shifts in species composition of natural ecosystems due to rising global temperatures and extreme events. On the other hand, the impact of climate change may potentially lead to the change of ecosystems no matter if they are novel or natural and thus, further challenge nature conservation.

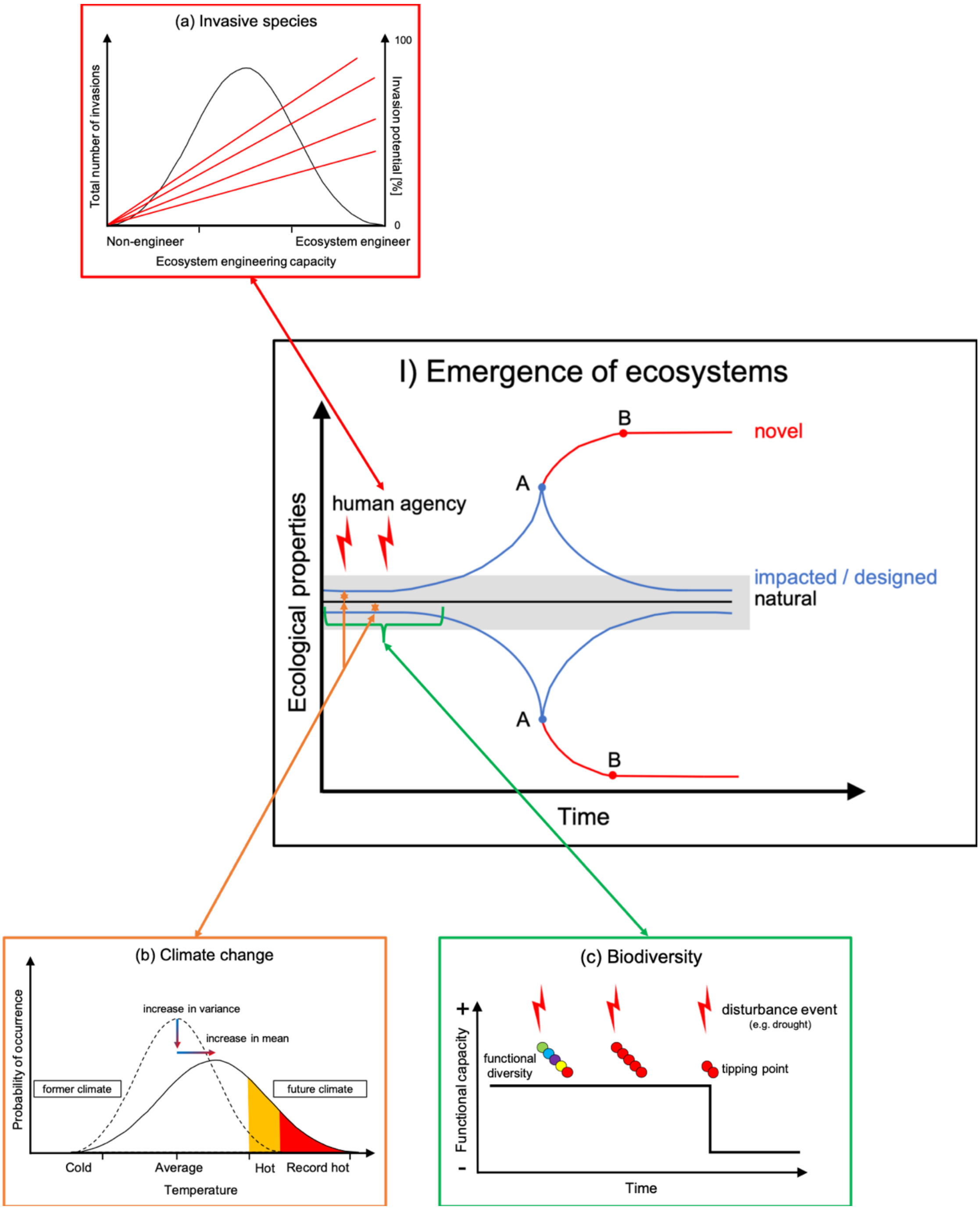


Figure 3: Drivers of (a,b) and buffer against (c) the emergence of novel and impacted ecosystems (I). **(a)** The total number of invasive species follows a normal distribution, with relatively less species holding either none (non-engineer) or very distinctive features of an ecosystem engineer, while the vast amount of invader species is something in-between both invader types. The invasiveness (red lines) increases along with the engineering capacity of an invasive species, while the slope of the respective line illustrates the invasion potential (the steeper the slope, the higher the invasiveness). The relative increase of invasion potential, as well as the shape of those curves, has not yet been clearly identified. This is illustrated by the fact that several potential straight lines with different slopes were drawn. **(b)** Climate change facilitates the emergence of impacted and novel ecosystems by shifting ecosystems away from their natural state: Due to climate change, an increase in mean and variance of temperature is expected. This leads to an increase in weather extremes, like e.g. drought. Figure adapted from IPCC (2013). **(c)** Biodiversity is the buffer against disturbance induced changes. But if a certain tipping point is crossed, e.g. the functional diversity of an ecosystem, then the buffering effect is lost. **I) Emergence of ecosystems:** human agency has an impact on ecosystems and may initiate the development towards a new ecosystem state. The grey bar indicates natural variability of ecosystems. **A:** At this point, the ecosystem either recovers to a near natural state, or the transformation to a novel ecosystem progresses. **B:** Starting with this point, the ecosystem is self-sustaining and has reached an alternative stable state. Now, the system may be called novel ecosystem. Figure adapted from Morse et al. (2014).

As soon as biodiversity is impacted too much by (single or multiple) human-induced disturbance(s), the buffering effect of biodiversity vanishes, and the affected ecosystem is tipping. This is when change happens, although impact – in the sense of reduced ecosystem functioning or loss of single key species – might have already occurred before. However, this change might not have been visible until now as it was intercepted by biodiversity, e.g. by species acting in asynchrony to the disturbance but being largely functionally redundant thus leading to a greater resistance stability of the respective ecosystem function/property (Blake and Duffy 2010). An ecosystem which has not yet crossed a tipping point but displays a certain degree of change, might be considered as a hybrid ecosystem. Ecosystems that have crossed the tipping point can either develop into an impacted or into a novel ecosystem (Figure 3), depending on the processes driving the recovery/succession. If recovery is assisted and planned by humans (Kreyling et al. 2011a), in this case recovery is called restoration, then a designed ecosystem may be the result of the process. 'Recovery' here means, return to a nearly natural state or to a state within the natural variability of the ecosystem.

Invasive species are able to impact native ecosystems with their presence or even change them to novel or hybrid ecosystems. However, when a change occurs is dependent on the vulnerability of the affected ecosystem. The majority of invasive species is something in-between an 'ecosystem engineer' (invader with distinct features of an ecosystem engineer) and a 'non-engineer invader' (invader with no distinct features of an ecosystem engineer), not clearly relatable to one of those invader types (Figure 3a). Due to the fact that invasive ecosystem engineers are able to change their physical environment to fit it to their needs and thus to increase their reproductive potential in the invasive range (Cuddington and Hastings 2004), the invasion potential of engineers may be higher than average (see e.g. Wright and Jones 2006). Consequently, Figure 3a depicts an increase of the invasion potential from non-engineering invaders to ecosystem engineers. The maximum invasion potential would be 100%, while no invasive species has an invasion potential of 0% (though always modified by the invasibility / invasiveness of the target community or site), because otherwise it would not be invasive. However, the shape and slope of the 'invasiveness curves' (Figure 3a, red lines) still have to be evaluated, as the number of different invasive species used in the manuscripts of this thesis is not enough to clearly evaluate this relationship. However, the future experiment described in chapter 6, could be used to determine this relationship. Consequently, for now I chose the simplest and most straight forward way to depict the invasion potential, a straight line but with different slopes (= different levels of invasiveness, Figure 3a). The red lines are only a trend, as the invasion potential of an invader also depends on the sensitivity of the affected ecosystem, as well as other external factors such as the prevailing weather conditions. (Sub-) arctic environments are more prone to nitrogen enrichment and are thus more vulnerable towards lupine invasion (**manuscript 5**; Hiltbrunner et al., 2014). Under drought, the invasiveness of the Mediterranean type invader *Senecio inaequidens* is probably higher than that of *Lupinus polyphyllus* (**manuscript 4**). Like many other invasive species, lupines were first introduced by humans, but nowadays are able to very effectively spread on their own. Thus, in case of the lupines, novel ecosystem emerge due to human action as well as the lack thereof (in case their spread is not prevented) (Evers et al. 2018).

Do plant invaders engineer novel and hybrid ecosystems under climate stress?

The higher the invasiveness of an invader (Figure 3b) and the lower the biodiversity / functional trait complementarity of the recipient community (Figure 3c) or the higher the background level of disturbance, e.g. due to climate change (Figure 3a), the smaller is generally the buffering capacity of the affected ecosystem (Figure 3c) and thus, the earlier change occurs. Consequently, plant invaders will certainly open opportunities for the emergence of novel and hybrid ecosystems under climate stress. The invaders studied in this thesis were able to germinate under a broad range of climatic conditions (**manuscript 1**), thus enabling the species to successfully establish themselves even under an uncertain range of future climate conditions. Invaders showed relatively better performance under combined drought and competition effects than native species (**manuscripts 2, 4**). Additionally, habitat suitability, at least of the legume ecosystem engineers *L. polyphyllus* and *L. nootkatensis*, is projected to increase under future climate change scenarios (**manuscripts 3, 5**), but will likely also increase for *S. inaequidens* – although we did not explicitly test the future habitat suitability for the pasture weed – as the highly competitive invader performed very well under future extreme drought events (and even better than the invasive legume *L. polyphyllus*) (**manuscript 4**). Both invader species, *L. polyphyllus* stemming from a rather cool origin and *S. inaequidens* from a warm origin, are able to change the recovery of native species communities and thus, further promote the formation of novel or hybrid ecosystems under climate stress in addition to their sheer presence (**manuscript 4**; Figure 3).

Invader species are able to change species richness and composition of the affected habitat (**manuscript 5**) as well as the nutrient pool (EPPO 2006; Fremstad 2010), two proficiencies that, as these species settle, very likely lead to the formation of novel or hybrid ecosystems (Hobbs et al. 2009). The invasive ecosystem engineers *L. polyphyllus* and *L. nootkatensis* are able to increase the soil nitrogen content, which is detrimental for native species that are adapted to nutrient-poor soils and may therefore possess poorer competitive performance when faced with increased nutrient availability (**manuscript 5**; Liška and Soldán 2004; Thiele et al. 2010; Hiltbrunner et al. 2014; Wasowicz 2016), especially under increased abiotic stress conditions. The increase in soil nitrogen can also lead to a so called ‘invasional meltdown’ (Simberloff and Von Holle 1999; Braga et al. 2018), an increase in settlement of native nitrophilous plants and/or further invasive species (Volz 2003; Magnusson et al. 2008; Magnusson 2010). In contrast, *S. inaequidens* increases the competitive pressure towards all native species by exploiting the top soil nutrient pool faster than natives, especially under abiotic stress conditions (**manuscript 4**; Dassonville et al., 2008; Global Invasive Species Database (GISD), 2015).

However, both effects may lead to novel or hybrid ecosystems while the latter might be monocultures of *S. inaequidens*.

In sum, the manuscripts of this thesis confirm that invasive species and extreme climatic events will work synergistically as catalysts for the emergence of novel and hybrid ecosystems (Figure 3). Individually, but especially when both global change drivers act in synchrony, this leads to negative synergistic effects, which are more powerful than the additive effects of the two single stressors.
Effects caused by the emergence of novel ecosystems, based on the results of this thesis, are 1) the deterioration of the biodiversity-stability relationship, 2) loss of diversity – in terms of species richness and subsequently resilience and functioning – if the emergence of the novel or hybrid ecosystem is due to the invasion in intact ecosystems (e.g. species-rich semi-natural grasslands), 3) increase in species richness, ecosystem functioning and services if the emergence of the novel or hybrid ecosystem takes place in highly degraded habitats, 4) induction of succession. Induction of succession is a good and wanted effect in highly degraded ecosystems as the overall biodiversity increases as succession progresses (compared to zero biodiversity in highly degraded ecosystems, e.g. in Iceland, and invader-monocultures). However, in species-rich habitats, e.g. semi-natural grasslands, succession is an unwanted effect, as in Europe it usually induces the formation of forest and forests harbor far less species than extensively managed semi-natural grasslands (Dengler and Tischew 2018). Invasive ecosystem engineers impact/change native ecosystem services, but also provide/build new ecosystem services. In the case of *L. polyphyllus* and *L. nootkatensis*, this means they change nutrient cycling by increasing the soil nitrogen content, change or increase productivity/resistance/recovery, increase soil quality and depth of degraded habitats, provide habitat for (few) species (less insects in general but e.g. good for bumble bees), etc. (Valtonen et al. 2006; Davidsdottir et al. 2016; Ramula and Sorvari 2017). Whether those services are perceived ‘positive’ or ‘negative’ depends on the affected habitat.

5.2 Crucial first steps for invader establishment

To what extent is the invasive potential of non-native species controlled by their pre-adaption to the recipient climate?
Species are adapted to climatic conditions of their source regions. Native populations originating from cool seed regions showed a higher germination rate in cool experimental climates and a lower germination rate in warmer experimental climates compared to non-native populations and vice versa (**manuscript 1**). In contrast to previous studies (Hierro et al. 2009; Beckmann et al. 2011; Hirsch et al. 2012; Xu et al. 2019), we were able to show that germination success of non-native populations is not superior to native populations per se, but depends on the adaption of a population to its seed region of origin and the climatic conditions of the recipient habitat (**manuscript 1**). Consequently, the import

of seeds from different source regions – thus, increasing within-species-diversity (Kreyling et al. 2011b, 2012a, b; Thiel et al. 2012) – could lead to a higher overall invasiveness and productivity of an invader species in the face of climate change (**manuscript 1**; Catford et al. 2009; Briski et al. 2018).

Manuscript 1 further revealed that all three invader species tested (*Verbascum thapsus*, *Senecio inaequidens* and *Lupinus polyphyllus*) are able to germinate and emerge in places outside their current distributions of their native and invasive ranges. Furthermore, species populations, stemming e.g. from the native and invasive range of an invader, may hold distinct stress/disturbance tolerance capabilities (**manuscript 1**). Besides the dry (humidity ≤ 50%, arid sub-tropical) and cool (≤ 5°C, humid sub-arctic) climates, all regions are in danger of being invaded as the native and non-native populations of the three global invaders were able to germinate and emerge in the remaining five biomes (**manuscript 1**).

Lupinus polyphyllus retains its high reproductive output even under drought and is able to germinate in large areas across the world (**manuscripts 1, 2**). Consequently, even under future extreme drought events *L. polyphyllus* may still be able to establish in the recipient community (**manuscripts 1, 2**; Tilman 2004; Ibanez et al. 2014; Pearson et al. 2018). Additionally, the high reproductive capacity of the invader after an extreme drought event stands in contrast to the declining seed output of native semi-natural grassland species due to dry spells (Zeiter et al. 2016) and consequently may lead to a dominance of the invader in the seed bank of native grasslands. Further spread (across Europe) seems highly probable (**manuscripts 1, 2**) as the predicted increase in drought events may favor the non-native legume over native species (**manuscript 2**). Extreme drought events that are uncharacteristic for Central Europe but more common in the western USA (McCabe et al. 2004; Loik et al. 2004), could provide an invasion window (Diez et al. 2012) for *L. polyphyllus* as the invader is less negatively affected than competing native species (**manuscript 2**).

In combination, **manuscripts 1, 2 & 3** seem to show contrasting effects of climate change (IPCC 2014) on invasive species performance, which can be attributed to their different areas of origin and consequently to their different preferences and traits. In accordance to Hulme (2017), **manuscripts 1 & 2** predict an enhanced potential of establishment and spread of invasive plant species after disturbance (climate events), here extreme drought events, as well as a higher benefit from climate change compared to native plant species (Liu et al. 2017). These effects were independent of invader origin. Climate change is predicted to lead to declining range sizes of invasive plant species on large spatial scales and an increase of range sizes on small spatial scales (Bellard et al. 2018). **Manuscripts 3 & 5** revealed that the amount of suitable habitat of the legume ecosystem engineers, *L. polyphyllus* in Europe and *L. nootkatensis* in Iceland, is projected to increase under future climate conditions (measured in total area suitable). However, the overall habitat suitability for *L. polyphyllus* is projected to decrease in both ranges, native and invasive, but especially in the invasive range of Europe: Large areas which are very well suited under current climate conditions are projected to be at the edge of suitability under future climate conditions (**manuscript 3**). This, again, could be attributed to the invader's pre-adaptation to its area of origin, where *L. polyphyllus* has the status of a facultative upland and wetland plant (Beuthin 2012), thus leaving it potentially maladapted for the increasingly warmer climate in Europe (IPCC 2014). Consequently, the long-term climate trends, based on global climate change models, seem not to particularly favor *L. polyphyllus*. While *L. nootkatensis* seems to profit from the potential warming and prolonged growing season of the projected future climate in Iceland (**manuscript 5**).

Additionally, **manuscript 3** showed that *L. polyphyllus'* realized niche may have expanded towards a broader range of suitable environmental conditions on the European continent compared to its native range North America (niche expansion 20.39%); while large parts of the invader's niche were stable between the two ranges (niche stability 79.61%) and only a very minor part of the native niche was non-overlapping with the invasive niche (niche unfilling 1.24%). Previous studies suggested that niche shifts are rare among most of the terrestrial plant invaders (Petitpierre et al. 2012) but in **manuscript 3** we have shown that the ecosystem engineer is experiencing a niche shift, which makes the accurate projection of potentially suitable habitat more difficult (Guisan et al. 2014; Tingley et al. 2014).

Senecio inaequidens seems to be better adapted to a possibly drier future climate (EPPO 2006) than *L. polyphyllus*. Thus, it might benefit from the increased disturbance and resource availability going along with climate warming, CO_2 enrichment and increased N deposition (e.g. Liu et al. 2017). Invaders of warm origin (like *S. inaequidens*) may profit from a drier future climate in Central Europe, while invaders from cold regions (like *L. polyphyllus*) may struggle with the combined effects of drought and native species competition (**manuscript 4**). Due to its superior performance under drought, *S. inaequidens* might form monocultures under future climate conditions as it may be able to outcompete inferior native species (**manuscript 4**).

5.3 Invader stress tolerance, prevalence and ability to spread

Will there be changes of biotic interactions due to climatic changes and how will this affect the spread of invasive species or the future invasiveness of communities?

Successful plant invasion may (indeed) be influenced by climate change in a positive way. **Manuscript 2** and **4** confirm that climate change may alter biotic interactions. Here, plant-plant interactions were changed by the increased relative competitiveness of invasive species. *Lupinus polyphyllus* showed inferior competitive ability compared to two native plant species under ambient climate conditions. However, during an extreme drought event, and although being negatively affected by the extreme drought event itself, *L. polyphyllus* maintained a relatively higher physiological performance than two dominant native species and derives a (slight) competitive advantage. This may be enough for the legume invader to outcompete native species during phases of increased abiotic stress. Hence, future extreme drought events likely reduce the biotic resistance of native species and thus, may open a potential ‘invasion window’ for establishment and population growth of invaders (**manuscript 2**; Diez et al., 2012). This phenomenon is observed in other invasive species, and not only non-native plants, too (Tucker and Williamson 2014; Kettenring et al. 2015).

A similar effect was found for the high-latitude invader *Lupinus nootkatensis* (**manuscript 5**). The ecosystem engineer seems also to be co-limited by biotic interactions (competition) as the colonization of *L. nootkatensis* was impeded in areas of only minor disturbance (**manuscript 5**). Thus, a change in one factor, here climate change altering the abiotic filter, can lead to changes in how the abiotic and biotic filters act together to shape species interactions (**manuscripts 2, 5**; Pearson et al., 2018). This may ultimately lead to synergistic effects of climate extremes and invasive species on physiological processes (Caldeira et al. 2015). Hence, the presence of highly invasive species might turn the insurance hypothesis ad absurdum (negative sampling effect), as the invader species are the resistant species here, but the native community surrounding the invaders is more negatively impacted by extreme drought events and thus potentially enabling the invader to become dominant after the disturbance.

In addition to the advantage in competitive performance of the selected invader species under future extreme events the total amount of suitable habitat is projected to increase (**manuscripts 3, 5**). This is in contrast to most other invasive species where a decline in their distribution is projected (Bellard et al. 2018). Consequently, it must be assumed that 1) communities will get more susceptible in the future due to climate change in general and extreme drought events in particular (**manuscripts 2, 3, 4, 5**), and 2) the ability of the invasive study species to spread will increase (**manuscripts 3, 5**). Hence, both factors are increasing the susceptibility of native communities as well as the hazardous potential of the invaders studied (more habitat, less resistance by natives).

Consequently, extreme climatic events (such as droughts) may facilitate biological invasion of non-native plant species of both, cool and warm source regions (**manuscript 2, 4**).

5.4 Impact of invader presence

How do plant invaders affect native species and the biodiversity-stability relationship?

Results of **manuscripts 1, 2 & 3** suggested a potential advantage of invasive versus native species due to climate change and extreme weather events and **manuscript 4** revealed that the joint forces of climate change and invasion may have a profound negative effect upon native species recovery from disturbance, thus probably speeding up/facilitating the emergence of novel or hybrid ecosystems. **Manuscript 4** revealed that invader presence may disrupt how native community interactions lead to stability of ecosystem functions (here productivity) in response to extreme climatic events. Species richness stabilized community productivity by increasing the ability of native species to recover from extreme drought events (**manuscript 4**), an effect which was also shown for pulse drought events in previous studies (Kreyling et al. 2017b; De Boeck et al. 2018). One year after the extreme drought event, community productivity without invader presence had fully recovered and in some cases even overcompensated, particularly in the high species richness mesocosms of native communities (**manuscript 4**). Native species richness improved the drought recovery of biomass production in our multisite experiment and, thus, provided ecosystem stability in the face of extreme climatic events in uninvaded assemblages (**manuscript 4**; Allison 2004; DeClerck et al. 2006; Van Ruijven and Berendse 2010; Vogel et al. 2012; Kreyling et al. 2017b). Invader presence turned the positive and stabilizing effects of diversity on native species recovery into a neutral relationship (*L. polyphyllus*), or even tended to reverse it in the presence of *S. inaequidens*. This effect was independent of the two invader's own capacity to recover from an extreme drought event (**manuscript 4**). Consequently, the interaction of the global change drivers, climate extremes, invasive species, and species richness decline may exacerbate their effects on ecosystem functioning even further. The invader impact upon native species performance was more pronounced in *S. inaequidens* relative to *L. polyphyllus* (**manuscript 4**). The presence of competitive and stress tolerant invaders may be able to overturn the positive diversity-stability relationship of native grassland communities (Wilsey et al. 2014). In sum, **manuscript 4** showed that the interaction of extreme climatic events and invasive species may not only disrupt the ability of native communities to recover from drought, but that extreme events may also facilitate non-native invaders, at least if they are well adapted to the future climate (Wilsey et al. 2014).

Combining the results from **manuscripts 1** and **2**, the ecosystem engineer *L. polyphyllus* seems to be a stress tolerant species with buffered population dynamics even under extreme abiotic conditions (LaForgia et al. 2018; Thomson et al. 2018). However, due to the only small advantage in the combined drought and competition experiment (**manuscript 2**) it remains questionable whether *L. polyphyllus* is able to competitively exclude native species under extreme climatic stress (Cleland et al. 2015; Thomson et al. 2018).

How do invasive ecosystem engineers create novel and hybrid ecosystems?

Lupinus polyphyllus, *L. nootkatensis*, *S. inaequidens* and *V. thapsus* are all invasive species with varying degrees of engineering capacities. While *L. polyphyllus* and *L. nootkatensis* are relatively strong ecosystem engineers, *S. inaequidens* seems to be from an intermediate level of engineering capacity. The major difference between the legume ecosystem engineers (*L. polyphyllus* and *L. nootkatensis*) and *S. inaequidens* seems to be that the former are able to pursue niche construction and thereby speed up succession by introducing an additional vegetation layer into open habitats as well as by increasing soil quality and depth (Fremstad 2010; Magnusson 2010; Thiele et al. 2010). Thus, they may lead to some kind of stable alternative ecosystem in heavily degraded systems (**manuscript 5**). While *Senecio inaequidens* seems to negatively impact native species more profoundly as it is highly efficient in exploiting the top soil nutrient pool (**manuscript 4**; Dassonville et al., 2008; Global Invasive Species Database (GISD), 2015). However, the stronger impact on native species under drought conditions may be due to the fact that *S. inaequidens* is a Mediterranean type invader that prefers soil dryness in its invasive habitats (Vacchiano et al. 2013). Thus, this species may be better able to deal with drought (**manuscript 4**; Dassonville et al., 2008; Global Invasive Species Database (GISD), 2015). Therewith, the stronger impact of *S. inaequidens* is likely not due to the difference in the engineering capacity per se. Due to its superior performance under drought, *S. inaequidens* might form monocultures under future climate conditions (as it may be able to outcompete inferior native species, **manuscript 4**; Heger and Böhmer 2006). However, as *S. inaequidens* is a highly effective competitor at least under drought conditions (natives growing with *L. polyphyllus* performed relatively better than natives growing with *S. inaequidens*, **manuscript 4**), these novel or hybrid ecosystems might prevail and lead to significant losses of biodiversity and functioning and likely also to a deterioration of soil conditions (EPPO 2006; Heger and Böhmer 2006). However, to date it is not quite clear if the changes in the physical environment induced by the presence of the invader outlive its own lifespan and/or presence (Heger and Böhmer 2006). Consequently, invasive ecosystem engineers can show constructive as well as rather destructive traits, in terms of their effect on other species, while forming the affected habitat. Hence, it may depend on the characteristics (e.g. mode of action, origin) of the respective ecosystem engineer whether or not the emerging novel or hybrid ecosystem is stable or sustainable.

While the ecosystem engineer, *L. polyphyllus*, showed consistently high germination and emergence rates across five climates, the results for the species with a relatively lower engineering capacity were more indifferent (**manuscript 1**). *Senecio inaequidens* had consistently low emergence rates, while *V. thapsus* showed very good emergence rates in three out of five climates, and low to intermediate germination in two climates (**manuscript 1**). In terms of germination success, the legume ecosystem engineer seems to be the more powerful invader, compared to the other species, when it comes to the sheer establishment phase.

Manuscript 4 revealed facilitation of invasive species in semi-natural grasslands due to extreme drought events, though the pathway to this effect varied between the invaders. *Senecio inaequidens* showed increased resistance of biomass production during drought as well as an increased ability to recover from such an extreme event compared to other native and invasive species. *Senecio inaequidens* invaded plant communities showed a stronger resistance and recovery than *L. polyphyllus* invaded plant communities and the native species communities. *Lupinus polyphyllus* invaded plant communities also showed a higher and overcompensating recovery compared to native species, despite an average drought resistance. Generalizing the results presented so far, invaders of warm origins (here *S. inaequidens*) may profit from a drier future climate in Central Europe as they are better adapted to warm temperatures and drought due to their native range (Vilà et al. 2007), while invaders from cold regions (here *L. polyphyllus*) may struggle with the combined effects of drought and native species competition. However, it is still very likely that both invader types are able to prevail under current and future climate conditions (**manuscripts 1, 2, 4, 5**).

In conclusion, the tested ecosystem engineers of this thesis showed a generally high invasiveness, but the impact upon native species, communities and ecosystems, and thus likely the structure of the emerging novel or hybrid ecosystem, depends on their origin, mode of action and the prevailing climate.

Does the occurrence of novel and hybrid ecosystems necessarily correlate with the degradation of the affected habitat, or with loss of biodiversity?

The answer to this question highly depends on the ecosystem in which the ecological novelty forms. Invasion of an ecosystem engineer can induce very different effects changing biotic interactions and ecosystem functioning into all sorts of directions: in heavily degraded habitats it can cause a fast increase in plant species richness and diversity while in native species-rich habitats it may lead to a reduction in plant species richness by outcompeting more sensitive species (**manuscript 5**).

In highly degraded ecosystems, the improvement of soil depth and quality, in terms of higher nutrient availability, induced by the lupine ecosystem engineers will likely lead to an overall improved biodiversity in comparison to the initial state. It is important to note that this may only apply to severely degraded ecosystems, such as bare soils, which are prone to erosion, as is the case in Iceland. However, it remains questionable whether the biodiversity of those invader-dominated novel or hybrid ecosystems is comparable with ecosystems of a similar succession stage (Evers et al. 2018). In Iceland, *L. nootkatensis* pursues niche construction (Fei et al. 2014) by eventually increasing soil quality (increased nutrients and improved water balance) and depth of the invaded habitats (Sigurdardottir 2008; Magnusson 2010). However, in most of the invaded habitats, *L. nootkatensis* eventually gets replaced by a birch forest in the course of succession. Nevertheless, recent studies showed that the vegetation structure of the habitats formerly invaded by *L. nootkatensis* is changed even after the disappearance of the invader (**manuscript 5**; Magnusson et al., 2008). Thus, those ecosystems are ecological novelties themselves (Evers et al. 2018). In addition, forests have a lower number of species per se, also in Iceland (**manuscript 5**).

In all other ecosystems void of degradation invader presence leads to a declining biodiversity (**manuscript 5**), and a decline in biodiversity leads to a tendency towards improved invasion success and invasiveness (**manuscript 4**). Species-rich habitats showed a loss in plant species diversity and richness as well as a change in community composition as soon as lupine invasion occurs even in low lupine cover classes (**manuscript 5**). In contrast, species-poor habitats showed an increase (**manuscript 5**). In Iceland, invasion of *L. nootkatensis* is most problematic in the heathlands as well as in the biodiversity hotspots: the mountainous regions and Central Highlands, especially of Northern Iceland (Wasowicz et al. 2014). Invader communities did not show the biodiversity-stability pattern (linear increase of recovery with increasing species richness) observed in native species under climate stress (**manuscript 4**). However, they showed higher and even over-compensating recovery compared to the native species communities, due to high individual invader performance when subjected to an extreme drought event (**manuscript 4**). Consequently, invaders may eventually replace natives, especially when invaders are able to outcompete natives during phases of increased abiotic stress (sensu invasion windows, Diez et al., 2012, **manuscript 2**) and when they show an increased ability of resistance and/or recovery (**manuscript 4**).

In accordance to recent publications (e.g. Wasowicz, 2016), we were able to verify the relation between human disturbance and occurrence of invasive species for *Lupinus nootkatensis* (**manuscript 5**). The legume ecosystem engineer may benefit from anthropogenic influences/disturbances, though it does not necessarily depend on human presence (**manuscript 5**). Summing up, once established legume ecosystem engineers are no longer dependent on human-induced rapid environmental change (HIREC) for their spread. However, when HIREC occurs (e.g. human disturbance of native ecosystems or climate change, both leading to a degradation of the affected habitats) it leads to a strong performance advantage of the invader (**manuscript 5**).

Does the stability concept stand in contrast to ecological novelty? / Are novel and hybrid ecosystems created by ecosystem engineers sustainable?

According to the findings presented in the manuscripts of this thesis, it seems as if the stability concept (e.g. MacArthur 1955; McNaughton 1977; Ives and Carpenter 2007; Loreau and de Mazancourt 2013) [in terms of resistance (*sensu* Pimm 1984)/recovery (*sensu* Hodgson et al. 2015)] stands in contrast to ecological novelty, but it depends on the respective invader and the affected habitat (**manuscripts 2, 4, 5**). **Manuscript 4** shows that biodiversity (here species richness) stabilizes community productivity by increasing the ability of native species to recover from extreme drought. Invader presence disturbs this stabilizing relationship and can even turn it into a negative relationship, depending on the invader. The negative invader impact is independent of the invaders own performance under increased abiotic stress (**manuscript 4**). Both invaders, *L. polyphyllus* and *S. inaequidens*, showed good or even overcompensating recovery compared to native species of different functional groups. Especially invader monocultures showed pronounced abilities of recovery (**manuscript 4**). Additionally, **manuscript 2** showed that the resistance of the legume ecosystem engineer *L. polyphyllus* is, despite being negatively impacted by extreme drought, still significantly better compared to two native common grassland species. Consequently, stability – in terms of sheer biomass production – may be inferred via two different mechanisms in native versus invader communities (**manuscript 4**; Wilsey et al. 2014): 1) stability of native species communities is inferred by species richness, that is a native species growing in a mixture of potentially asynchronous and diverse, but partially functionally redundant species, 2) stability of invader communities is largely due to highly productive invasives and their relative share in the entire community (**manuscript 4**).

During lupine invasion biodiversity is reduced, as the invader reduces species richness, changes community composition of the affected habitats (**manuscript 5**; Hejda et al., 2017) and reduces the habitat availability for wildlife (Hejda et al. 2009; Thiele et al. 2010; Ramula and Pihlaja 2012; Ramula and Sorvari 2017). In addition to the loss of habitat provision, further ecosystem services delivered by the semi-natural grasslands (hay, meat and dairy production) are not necessarily preserved during lupine invasion (Volz and Otte 2001; Otte et al. 2002; Otte and Maul 2005; Dengler and Tischew 2018). Hay meadows invaded by *L. polyphyllus* may lose their economic value due to the piperidine alkaloid content of the legume invader and its indigestibility for livestock (Beuthin 2012; Panter et al. 2017).

Consequently, if we interpret the ‘stability concept’ (aka resistance/recovery) as ‘being able to keep or to return to pre-disturbance levels of an ecosystem function’, only in terms of productivity, then it does not stand in contrast to ecological novelty, as the invaders were able to keep up or return to pre-drought productivity levels (**manuscripts 2, 4**). However, if we interpret stability in a wider definition as maintaining functionality (e.g. Hautier et al. 2018), protection against further changes (resilience aka resistance and recovery) (e.g. Ives and Carpenter 2007; Hodgson et al. 2015), but also ecological integrity and biodiversity (Hobbs et al. 2009; Hautier et al. 2015; Pauchard et al. 2018), then the answer is likely “no”. However, it definitively depends on the ecosystem function we are looking at. Invader mesocosms were perfectly able to maintain the ecosystem function/service ‘productivity’, in terms of absolute biomass production, but will certainly fail to keep up or tremendously change with respect to biodiversity/species richness, habitat provision, nutrient cycling, water regulations, provision of fodder value etc. (**manuscript 2, 4, 5**; Thiele et al. 2010; Beuthin 2012; Ramula and Sorvari 2017; Klinger et al. 2019). It is currently being investigated to what extent the high productivity / the biomass produced by the invasive *L. polyphyllus* can be used economically if not for hay production. Use of the invaded biomass for biogas and solid fuel production seems to be a good solution (Hensgen and Wachendorf 2016). On the other hand, and especially if they are introduced for management purposes, lupine ecosystem engineers secure and develop soils (Liška and Soldán 2004; Hiltbrunner et al. 2014; Wasowicz 2016; **manuscript 5**), so that soil degradation does not progress further and the affected areas can be used again for agricultural purposes or nature conservation.

Consequently, functionality of the affected habitats is not or only limitedly or fully preserved depending on the habitat and the recipient community. An increase in the recurrence of extreme drought events likely leads to an increase in invader presence in the affected semi-natural grasslands and consequently less biodiversity due to the competitive advantage of the invader. In sum, these effects stand in contrast to the stability concept and thus, novel or hybrid ecosystems should not necessarily be perceived as sustainable (Evers et al. 2018).

However, the main reason why novel or hybrid ecosystems initiated by the lupine ecosystem engineers might be sustainable after all (without any options to return to pre-invasion reference dynamics) is that they are able to secure and develop soils, as well as to speed up succession to higher plant life in highly degraded ecosystems (**manuscript 5**; Magnusson et al., 2008). Those plant communities are then able to stabilize the barren and sometimes degraded soils and subsequently reduce desertification and dust storms on Iceland (**manuscript 5**; Arnalds and Runolfsson 2008; Magnusson et al. 2008; Riege 2008), which are due to the man-made, large-scale deforestation of the island since the Viking Age (Arnalds and Runolfsson 2008). Further case studies, which acknowledge the protective value of the ecological novelty phenomena for degraded ecosystems (protection against further damage), exist (Kueffer et al. 2010; Wolfe and Van Bloem 2012). *Lupinus nootkatensis* and *L. polyphyllus* both speed up succession and thus, are only a transitional stage themselves. The most likely ‘climax’ vegetation, however is some kind of forest, as seen in Iceland. In Iceland those follow-up ecosystems, especially the forests, show a reasonable biodiversity (**manuscript 5**) and seem to be sustainable in the longer perspective (Arnalds and Runolfsson, 2008; Magnusson et al., 2008). However, forests in Europe are usually less species-rich compared to semi-natural grasslands and heathlands and these follow-up forests differ in their species composition to native forests (**manuscript 5**). Additionally, ecosystem engineers can also lead to the establishment of more invasive species or nitrophilous cosmopolitans and thus, to an invasional meltdown (**manuscript 5**; Magnusson et al. 2008; Thiele et al. 2010; Braga et al. 2018). Consequently, systems created by legume ecosystem engineers possess the potential to become sustainable and valuable novel or hybrid ecosystems, if the initial situation was a highly degraded ecosystem. However, to ensure their proper development, the succession process needs to be guided by restoration managers (Kreyling et al. 2011a; Kueffer and Kaiser-Bunbury 2014).

At which point do hybrid ecosystems turn into novel ecosystems?

Hybrid ecosystems can return to their reference or historical state, while a novel ecosystem cannot reach its former status again (Hobbs et al. 2009; Figure 1b and 2). Consequently, novel ecosystems have crossed a threshold in their development away from the former reference status (Collier and Devitt 2016; Higgs 2017). In contrast, hybrid ecosystems are simply a blend of new and old elements. As soon as this mixture status is surpassed and (unpredictable) diverging traits emerge, a novel ecosystem is formed (Hobbs et al. 2009; Collier and Devitt 2016; Higgs 2017).

A fundamental trait of lupines is the addition of inactive atmospheric nitrogen to reactive plant-available nitrogen to ecosystems. Naturally - meaning without anthropogenic input - most ecosystems lack reactive nitrogen, as only few organisms can acquire atmospheric nitrogen. Therefore, lupines and other legumes are biogeochemical ecosystem engineers (by symbiotic nitrogen fixation) with massive and sustainable impact. So, if legumes are not native to an ecosystem, they start transforming it massively. The question of when the tipping point or threshold from a hybrid to a novel ecosystem is crossed in terms of nitrogen accumulation by invasive lupines depends on the previous nitrogen status and the duration of nitrogen accumulation. On Iceland, being a cold and volcanic island with nutrient-poor arctic soils, ecosystems are mostly in a very early successional stage, and therefore it takes only small changes in the nitrogen status to cross the tipping point as compared to Germany, where ecosystems are further developed and adapted to atmospheric anthropogenic nitrogen depositions.

In Iceland, restoration of ecosystems invaded by *Lupinus nootkatensis* to the original / historical reference ecosystem state is hardly possible at least in the foreseeable future. The changes in solid nitrogen content and shifts from nutrient-poor to nutrient-rich soils in Iceland is accompanied by substantial vegetation changes. In places where *L. nootkatensis* was successfully eradicated, grassland instead of heath emerges. This indicates that a tipping point (here nitrogen addition in nutrient-poor artic soils) has been exceeded and a novel ecosystem has emerged. (pers. communication Pawel Wasowicz, Icelandic Institute of Natural History, 26.05.2020 and 16.03.2022)

In Germany, the presence of *Lupinus polyphyllus* leads to the formation of hybrid ecosystems. *L. polyphyllus* frequently occurs in semi-natural ecosystems e.g. in the Rhön UNESCO Biosphere Reserve, in Germany. However, by intense restauration effort, aiming at the reduction of the nitrogen addition caused by *L. polyphyllus*, the invaded systems can potentially be returned to their original ecosystem state (pers. communication Ranger Office hessian part of the Rhön UNESCO Biosphere Reserve, ranger Hubert Heger, 25.03.2014; Volz 2003; Valtonen 2006; Hansen et al. 2022), indicating that no tipping point has been crossed so far. However, these management options are very laborious (e.g. hand mowing 3 to 4 times per year) and must be maintained over decades (> seed longevity in seed banks of *L. polyphyllus*) to ensure effective removal of the lupine from those semi-natural ecosystems (pers.

communication Ranger Office hessian part of the Rhön UNESCO Biosphere Reserve, ranger Hubert Heger, 25.03.2014; Volz 2003).

5.5 The conservation aspect

Can we use/engineer novel and hybrid ecosystems to solve environmental problems?

Of course, ecosystem engineers – both, invasive and native – can be and are used to solve environmental problems (**manuscript 5**; Pejchar and Mooney 2009; Schlaepfer et al. 2011; Beuthin 2012; Ayanu et al. 2015). But, the usage of invasive ecosystem engineers for this purpose may quickly develop into a double-edge sword (Schlaepfer et al. 2011). Especially in times of rapid environmental changes, a targeted application for restoration purposes, only at the desired locations, may not be feasible. A prime example is *Lupinus nootkatensis* in Iceland. The non-native ecosystem engineer was widely and deliberately applied by conservation agencies to restore the highly degraded soils of Iceland and to stop desertification (Arnalds and Runolfsson 2008; Magnusson 2010). And it works, the non-native legume stabilizes soils, increases soil quality and depth and induces the urgently needed succession to higher plant life in eroded ecosystems (Arnalds and Runolfsson, 2008; Magnusson et al., 2008; Riege, 2008). But these beneficial effects come at two costs: 1) the lupine is an effective disperser, which spreads beyond the areas designated for its application, and 2) if *L. nootkatensis* is able to establish itself, it also permanently changes intact plant communities (**manuscript 5**) and wildlife habitat thereby degrading native biodiversity (Davidsdottir et al. 2016). Therefore, the invader engineers novel or hybrid ecosystems even in areas void of any restoration needs.

Invasion of an ecosystem engineer can induce very different effects: in heavily degraded habitats it can cause a fast increase in plant species richness and diversity while in native cold-adapted habitats it may lead to a reduction in plant species richness by outcompeting more sensitive species (**manuscript 5**). The abundance of species that rely on soils with low nitrogen content (small rosettes, cushion plants, orchids, and small woody long-lived plants of the heath in Iceland) declined with invader presence, while the abundance of late successional species and widespread nitrophilous ruderals in wood- and grasslands increased (**manuscript 5**). In terms of alpha, beta and gamma diversity, the affected habitats deteriorated owing to the presence of *L. nootkatensis*, which acts as 'transformer species' whose presence leads to lupine induced homogenization (Davidsdottir et al. 2016).

Additionally, if one or more factors, which control the spread of the invasive ecosystem engineer under current conditions, changes, a massive further spread of the intruder must be assumed. In Iceland the changing factor will be climate, as the habitat suitability of Iceland's land surface area will significantly increase for *L. nootkatensis*, giving the invader the opportunity to greatly expand into the Central

Mountains of Iceland, which are of high conservational value (**manuscript 5**). This additionally hampers the targeted application of the ecosystem engineer and facilitates invasion. Under current as well as future climate conditions, the amount of projected suitable habitat for *L. nootkatensis* will mainly cover areas without native vegetation and thus, may induce the urgently needed succession to higher plant communities. However, 86.9% of the area that is currently inhabited by the native vegetation of Iceland is projected to become suitable lupine habitat under future climate conditions. Thus, this area is at risk of being permanently changed to a secondary vegetation as the emerging plant community of the novel or hybrid ecosystem induced by lupine succession differs in structure and composition from native plant communities (**manuscript 5**; Magnusson et al., 2008). In areas where positive aspects prevail, ecosystem engineers may carefully by used for restoration purposes e.g. to speed up succession toward a stable vegetation cover on severely degraded soils. However, the spread of an invader beyond such areas is very likely leading to altered energy and nutrient fluxes (**manuscript 5**). Consequently, ecosystem engineers may be used to successfully engineer novel or hybrid ecosystems, however, while their use always leads to the emergence of novel or hybrid ecosystems, their effects depend on the recipient community/habitat and are not necessarily desirable (**manuscript 5**). Using invasive ecosystem engineers to solve environmental problems (**manuscript 5**; Ayanu et al., 2015) may come at a high risk owing to HIREC. Consequently, it is advisable to use them only very carefully and maybe consider other, less dangerous options to solve the respective environmental problem first.

Management recommendations

During drought the ripening and spreading of lupine seeds should be prevented. The seeds of *L. polyphyllus*, even if the plant is cut before seed maturity, can still ripen in the mown state and the lupine thus spread further (Klinger et al. in prep.). Therefore, the removal of mown aboveground biomass of *L. polyphyllus* is very important because, as shown by **manuscripts 1** and **2**, the invader may be able to use the invasion window arising during and after an extreme drought event and *L. polyphyllus* is additionally able to germinate in a great variety of climate conditions, while native species reproduction may be negatively affected by a drought event (Zeiter et al. 2016). It might be advisable to combine management measures that aim to reduce invader presence (ripening and spreading of seeds should be prevented in any case) of non-native species from a northern-cool origin with the occurrence of extreme drought events. By combining the effects of decrease in habitat suitability, due to climate trends, with the temporary deterioration of performance of *L. polyphyllus*, due to the extreme drought event, the targeted eradication of the invader may be promoted (Guo et al. 2018). In this way, conservation may be able to prevent the usage of the arising invasion window by lupines (see **manuscripts 1, 2**).

Management measures should be very targeted to the respective invader, as additional stress (e.g. due to mowing) could impact the stressed native plant species more negatively than the (slightly less stressed) invader (**manuscripts 2, 4**). Therefore, natives are at risk of taking unwanted additional impact, e.g. through broad-based management measures that affect the native vegetation as well. However, since the invader from a norther-cool region is stressed by an extreme drought event, too, a combination of management measures supported by the negative effects of an extreme drought event might be more effective in invader containment. One, although not very practical (depending on the invasion status) solution therefore would be removal of the invader by hand.

Better safe than sorry, the use of lupines for the restoration of degraded ecosystems should be avoided as far as possible. However, if the ecosystem engineers are used anyways, it should be done with caution: assess beforehand if they can spread to vulnerable habitats and have a negative impact there. In addition, and in order to reduce the invasion potential of lupines, no seed imports from climatically different origins should be made (**manuscript 1**).

6 EMERGING RESEARCH CHALLENGES AND FRONTIERS ON THE TOPIC OF NOVEL ECOSYSTEMS AND INVASIVE ECOSYSTEM ENGINEERS

In my dissertation, I use a versatile approach combining experiments with data recording in the field as well as modelling. Being a field ecologist and modeler, I know and value the importance of experiments. They not only advance our knowledge in ecology by providing essential insights for the understanding of ecological processes and relations, but also provide an urgently needed and valuable data basis for modelling. Modelling, on the other hand, can be used to scale the insights gained by experiments up to the landscape/ecosystem level and/or to project into future/past conditions, e.g. future climate change conditions. Thus, modelling is able to bridge the 'time and scale gap' which often limits experiments. Therefore, I would like to conclude by (roughly) describing an experiment on the basis of which important information could be obtained in order to further develop our ecological knowledge regarding novel ecosystems and invasive ecosystem engineers and which would provide an important data basis for future modeling.

In general, my dissertation gives first insights into the interplay of climatic pre-adaptation and the invasion potential of non-native species, the impacts of invasive species on the biodiversity-stability relationship of native communities, the impacts of (engineering) invasive species on native communities, biotic interactions and their constrains to the future invasiveness of non-native species, the emergence of novel ecosystems due to the interplay of invasive species and climate change, the ecological consequences of the emergence of novel ecosystems, and the ecological impacts of invasive ecosystem engineers across different habitats.

A potential future experiment

To further determine the invasiveness of ecosystem engineers (e.g. lupines; and maybe additionally other invasive species with no distinctive features of an ecosystem engineer), as well as to investigate how they contribute to the emergence of novel ecosystems, the next necessary step would be to test the combined filter effect (combined abiotic and biotic stress: e.g. extreme drought events and competition by native species) along a larger environmental gradient (e.g. sub-polar to tropical) and against the competitive power of a larger set of native species that includes different grassland types of the world (e.g. prairie, steppe, etc.).

Concerning the dimensions and the globality of the experiment, it would resemble those of the large grassland experiments, e.g. Drought-Net, Nutrient Network (NutNet) or HerbDivNet. Or precisely, it would be feasible to 'add some more plots' to the already existing sites of those globally distributed experiments. Although, these experiments could test the emergence of novel ecosystems owing to the pressure of other disturbances (drought, nutrient addition etc.), they lack the invader aspect. Globally distributed experiments are able to bridge the gap between repeated measurements across large spatial and temporal scales and the in-depth exploration of the processes as well as the ecology of a particular location (Kueffer 2014). In this way it is feasible to study different locations, species and climates with the precision of a single case study. Therefore, I advocate the addition of disturbance x invader presence plots to those large grassland experiments. As an example, I describe the procedure for plot addition to the Drought-Net experiment. The factors suggested to test in this hypothetical experiment are based on those tested in the manuscripts of this PhD thesis (drought x invader), as the task of this section is to provide emerging research challenges based on the thesis on hand. However, a similar procedure would also be feasible for the NutNet or HerbDivNet experiment.

The easiest solution would be to add new plots to already existing sites partitioning e.g. in the Drought-Net community (https://wp.natsci.colostate.edu/droughtnet/). In this case, the already existing drought plots as well as the plots under ambient weather conditions could serve as control without invader presence. Thus, it would be sufficient to add 6 plots per invader species (3 x invader presence under ambient weather conditions; 3 x invader presence under drought). The experimental set-up should follow the Drought-Net protocol for the installation of the climate treatment plots (see appendix to have a look into the protocol). Due to the fact that Drought-Net is a globally distributed experiment, it may be sufficient to test one invader species per site. All the single case studies of one invader species per site will ultimately sum-up to a large multi-species invader experiment (Kueffer et al. 2013). More invader species or more replicates per invader species could be tested if feasible for the respective site. However, care should be taken to ensure that the controls and invader treatments have the same sample sizes.

Invader species

Possible criteria for choosing the invader species. The invader should:

- already be present in the respective country to avoid introductions of non-native species into new areas/countries/continents.
- display traits which are characteristic for an ecosystem engineer, e.g. be able to modify
    - the biogeochemical cycle of the recipient habitat
    - the physical space in which they and other species live
    - the availability of resources for other species
- be able to induce changes that extend beyond its life span and/or presence

Additionally, the steering board of this experiment could provide a list with a basis set of invader species that fit to those criteria (*Lupinus polyphyllus*, *Lupinus nootkatensis*, *Senecio inaequidens* etc.). Invaders should be planted as seedlings (e.g. 5 per plot) into the native matrix vegetation of the respective site. After an establishment phase (e.g. 4 weeks), during which deceased seedlings can still be exchanged, the drought treatment starts. A standardized planting scheme would be necessary to ensure uniform starting conditions for each invader species of every site.

Drought treatment

The extreme drought event should be tested with a flexible definition, because those are ecologically more meaningful than comparing a fix drought duration. The Drought-Net consortium tests a chronic extreme drought event in terms of percentage reduction of each rainfall event, calculated specifically for every site. The percentage of rainfall reduction for each site is based on the 1st percentile of either a site-specific climate data with > 50 year recording time or based on 100-year interpolated climate data (see Drought-Net protocol in the appendix).

The chronic drought treatment is installed for 4 consecutive years, following the instructions given in the Drought-Net protocol. The course of the drought over those years as well as the development of the communities and the potentially arising novel ecosystem is monitored. After termination of the drought phase, recovery is monitored for an equally long period of time.

Measurements

The basic measurements, required from all participating sites, include primary productivity and plant community composition. On an annual basis, the following parameters should be measured:

- aboveground productivity and standing biomass: community biomass per plot, biomass sorted into species, functional group biomass
    - resampling should be avoided; harvest of 25% of the plots per year; repetition of the harvest cycle in the recovery phase
- plant community composition: species richness, species abundance (cover, density)

The following measurements are also mandatory, however, they only take place at specific time points during the different experimental phases:

- soil C and N concentration: will be measured 3 times during the experiment
    - before the onset of drought
    - at the end of the drought treatment
    - at the end of the recovery phase
- traits of the species: will be recorded once upon first appearance of a species
    - growth forms: graminoids, forbs, legumes, etc.
    - photosynthetic pathway: C4, C3, CAM
    - N-fixer
    - Life history: perennial, annual, etc.
    - Clonality: stoloniferous, rhizomatous, caespitose

- Soil moisture in 10-15 cm depth: continuous recording

Additional measurements, which are not mandatory, can be taken from the level 2 measurements of the Drought-Net protocol (see appendix chapter 8.1).

Resistance and recovery ratios will be calculated for communities with and without invader presence. Based on the recorded parameters, which are monitoring the course of the drought treatment and recovery, this experiment is additionally able to provide insights into spatial and temporal trajectories of resistance and recovery to an extreme chronic drought event in native versus invader communities. The naturally grown communities of the Drought-Net experiment could be sorted into a global gradient of species and functional group richness. Thus, it can be observed how extreme weather events, like extreme drought events, in combination with invader presence form novel ecosystems and how this transformation and speed of the process differs in dependence of a global diversity gradient.

According to the most simplest definition of a novel ecosystem 'new and unique set of species and/or relative abundances of species which has not previously occurred in any native ecosystem' (e.g. Morse et al. 2014; Higgs 2017) tracking of the changes in species richness, composition and relative abundance of plots with and without the two stress factors invader presence and extreme drought would be enough to observe the emergence of a 'novel' ecosystem. All additionally measured parameters (e.g. soil C and N) help to underpin these observations. Whether or not those changes are reversible [the threshold to a novel ecosystem is only crossed if the changes are not reversible (according to Morse et al. 2014)], retained, or continue to develop needs to be tested in the recovery phase of this experiment. In case the observed changes in species richness, composition and abundance relative to the control plots are statistically significant ($\alpha < 0.05$) and unique, and if the temporal trajectory of the affected ecosystem is irreversible, then a novel ecosystem has emerged.

Possible variations and additions of the basic experiment

- <u>Variation:</u> permanent installation of the chronic drought experiment (no recovery phase)
- <u>Variation:</u> test invasive species with increasing degrees of characteristics of an ecosystem engineer
- <u>Addition:</u> test an extreme pulse drought event of 1000 year recurrence rate of the respective climate (Jentsch 2013). Testing a pulse drought event in addition to a chronic drought event leads to 12 additional plots, which would need to be added to the original Drought-Net experiment:
    - 3 x invader presence in chronic drought
    - 3 x invader presence in ambient weather conditions
    - 3 x invader presence in pulse drought
    - 3 x pulse drought without invader

- Addition: test the ability of invaders to establish after an extreme pulse or chronic drought event by seeding invaders into the plots after the first phase of drought treatment. Tracking of invader establishment success.
    - 3 x seed addition after drought
    - 3 x seed addition in control
- Addition: removal of the invader species after the drought event and/or after 4 years of recovery. Another 4 years of recovery without invader presence.
    - 3 x invader presence removed after drought
    - 3 x invader presence removed in ambient weather conditions at the end of the drought treatment
    - 3 x invader presence removed after recovery
    - 3 x invader presence removed in ambient weather conditions after recovery

The decision to include one or several additional scenarios would lay by the respective site PIs.

Emerging research challenges

Based on the experiment, a plethora of questions could be answered, which can be summarized under the following topics:

Emergence of novel ecosystems

So far, we know relatively little about novel ecosystems and their emergence besides the fact that we are able to identify them, and even this is debatable and depends on the chosen definition [e.g. Higgs (2017) versus Hobbs et al. (2009)]. When do they form, how do they form, how much pressure is needed? Are there any basic requirements for the emergence of novel ecosystems besides the ones given in the definitions (human agency, self-sustaining etc.) (Morse et al. 2014; Truitt et al. 2015; Higgs 2017)? Is chance an important component in the formation of novel ecosystems or do they always emerge under a certain set of requirements? Do the same invaders form similar novel ecosystems in the affected grasslands [similar in terms of vegetation type/set of species/functional groups (and their relative abundance), succession stage, level of diversity, ecosystem functions; despite the similarities characteristics will vary dependent on the continent/ecozone in which the ecosystem lies] across a global climate gradient? As ecosystem engineers shape their environment according to their demands, do those invaders increase the similarity between the affected grassland habitats across a global gradient, thus decrease global beta and gamma diversity? Is the emergence of novel ecosystems dependent upon the sensitivity against disturbance of the recipient habitat? Are invasive species a leading element in the creation of novel ecosystems or do resistant/strong performing native species, which may become dominant after a disturbance event, take over and lead to novel ecosystems in the absence of invaders (maybe also in the presence of invaders)? How do novel ecosystems, which emerge only due to the presence of an invader species differ compared to those which emerge by invader presence x drought treatment (set of species, relative abundance, speed of emergence etc.)? Does drought on its own lead to the formation of novel ecosystems? Questions like these could be answered with the new experiment. Additionally, based on the results of this experiment, we may be able to predict the emergence of novel ecosystems.

Resistance and recovery of grasslands to disturbances on a global scale

It is necessary to further outline the invasion potential of invader species and types in comparison to the performance of native species under disturbance/extreme weather events. With the new experiment it would be feasible to test the performance and competitive ability of more invader species against a variety of native species from different functional groups.

Knowing when and how invasive species change/affect the ability of native communities to resist/recover from a disturbance event likely means knowing under which circumstances ecosystems will be negatively impacted and/or under which circumstances novel ecosystems will emerge.

Tipping points of native and impacted ecosystems

The point at which human induced disturbance is such pronounced that ecosystems are tipping remains to be clarified. The experiment described above is designed to track the change in the invader versus control plots under two different climate conditions (ambient versus extreme weather event). A yearly calculation of the amount of change relative to the control plots (plots without invader presence) may give first insights if and when the trajectories of the plots begin to diverge. A tipping point is crossed when there is a statistically significant difference ($\alpha < 0.05$) between the invader and the native species plots and if this change persists or continuous to evolve after the end of the disturbance event (here extreme chronic drought and/or invader presence). How much disturbance can ecosystems endure before shifting away from their original state (amount of resilience)? Are there general rules when tipping points occur or are there signs that a tipping point is imminent? Being able to answer these questions would help conservation management. Additionally, tipping points might be invader-dependent and/or dependent upon the affected ecosystem. (Dakos and Hastings 2013)

Additionally, the data and results collected in this experiment could further be used in predictive regime and population shift modelling (see e.g. Takimoto 2009; Weissmann and Shnerb 2015; Xie et al. 2018).

Invasiveness of non-native species

In the manuscripts of this thesis the performance of four invasive species was tested and the insights gained are a good basis to start from. However, the number of invader case studies arising due to the conduct of this experiment provide insights to 1) the individual invader performance/invasiveness under ambient and future climate change conditions, 2) the invader impact on native species

resistance and recovery, 3) the invasibility of the affected ecosystems – all on a regional and global scale (Kueffer et al. 2013). The experiment may also be used to review some of the hypotheses in invasion ecology across larger spatial scales (Fridley et al. 2007; Jeschke 2014), e.g. the biotic resistance and the diversity-invasibility hypothesis. Furthermore, the following questions may be answered:
Are the majority of invasive plant species ecosystem engineers? How do invasive ecosystem engineers create novel ecosystems? Do they always create novel ecosystems? So, is their sheer presence enough or are there other requirements which need to be given? Do extreme drought events, chronic and pulse, facilitate the settlement of invaders in all habitats along the climate gradient? Which invader species profit from an extreme drought event; only invaders from warm origins?

Conservation approaches

Novel ecosystems will likely require novel management structures (Bridgewater et al. 2011). Further knowledge on how extreme weather events and invasive species, on their own but especially in combination work to build impacted or novel ecosystems, and if this process is reversible (to which degree) or permanent, is needed. Building on the results of this new experiment, it would be possible to guide restoration managers.

However, the question of how far invader species are able to spread, may only be answered with species distribution modelling. Therefore, it is important to enlarge the available data concerning species occurrences in their native and invasive range. Insufficient monitoring of invasive species in their native as well as in their invasive range, and consequently insufficient species occurrence data is still a challenge which, besides further knowledge on the species and their behavior under different abiotic and biotic conditions, limits species distribution modelling. Since some invader species in their native range may even be endangered under future climatic conditions, nature conservation and research (e.g. invasion biology) should work hand-in-hand and, above all, make species occurrence records, especially in their native range, accessible.

A detailed collection of further research questions emerging from the results of this thesis can be found in the appendix (chapter 8.2).

7 DECLARATION OF OWN CONTRIBUTION TO EACH PAPER, PRESENTATIONS AT SCIENTIFIC CONFERENCES AND TEACHING EXPERIENCE

In this section, I shortly summarize my own contribution to each of the manuscripts presented in this thesis. Additionally, I give an overview of the courses which I have given during my doctorate. Finally, Table 3 summarizes all the presentations I have given during my doctorate at various scientific conferences, meetings and workshops.

Manuscript 1:

Title: **Factors influencing seedling emergence of three global invaders in greenhouses representing major eco-regions of the world**

Authors: Arfin-Khan MAS, Vetter VMS, Reshi ZA, Dar PA, Jentsch A

Journal: **Plant Biology,** 20, p. 610-618, (2018)

Personal contribution: field work: 0%, data analysis: 10%, figures: 10%, writing: 20%, idea and concept of the manuscript: 20%, corresponding author

Manuscript 2:

Title: **Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters**

Authors: Vetter VMS, Walter J, Wilfahrt PA, Buhk C, Braun M, Clemens S, Dinkel E, Dubbert M, Schramm A, Wegener F, Werner C, Jentsch A

Journal: **Plant Biology**, 21, p. 832-843, (2019)

Personal contribution: field work: 30%, data analysis: 60%, figures: 80%, writing: 70%, idea and concept of the manuscript: 50%, corresponding author

Manuscript 3:

Title: **Niche conservatism or niche shift? Implications for the management of a legume invader**

Authors: Vetter VMS, Jaeschke A, Buhk C, Jentsch A

Journal: in preparation for resubmission

Personal contribution: data collection: 80%, data analysis: 80%, figures: 90%, writing: 70%, idea and concept of the manuscript: 80%, corresponding author

Manuscript 4:

Title: **Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought**

Authors: Vetter VMS, Kreyling J, Dengler J, Apostolova I, Arfin-Khan MAS, Berauer B, Berwaers S, De Boeck HJ, Nijs I, Schuchardt M, Sopotlieva D, von Gillhausen P, Wilfahrt PA, Zimmermann M, Jentsch A

Journal: **Global Change Biology**, 26, p. 3539-3551 (2020)

Personal contribution: field work: 5%, data analysis: 80%, figures: 20%, writing: 80%, idea and concept of the manuscript: 50%, corresponding author

Manuscript 5:

Title: **Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity**

Authors: Vetter VMS, Tjaden NB, Jaeschke A, Buhk C, Wahl V, Wasowicz P, Jentsch A

Journal: **Frontiers in Plant Science**, 9 (715), p. 1-12 (2018)

Personal contribution: data collection: 40%, data analysis: 60%, figures: 90%, writing: 70%, idea and concept of the manuscript: 40%, corresponding author

Teaching experiences

University of Bayreuth

- Spatial Ecology (seminar)
- Modelling of spatial ecological processes (exercise)
- Concepts in Biogeographical Modelling (seminar)
- Invasion processes, 1 session of the lecture Disturbance Ecology

University of Koblenz-Landau, Campus Landau

- Introduction to Geography and geographical methods
  (Einführung in die Geographie und geographischen Arbeitsweisen; seminar)
- Regional Geography of Germany
  (Spezielle Regionale Geographie Deutschlands; seminar)
- Excursion North Carolina, USA, 10 days

Table 2: Presentations of my research at (scientific) conferences, workshops and meetings.

Date	Organization	Conference	Title	Type
10/2018	Bayreuth Center of Ecology and Environmental Research (BayCEER)	BayCEER workshop, Bayreuth, Germany	Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity	Talk
09/2018	Society for Ecological Restoration Europe (SER)	Restoration in the Era of Climate Change, Reykjavik, Iceland	A global legume invader benefits from extreme events under competition	Talk
09/2018	Society for Ecological Restoration Europe (SER)	Restoration in the Era of Climate Change, Reykjavik, Iceland	Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity (on behalf of Prof. Dr. Anke Jentsch)	Talk
12/2017	BES, GFÖ, NECOV, EEF	Ecology Across Boarders: Joint Annual Meeting 2017, Ghent, Belgium	Invasion of the legume ecosystem engineer *Lupinus nootkatensis* alters plant biodiversity and ecosystem functioning in Iceland	Poster
10/2016	INRA Auvergne – Rhône-Alps	SIGNAL meeting Clermont-Ferrand, France	A global legume invader shows high resistance towards extreme weather events and competition – implications for the future invasion success of *Lupinus polyphyllus*	Talk
09/2016	Ecological Society of Germany, Austria and Switzerland (GFÖ)	46th Annual Meeting: 150 years of ecology – lessons for the future, Marburg, Germany	A global legume invader shows high resistance towards extreme weather events and competition – implications for the future invasion success of *Lupinus polyphyllus*	Talk
03/2016	Ulstertalschule in Hilders, Dr. Rainer Heimerich	Forum im Foyer, Hilders, Germany	Lupineninvasion in Zentraleuropa – Ursachen, Prozesse und Ausblicke	Talk
06/2015	INRA Avignon, Dept. of Biostatistics and Spatial Processes Twente University, Faculty of Geoinformation Science and Earth Observation (ITC)	Spatial Statistics 2015: Emerging Patterns, Avignon, France	Predicting the potential distribution and ecological effects of *Lupinus polyphyllus* (Lindl.) in Germany	Poster

8 APPENDIX

8.1 Drought-Net experimental set-up protocol

DRAFT PROTOCOL V1
6 January 2015

The International Drought Experiment: a distributed approach to assess terrestrial ecosystem responses to extreme drought

The goal of the International Drought Experiment (IDE) is to determine how and why terrestrial ecosystems may differ in their sensitivity to extreme drought. To accomplish this goal, a coordinated, distributed experiment imposing an extreme drought over a four-year period will be established in range of ecosystem types across the globe. Below is a description of the IDE experimental design, measurements, and sampling protocols. Please refer to the Drought-Net website for additional details about IDE (www.drought-net.org).

I. Experimental Design

A. Site Selection

- Participation is encouraged for, but not limited to, unmanaged ecosystems.
- Because of the relatively low sample size at each site, the site selected for establishment of the experiment should be relatively homogeneous, with respect soil properties and plant species composition.
- Ideally, the study site should not have experienced a major disturbance event (such as nutrient addition, severe soil disturbance, seed addition, etc.) within past several years or have been recently grazed by livestock (i.e., within the last 3-5 years) to avoid confounding the effects of disturbance or grazing release with the experimental treatments.

B. Treatments

Drought will be imposed using fixed shelters that passively reduce precipitation events by a constant, site-specific percentage (Fig. 1; also see Yahdjian & Sala 2002, Gherardi & Sala 2013). The manipulation will occur year-round where possible. In those instances where snowfall is significant, alternative means of precipitation reduction may be used (e.g., snow removal) or, alternatively, the roof can be removed during the period of heavy snowfall. In all cases, the total amount of precipitation reduction that is imposed must be quantified.

1. Core treatments – The core treatments will consist of 1) an ambient precipitation treatment (unsheltered control) and 2) an extreme drought treatment. The extreme drought treatment will be imposed for four consecutive years. For the drought treatment, the percentage reduction of each

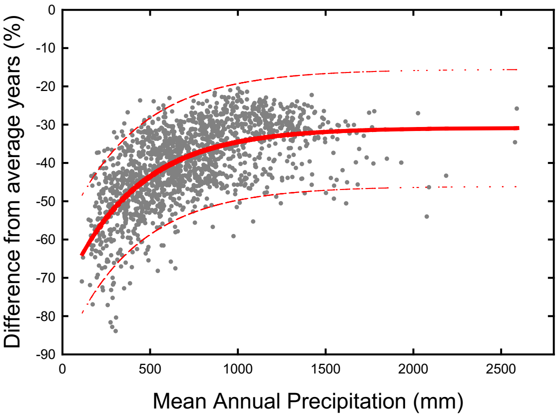


Fig. 1. Relationship between the difference (%) in precipitation amounts between normal years (amounts between the 45-55th % of years within a 100 year record) and extremely dry years (precipitation amounts in the lowest 10th % of years for a 100 yr record) and mean annual precipitation. Data (grey dots) are from 1614 climate stations arrayed across the globe, representing 12 ecoregions. Shown is the predicted relationship (solid red line) with upper and lower bounds of the 95% confidence interval (dashed red lines). Smith *et al*. in prep.

rainfall event will mimic an extreme drought, defined as an extreme reduction in precipitation (based on the 1st percentile of the long-term record), which is specific to a particular site. Sites will be asked to determine this level of extremity in one of two ways: 1) based on site-specific climate data greater than 50 years in length, or 2) based on interpolated 100-yr data. To assist with determination of extremity, an online tool will be made available on the Drought-Net website (www.drought-net.org).

2. Optional treatments – Sites are encouraged to implement the optional treatments, but these are not required for participation in the network.
    a. Fixed treatment - Each site will reduce annual precipitation by 50% using passive shelters.
    b. Infrastructure control – To account for shelter effects, sites are encouraged to establish infrastructure controls, which can be either inverted slats or deer netting (choice to be determined based on cost).

C. Replication and plot size

- The level or replication will, in part, be dependent upon cost. For herbaceous systems, each core treatment will be, at minimum, replicated <u>three</u> times. For those systems requiring larger plots (shrublands, forests), at least <u>two</u> replicates per core treatment are recommended (but not required). Plots can be set up randomly or in a blocked design if appropriate.
- Sampling plot size will be matched to vegetation structure (i.e., height, density, crown width). For short-stature vegetation (<2 m), minimum sampling plot size is 2 x 2 m with a 50 cm buffer surrounding the plot. In cases where larger plots are appropriate, a 4 x 4 m sampling plot with a 1 m buffer is recommended. Forest and savanna sites will need to scale their plot size appropriately.
- The shelter roof will be large enough to cover both the sampling plot plus buffer area (i.e. 3 x 3 m or 6 x 6 m). Shelters should not be installed lower than 80 cm above ground to avoid modifying microclimatic conditions.

D. Trenching

Trenching (to a depth of > 0.5 m) along the border of each shelter (and control plot) is encouraged but not mandatory in order to hydrologically isolate each plot. Depth will be dependent on vegetation; a depth of at least 0.5 m or greater is recommended for herbaceous systems, and deeper depths (at 1 m depth) are encouraged for shrublands and forests. Excavated trenches should be lined with an impermeable barrier (e.g., 6 mm plastic) and refilled prior to the initiation of the experiment. Given that trenching is not feasible at all sites, an alternative to trenching is to increase the size of the shelter to accommodate a larger buffer. If a site is located on a slope (>2%), the mitigation of run-on (e.g., via flashing or other means) is encouraged.

II. Measurements

Two levels of measurements are proposed. Level-1 measurements are designed to quantify three key response variables that will allow us to test network-level hypotheses, as well as provide important site characteristics. These measurements are <u>required</u> for inclusion in the network. Level-2 measurements provide additional response and explanatory variables. Level-2 measurements, although optional for inclusion in the network, should be made <u>if possible</u>. Many additional measurements may be of interest to network participants, but the two levels of measurements are meant to capture key responses and explanatory variables to address a range of network-level questions. Detailed methodologies will be provided on the Drought-Net website (www.drought-net.org).

A. Level 1 measurements

1. **Site level**

   Each site must provide the following information:
   - Latitude, longitude
   - Bailey biogeographic region, biome type, ecosystem type, a more detailed description based on dominant vegetation/species
   - Slope, aspect, elevation
   - Long-term air temperature and precipitation data (preferably 50-100yr record, daily time scale)
     - These data can be from a nearby representative weather station or based on interpolated data
   - Other site characteristics (if known)
     - Disturbance history
     - Depth of known soil impediment (shallow bedrock, caliche layer, etc.)
     - Average water table depth
     - Other unusual site characteristics (saline, serpentine, etc.)

   In addition, each site is required to make the following measurements during the study period:
   - Annual precipitation for each year of the study based on daily precipitation if possible, or less frequent data (i.e., weekly, monthly) if appropriate.
   - Annual average air temperature of each year of the study based on daily measurements, or less frequently if appropriate.
   - List of plant species for the study site.
   - Soil texture, bulk density, chemical characterization (pH, Ca, C, N, P, %OM, etc.).

2. **Plot level**

   The core measurements required for participation in the network are focused on primary productivity, soil CN, and plant community composition.
   1. Aboveground productivity and standing biomass will be measured annually using methods appropriate for a particular ecosystem (refer Fahey & Knapp 2007). These can include both destructive and/or non-destructive measurements. Estimates of biomass will be separated into live and dead biomass. Live biomass will be further separated by growth form (grass, forb, woody). Dead biomass will be separated into current and previous year's when appropriate. For herbaceous-dominated systems, we recommend following the Nutrient Network protocol (www.nutnet.umn.edu). For destructive measurements, no more than 25% of the subplot dedicated to productivity measurements will be harvested each year to avoid resampling over the 4-year study period.

   2. Soil C and N concentration will be measured twice, once during the pre-treatment data collection year and in year 4 of the drought. For each plot, two to three soil samples will be collected to a depth of 0-15 cm and composited. Samples will be sent to a central lab (tbd) for analysis and archived. Standard protocols will be used for the analysis (including correcting for inorganic C if necessary, Robertson *et al*. 2007).

   3. Plant community composition will be measured at least on an annual basis. Abundance (cover, density) will be estimated separately for each species rooted within each plot. For herbaceous-dominated vegetation, the Nutrient Network protocol is recommended

(www.nutnet.umn.edu). This protocol utilizes 1 x 1 m permanent sampling plots. For other systems, sampling plot size will increase dependent on vegetation type and protocol used (e.g., line intercept, laser point frame/pin frame, etc.).

4. Each site will provide qualitative trait data for all species found in the species composition sampling plots. These traits include: growth form (grass, forb, shrub, tree, succulent), photosynthetic pathway (C4, C3, CAM), N-fixer, life history (perennial, biennial, annual), and clonality (stoloniferous, rhizomatous, and for grasses caespitose or not).

B. Level 2 measurements

Level 2 measurements are not required for participation in the network but are strongly encouraged. These measurements include quantifying shelter effects and performance, precipitation inputs and changes in soil moisture, belowground productivity, decomposition rates, and plant traits. Of these, quantifying soil moisture content is the ***highest priority*** and most valuable for understanding drought impacts.

1. Soil moisture content will be measured for the drought and control treatments at a depth of at least 10 cm (preferred >= 15 cm). These measurements will be made as frequently as possible (e.g., continuous, bi-weekly, monthly). Ideally, continuous soil moisture measurements at two depths (0-15 cm and a deeper depth) are recommended.

2. Quantifying shelter effects and performance
   - Shelter effects will be quantified by measuring PAR interception, air temperature and soil temperature beneath the shelters and outside the shelters.
   - Shelter performance will be quantified for as many precipitation events as possible by measuring the amount of precipitation reaching each sheltered plot relative to outside the plot.

3. Root production and biomass
   - Annual root production will be estimated with root-ingrowth cores (recommended minimum of n = 2 per plot; Smit *et al*. 2000). In-growth core diameter and depth may vary by soil depth and/or type of vegetation. In-growth cores will be installed at end of each growing season and removed a year later. Estimates of root production will be provided in 10 cm intervals (0-10, 10-20, 20-30, etc.) for all sites.
   - Standing root biomass will be estimated from the cores extracted for root-ingrowth measurements.

4. As an index of decomposition, standardized substrates and protocols will be used at all sites (e.g., tea bags for aboveground, Keuskamp *et al*. 2013; wooden dowels/ tongue depressors for belowground, Robertson *et al*. 2007).

5. Light availability will be measured at the beginning and end of each growing season in the subplot designated for the plant species composition measurements.

6. For the most common plant species (those collectively comprising 90% of relative cover in plots), additional plant traits will be measured, including height, specific leaf area, and estimated rooting depth.

Literature Cited

Fahey, T.J. and A.K. Knapp (eds). 2007. Principles and Standards for Measuring Primary Production. Oxford University Press.

Gherardi, L.A. & O.E. Sala. 2013. Automated rainfall manipulation system: a reliable and inexpensive tool for ecologists. Ecosphere 4:

Roberston, G.P., D.C. Coleman, C.S. Bledsoe, and P. Sollins (eds). 1999. Standard Soil Methods for Long-term Ecological Research. Oxford University Press.

Oliveira, M.R.G., M. van Noordwijk, S.R. Gaze, G. Brouwer, S. Bona, G. Mosca, and K. Hairiah. 2000. Auger sampling, ingrowth cores and pinboard methods. In: Root Methods, Smit, A.L., A.G. Bengough, C. Engels, M. van Noordwijk, S. Pellerin, and S.C. van de Geijn (eds). pp. 175-210.

Yahdjian, L. & O.E. Sala. 2002. A rainout shelter design for intercepting different amounts of rainfall. Oecologia 133:95-101.

8.2 Detailed collection of emerging research questions and challenges

Table A1: Detailed collection of emerging research questions and challenges based on and in addition to the results of this thesis. Some of the emerging research questions/challenges could be answered based on the results of the future experiment described in chapter 6, others need further experimental testing.

Topic	Related research questions/challenges based on the manuscripts of this thesis
Diversity-stability	• Does the disturbance of the diversity-recovery relationship by the presence of non-native species hold true on a global scale? • Do invaders disturb the resistance of native communities when exposed to a chronic drought event instead of a pulse drought (this is what was tested so far)? • What kind of novel ecosystems will develop, if invasive ecosystem engineers, e.g. *Lupinus polyphyllus*, are not prevented from invading ecosystems? • Do, and if so to what degree, the novel ecosystems emerging from lupine induced succession differ in their species composition from historic or present uninvaded ecosystems of the same succession stage? • Is the final succession stage of those novel ecosystems self-sustaining and does it provide a reasonable amount of biodiversity? • Do those ecosystems show novel rules of interaction?
Crucial first steps	• Test the germination success of diverse invasive ecosystem engineers across a global climate gradient; ideally with native and invasive populations of those invaders stemming from different climate regions. • Test the germination of plant invaders across several representative climates after a drought event, which is designed to be extreme for the respective biome (1000-year recurrence rate). • Test the reproductive output of the invaders (e.g. *L. polyphyllus*) under a combined drought and competition treatment in comparison to the reproductive output of a great variety of native species. • Compare reproductive output of the invaders (e.g. *L. polyphyllus*) under ambient conditions but in competition with a great variety of native species across a global climate gradient
Invader stress tolerance	• Test the competitive ability of *L. polyphyllus* in the establishment phase, in terms of above- and belowground biomass production, against various native representatives from different functional groups (grasses, forbs, legumes). • Test if native species are also able to accumulate compatible solutes to retain cell turgor under extreme drought, like *L. polyphyllus* does with glutamic acid (so far we only tested *L. polyphyllus*, not the natives).
Invasion and conservation	• Examine if and how limiting effects of occurring weather extremes (e.g. early summer droughts), can be combined with restoration measures, so that the invader is harmed, but the stressed native plants are spared. • Are management measures useful? Or would it be better to run the succession (e.g. in semi-natural European grasslands) and create a novel, more stable ecosystem? • Are the novel ecosystems arising due to disturbance stable against further disturbances? • Do novel ecosystems necessarily hold a lower biodiversity compared to historical/present ecosystems of the same succession stage or relative to the ecosystem they originate from? Do novel ecosystems, emerging from the invasion of non-native species, only show increased biodiversity when compared to highly degraded ecosystems due to the characteristics of invaders (high competitive ability etc.)? • On a landscape or global scale, is the beta and gamma diversity of novel ecosystems, created by the invasion of ecosystem engineers, reduced in comparison to natural ecosystems? • What kind of ecosystem engineer invaders lead to a final stable stage of a novel ecosystem? • How do ecosystem engineers, which lead to a stable alternative ecosystem, differ in their impact/mode of action from those, which do not lead to stable novel ecosystems? Have the unstable new ecosystems just not reached their climax vegetation? • Is the invasion-related species loss induced by ecosystem engineers permanent? Do climax novel ecosystems show an adequate level of biodiversity in comparison to 1) climax vegetation of similar succession stages, 2) the habitat of origin.
Tipping points	• Are novel ecosystems preceded by a tipping point? • Under which circumstances do ecosystem engineers shift ecosystems behind the tipping point where resilience is not possible anymore? o What length/intensity does the drought need to have? /When does change begin?
How far will they come?	• Can we proof a niche shift for *L. polyphyllus* in other regions? E.g. North America vs. Chile, North America vs. Australia and New Zealand. So far it was not possible to test this because too few occurrences from these non-native regions are available.

Biotic interactions	- Do positive plant-plant interactions between invasive ecosystem engineers and native species lead to the formation of novel ecosystems and, if so, do those novel ecosystems show higher rates of stability in terms of functionality, sustainability and biodiversity compared to novel ecosystems emerging from disturbance events?

9 REFERENCES IN INTRODUCTION AND SYNTHESIS

Alba C, NeSmith JE, Fahey C, et al (2017) Methods to test the interactive effects of drought and plant invasion on ecosystem structure and function using complementary common garden and field experiments. Ecol Evol 7:1442–1452. doi: 10.1002/ece3.2729

Allison G (2004) THE INFLUENCE OF SPECIES DIVERSITY AND STRESS INTENSITY ON COMMUNITY RESISTANCE AND RESILIENCE. Ecol Monogr 74:117–134. doi: 10.1890/02-0681

Anderson CB, Pastur GM, Lencinas MV, et al (2009) Do introduced North American beavers Castor canadensis engineer differently in southern South America? An overview with implications for restoration. Mammal Rev 39:33–52. doi: 10.1111/j.1365-2907.2008.00136.x

Andrade C, Leite SM, Santos JA (2012) Temperature extremes in Europe: overview of their driving atmospheric patterns. Nat Hazards Earth Syst Sci 12:1671–1691. doi: 10.5194/nhess-12-1671-2012

Arnalds A, Runolfsson S (2008) The role of Nootka Lupin (Lupinus nootkatensis) for revegetation in Iceland. In: Palta JA, Berger JD (eds) Lupins for health and wealth: 12th International Lupin Conference , Fremantle, Western Australia, 14-18 September 2008. International Lupin Association, Canterbury, New Zealand

Ayanu Y, Jentsch A, Müller-Mahn D, et al (2015) Ecosystem engineer unleashed: Prosopis juliflora threatening ecosystem services? Reg Environ Change 15:155–167. doi: 10.1007/s10113-014-0616-x

Bahn M, Ingrisch J (2018) Accounting for Complexity in Resilience Comparisons: A Reply to Yeung and Richardson, and Further Considerations. Trends Ecol Evol 33:649–651. doi: 10.1016/j.tree.2018.06.006

Bahn M, Jentsch A, Ingrisch J (2019) Grünlandnutzung. In: Störungsökologie, UTB 5018. Verlag Haupt, Stuttgart, pp 304–324

Barnosky AD, Hadly EA, Gonzalez P, et al (2017) Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science 355:eaah4787. doi: 10.1126/science.aah4787

Batavia C, Nelson MP (2017) For goodness sake! What is intrinsic value and why should we care? Biol Conserv 209:366–376. doi: 10.1016/j.biocon.2017.03.003

Bathiany S, Dakos V, Scheffer M, Lenton TM (2018) Climate models predict increasing temperature variability in poor countries. Sci Adv 4:eaar5809. doi: 10.1126/sciadv.aar5809

Beckmann M, Bruelheide H, Erfmeier A (2011) Germination responses of three grassland species differ between native and invasive origins. Ecol Res 26:763–771. doi: 10.1007/s11284-011-0834-3

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biol Lett 12:20150623. doi: 10.1098/rsbl.2015.0623

Bellard C, Jeschke JM, Leroy B, Mace GM (2018) Insights from modeling studies on how climate change affects invasive alien species geography. Ecol Evol 8:5688–5700. doi: 10.1002/ece3.4098

Bengtsson J, Bullock JM, Egoh B, et al (2019) Grasslands-more important for ecosystem services than you might think. Ecosphere 10:e02582. doi: 10.1002/ecs2.2582

Beuthin M (2012) Plant guide for bigleaf lupine (Lupinus polyphyllus). USDA-Nat Resour Conserv Serv Plant Mater Cent Corvallis OR

Blake RE, Duffy JE (2010) Grazer diversity affects resistance to multiple stressors in an experimental seagrass ecosystem. Oikos 119:1625–1635. doi: 10.1111/j.1600-0706.2010.18419.x

Boltovskoy D, Sylvester F, Paolucci EM (2018) Invasive species denialism: Sorting out facts, beliefs, and definitions. Ecol Evol 8:11190–11198. doi: 10.1002/ece3.4588

Braga RR, Gómez-Aparicio L, Heger T, et al (2018) Structuring evidence for invasional meltdown: broad support but with biases and gaps. Biol Invasions 20:923–936. doi: 10.1007/s10530-017-1582-2

Bridgewater P, Higgs ES, Hobbs RJ (2011) Engaging with novel ecosystems. Front Ecol Environ 8:1

Briski E, Chan FT, Darling JA, et al (2018) Beyond propagule pressure: importance of selection during the transport stage of biological invasions. Front Ecol Environ 16:345–353. doi: 10.1002/fee.1820

Butchart SHM, Walpole M, Collen B, et al (2010) Global Biodiversity: Indicators of Recent Declines. Science 328:1164–1168. doi: 10.1126/science.1187512

Caldeira MC, Lecomte X, David TS, et al (2015) Synergy of extreme drought and shrub invasion reduce ecosystem functioning and resilience in water-limited climates. Sci Rep 5:15110. doi: 10.1038/srep15110

Cantarel AAM, Bloor JMG, Soussana J-F (2013) Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. J Veg Sci 24:113–126. doi: 10.1111/j.1654-1103.2012.01452.x

Cardinale BJ, Duffy JE, Gonzalez A, et al (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67. doi: 10.1038/nature11148

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers Distrib 15:22–40. doi: 10.1111/j.1472-4642.2008.00521.x

Catford JA, Vesk PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Glob Change Biol 18:44–62. doi: 10.1111/j.1365-2486.2011.02549.x

Chytrý M, Pyšek P, Wild J, et al (2009) European map of alien plant invasions based on the quantitative assessment across habitats. Divers Distrib 15:98–107. doi: 10.1111/j.1472-4642.2008.00515.x

Cleland EE, Esch E, McKinney J (2015) Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. Oikos 124:33–40. doi: 10.1111/oik.01433

Clement S, Standish RJ (2018) Novel ecosystems: Governance and conservation in the age of the Anthropocene. J Environ Manage 208:36–45. doi: 10.1016/j.jenvman.2017.12.013

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule Pressure: A Null Model for Biological Invasions. Biol Invasions 8:1023–1037. doi: 10.1007/s10530-005-3735-y

Collier MJ (2014) Novel ecosystems and the emergence of cultural ecosystem services. Ecosyst Serv 9:166–169. doi: 10.1016/j.ecoser.2014.06.002

Collier MJ, Devitt C (2016) Novel ecosystems: Challenges and opportunities for the Anthropocene. Anthr Rev 3:231–242. doi: 10.1177/2053019616662053

Cook BI, Mankin JS, Anchukaitis KJ (2018) Climate Change and Drought: From Past to Future. Curr Clim Change Rep 4:164–179. doi: 10.1007/s40641-018-0093-2

Costanza R, de Groot R, Braat L, et al (2017) Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosyst Serv 28:1–16. doi: 10.1016/j.ecoser.2017.09.008

Craine JM, Nippert JB, Elmore AJ, et al (2012) Timing of climate variability and grassland productivity. Proc Natl Acad Sci 109:3401–3405. doi: 10.1073/pnas.1118438109

Craven D, Eisenhauer N, Pearse WD, et al (2018) Multiple facets of biodiversity drive the diversity–stability relationship. Nat Ecol Evol 2:1579–1587. doi: 10.1038/s41559-018-0647-7

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166. doi: 10.1034/j.1600-0706.2002.970201.x

Cuddington K, Hastings A (2004) Invasive engineers. Ecol Model 178:335–347. doi: 10.1016/j.ecolmodel.2004.03.010

Dai A (2013) Increasing drought under global warming in observations and models. Nat Clim Change 3:52–58. doi: 10.1038/nclimate1633

Dakos V, Hastings A (2013) Editorial: special issue on regime shifts and tipping points in ecology. Theor Ecol 6:253–254. doi: 10.1007/s12080-013-0197-1

Dassonville N, Vanderhoeven S, Vanparys V, et al (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia 157:131–140. doi: 10.1007/s00442-008-1054-6

Davidsdottir B, Gunnarsson TG, Halldorsson G, Sigurdsson BD (2016) Avian abundance and communities in areas revegetated with exotic versus native plant species. Icel Agric Sci 29:21–37. doi: 10.16886/IAS.2016.03

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

De Boeck HJ, Bloor JMG, Kreyling J, et al (2018) Patterns and drivers of biodiversity-stability relationships under climate extremes. J Ecol 106:890–902. doi: 10.1111/1365-2745.12897

de Mazancourt C, Isbell F, Larocque A, et al (2013) Predicting ecosystem stability from community composition and biodiversity. Ecol Lett 16:617–625. doi: 10.1111/ele.12088

DeClerck FAJ, Barbour MG, Sawyer JO (2006) SPECIES RICHNESS AND STAND STABILITY IN CONIFER FORESTS OF THE SIERRA NEVADA. Ecology 87:2787–2799. doi: 10.1890/0012-9658(2006)87[2787:SRASSI]2.0.CO;2

Dengler J, Biurrun I, Apostolova I, et al (2016) Scale-dependent plant diversity in Palaearctic grasslands: a comparative overview. Bull Eurasian Dry Grassl Group 16

Dengler J, Janišová M, Török P, Wellstein C (2014) Biodiversity of Palaearctic grasslands: a synthesis. Agric Ecosyst Environ 182:1–14. doi: 10.1016/j.agee.2013.12.015

Dengler J, Tischew S (2018) Grasslands of Western and Northern Europe—Between intensification and abandonment. In: Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton, US, pp 27–63

Diaz S, Settele J, Brondizio E, et al. (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services - Advance Unedited Version -. Intergov Sci-Policy Platf Biodivers Ecosyst Serv IPBES Bonn Ger

Diez JM, D’Antonio CM, Dukes JS, et al (2012) Will extreme climatic events facilitate biological invasions? Front Ecol Environ 10:249–257. doi: 10.1890/110137

Divíšek J, Chytrý M, Beckage B, et al (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat Commun 9:4631. doi: 10.1038/s41467-018-06995-4

Doney SC, Ruckelshaus M, Emmett Duffy J, et al (2012) Climate Change Impacts on Marine Ecosystems. Annu Rev Mar Sci 4:11–37. doi: 10.1146/annurev-marine-041911-111611

Dornelas M, Gotelli NJ, McGill B, et al (2014) Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science 344:296–299. doi: 10.1126/science.1248484

Ehrenfeld JG (2003) Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. Ecosystems 6:503–523. doi: 10.1007/s10021-002-0151-3

Ehrenfeld JG (2010) Ecosystem Consequences of Biological Invasions. Annu Rev Ecol Evol Syst 41:59–80. doi: 10.1146/annurev-ecolsys-102209-144650

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London, UK

EPPO (2006) Data sheet on Invasive Plants Senecio inaequidens. Eur Mediterr Plant Prot Organ EPPO

Evers CR, Wardropper CB, Branoff B, et al (2018) The ecosystem services and biodiversity of novel ecosystems: A literature review. Glob Ecol Conserv 13:e00362. doi: 10.1016/j.gecco.2017.e00362

Fei S, Phillips J, Shouse M (2014) Biogeomorphic Impacts of Invasive Species. Annu Rev Ecol Evol Syst 45:69–87. doi: 10.1146/annurev-ecolsys-120213-091928

Folke C, Carpenter S, Elmqvist T, et al (2002) Resilience and Sustainable Development: Building Adaptive Capacity in a World of Transformations. AMBIO J Hum Environ 31:437–440. doi: 10.1579/0044-7447-31.5.437

Folke C, Carpenter S, Walker B, et al (2004) Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. Annu Rev Ecol Evol Syst 35:557–581. doi: 10.1146/annurev.ecolsys.35.021103.105711

Fremstad E (2010) NOBANIS - Invasive Alien Species Fact Sheet - Lupinus polyphyllus.

Fridley JD, Stachowicz JJ, Naeem S, et al (2007) THE INVASION PARADOX: RECONCILING PATTERN AND PROCESS IN SPECIES INVASIONS. Ecology 88:3–17. doi: 10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Global Invasive Species Database (GISD) (2015) Species profile Senecio inaequidens

Goodenough A (2010) Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. Community Ecol 11:13–21. doi: 10.1556/ComEc.11.2010.1.3

Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334. doi: 10.1007/s004420050090

Gross K, Cardinale BJ, Fox JW, et al (2014) Species Richness and the Temporal Stability of Biomass Production: A New Analysis of Recent Biodiversity Experiments. Am Nat 183:1–12. doi: 10.1086/673915

Guisan A, Petitpierre B, Broennimann O, et al (2014) Unifying niche shift studies: insights from biological invasions. Trends Ecol Evol 29:260–269. doi: 10.1016/j.tree.2014.02.009

Guo Q, Brockway DG, Larson DL, et al (2018) Improving Ecological Restoration to Curb Biotic Invasion—A Practical Guide. Invasive Plant Sci Manag 11:163–174. doi: 10.1017/inp.2018.29

Habel JC, Dengler J, Janišová M, et al (2013) European grassland ecosystems: threatened hotspots of biodiversity. Biodivers Conserv 22:2131–2138. doi: 10.1007/s10531-013-0537-x

Hansen W, Klinger YP, Otte A, Eckstein RL, Ludewig K (2022) Constraints in the restoration of mountain meadows invaded by the legume *Lupinus polyphyllus*. Restoration Ecology. https://doi.org/10.1111/rec.13682

Hastings A, Byers JE, Crooks JA, et al (2007) Ecosystem engineering in space and time. Ecol Lett 10:153–164. doi: 10.1111/j.1461-0248.2006.00997.x

Hautier Y, Isbell F, Borer ET, et al (2018) Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nat Ecol Evol 2:50–56. doi: 10.1038/s41559-017-0395-0

Hautier Y, Tilman D, Isbell F, et al (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348:336–340. doi: 10.1126/science.aaa1788

Heger T, Böhmer HJ (2006) NOBANIS - Invasive Alien Species Fact Sheet - Senecio inaequidens. Online Database Eur Netw Invasive Alien Species - NOBANIS Wwwnobanisorg

Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97:393–403. doi: 10.1111/j.1365-2745.2009.01480.x

Hejda M, Štajerová K, Pyšek P (2017) Dominance has a biogeographical component: do plants tend to exert stronger impacts in their invaded rather than native range? J Biogeogr 44:18–27. doi: 10.1111/jbi.12801

Hendrix PF, Callaham MA, Drake JM, et al (2008) Pandora’s Box Contained Bait: The Global Problem of Introduced Earthworms. Annu Rev Ecol Evol Syst 39:593–613. doi: 10.1146/annurev.ecolsys.39.110707.173426

Hensgen F, Wachendorf M (2016) The Effect of the Invasive Plant Species Lupinus polyphyllus Lindl. on Energy Recovery Parameters of Semi-Natural Grassland Biomass. Sustainability 8:998. doi: 10.3390/su8100998

Hierro JL, Eren Ö, Khetsuriani L, et al (2009) Germination Responses of an Invasive Species in Native and Non-Native Ranges. Oikos 118:529–538. doi: 10.1111/j.1600-0706.2009.17283.x

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J Ecol 93:5–15

Higgs E (2017) Novel and designed ecosystems. Restor Ecol 25:8–13. doi: 10.1111/rec.12410

Hiltbrunner E, Aerts R, Bühlmann T, et al (2014) Ecological consequences of the expansion of N2-fixing plants in cold biomes. Oecologia 176:11–24. doi: 10.1007/s00442-014-2991-x

Hirsch H, Wypior C, von Wehrden H, et al (2012) Germination performance of native and non-native Ulmus pumila populations. NeoBiota 15:53–68. doi: 10.3897/neobiota.15.4057

Hobbs RJ, Arico S, Aronson J, et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob Ecol Biogeogr 15:1–7. doi: 10.1111/j.1466-822X.2006.00212.x

Hobbs RJ, Higgs E, Hall CM, et al (2014) Managing the whole landscape: historical, hybrid, and novel ecosystems. Front Ecol Environ 12:557–564. doi: 10.1890/130300

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends Ecol Evol 24:599–605. doi: 10.1016/j.tree.2009.05.012

Hodgson D, McDonald JL, Hosken DJ (2015) What do you mean, ‘resilient’? Trends Ecol Evol 30:503–506

Hooper DU, Chapin FS, Ewel JJ, et al (2005) EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING: A CONSENSUS OF CURRENT KNOWLEDGE. Ecol Monogr 75:3–35. doi: 10.1890/04-0922

Hulme PE (2017) Climate change and biological invasions: evidence, expectations, and response options: Alien species and climate change in Great Britain. Biol Rev 92:1297–1313. doi: 10.1111/brv.12282

Hunter Jr. ML, Gibbs J (2007) Fundamentals of Conservation Biology, Third Edition. Blackwell Publishing

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460. doi: 10.1007/s004420050180

Ibanez I, Diez JM, Miller LP, et al (2014) Integrated assessment of biological invasions. Ecol Appl 24:25–37

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

IPCC (2014) Climate change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Camb Univ Press Camb U K N Y NY USA 688

Isbell F, Craven D, Connolly J, et al (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577. doi: 10.1038/nature15374

Ives AR, Carpenter SR (2007) Stability and Diversity of Ecosystems. Science 317:58–62. doi: 10.1126/science.1133258

Jakobsson A, Padrón B, Ågren J (2015) Distance-dependent effects of invasive Lupinus polyphyllus on pollination and reproductive success of two native herbs. Basic Appl Ecol 16:120–127. doi: 10.1016/j.baae.2014.12.005

Jentsch A (2013) Sending a SIGNAL – the mechanisms of grassland resilience. Res Media EU 21–23

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374

Jentsch A, Kreyling J, Elmer M, et al (2011) Climate extremes initiate ecosystem-regulating functions while maintaining productivity: Drought effect on multiple ecosystem services. J Ecol 99:689–702. doi: 10.1111/j.1365-2745.2011.01817.x

Jentsch A, White P (2019) A theory of pulse dynamics and disturbance in ecology. Ecology e02734. doi: 10.1002/ecy.2734

Jeschke JM (2014) General hypotheses in invasion ecology. Divers Distrib 20:1229–1234. doi: 10.1111/ddi.12258

Jeschke JM, Enders M, Bagni M, et al (2018) Hi-Knowledge. Hi-Knowledge.org

Jeschke JM, Keesing F, Ostfeld RS (2013) Novel Organisms: Comparing Invasive Species, GMOs, and Emerging Pathogens. AMBIO 42:541–548. doi: 10.1007/s13280-013-0387-5

Jones CG, Gutiérrez JL, Byers JE, et al (2010) A framework for understanding physical ecosystem engineering by organisms. Oikos 119:1862–1869. doi: 10.1111/j.1600-0706.2010.18782.x

Jones CG, Lawton JH, Shachak M (1994) Organisms as Ecosystem Engineers. Oikos 69:373. doi: 10.2307/3545850

Jylhä K, Fronzek S, Tuomenvirta H, et al (2008) Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. Clim Change 86:441–462. doi: 10.1007/s10584-007-9310-z

Kettenring KM, Whigham DF, Hazelton ELG, et al (2015) Biotic resistance, disturbance, and mode of colonization impact the invasion of a widespread, introduced wetland grass. Ecol Appl 25:466–480. doi: 10.1890/14-0434.1

King AD, Karoly DJ (2017) Climate extremes in Europe at 1.5 and 2 degrees of global warming. Environ Res Lett 12:114031. doi: 10.1088/1748-9326/aa8e2c

Klein A, Cameron EK, Heimburger B, et al (2017) Changes in the genetic structure of an invasive earthworm species (Lumbricus terrestris, Lumbricidae) along an urban – rural gradient in North America. Appl Soil Ecol 120:265–272. doi: 10.1016/j.apsoil.2017.08.009

Klinger YP, Harvolk-Schöning S, Eckstein RL, et al (2019) Applying landscape structure analysis to assess the spatio-temporal distribution of an invasive legume in the Rhön UNESCO Biosphere Reserve. Biol Invasions. doi: 10.1007/s10530-019-02012-x

Knapp AK (2002) Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland. Science 298:2202–2205. doi: 10.1126/science.1076347

Koutika L-S, Rainey HJ (2015) A REVIEW OF THE INVASIVE, BIOLOGICAL AND BENEFICIAL CHARACTERISTICS OF AQUATIC SPECIES EICHHORNIA CRASSIPES AND SALVINIA MOLESTA. Appl Ecol Environ Res 13:. doi: 10.15666/aeer/1301_263275

Kreyling J (2010) Winter climate change: a critical factor for temperate vegetation performance. Ecology 91:1939–1948

Kreyling J, Arfin Khan MAS, Sultana F, et al (2017a) Drought Effects in Climate Change Manipulation Experiments: Quantifying the Influence of Ambient Weather Conditions and Rain-out Shelter Artifacts. Ecosystems 20:301–315. doi: 10.1007/s10021-016-0025-8

Kreyling J, Beierkuhnlein C, Ellis L, Jentsch A (2008) Invasibility of grassland and heath communities exposed to extreme weather events–additive effects of diversity resistance and fluctuating physical environment. Oikos 117:1542–1554

Kreyling J, Bittner T, Jaeschke A, et al (2011a) Assisted Colonization: A Question of Focal Units and Recipient Localities. Restor Ecol 19:433–440. doi: 10.1111/j.1526-100X.2011.00777.x

Kreyling J, Dengler J, Walter J, et al (2017b) Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment. Ecol Lett 20:1405–1413. doi: 10.1111/ele.12848

Kreyling J, Henry H (2011) Vanishing winters in Germany: soil frost dynamics and snow cover trends, and ecological implications. Clim Res 46:269–276. doi: 10.3354/cr00996

Kreyling J, Huber G, Jentsch A, et al (2011b) Innerartliche Plastizität und lokale Anpassungen von Waldbäumen. Die innerartliche Vielfalt ist ein Schlüsselkriterium für eine erfolgreiche Klimaanpassung. LWF Aktuell 12–14

Kreyling J, Thiel D, Simmnacher K, et al (2012a) Geographic origin and past climatic experience influence the response to late spring frost in four common grass species in central Europe. Ecography 35:268–275. doi: 10.1111/j.1600-0587.2011.07173.x

Kreyling J, Wiesenberg GLB, Thiel D, et al (2012b) Cold hardiness of Pinus nigra Arnold as influenced by geographic origin, warming, and extreme summer drought. Environ Exp Bot 78:99–108. doi: 10.1016/j.envexpbot.2011.12.026

Kueffer C (2014) Ecological Novelty: Towards an Interdisciplinary Understanding of Ecological Change in the Anthropocene. In: Greschke H, Tischler J (eds) Grounding Global Climate Change. Springer Netherlands, Dordrecht, pp 19–37

Kueffer C, Kaiser-Bunbury CN (2014) Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. Front Ecol Environ 12:131–137. doi: 10.1890/120201

Kueffer C, Pyšek P, Richardson DM (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytol 200:615–633. doi: 10.1111/nph.12415

Kueffer C, Schumacher E, Dietz H, et al (2010) Managing successional trajectories in alien-dominated, novel ecosystems by facilitating seedling regeneration: A case study. Biol Conserv 143:1792–1802. doi: 10.1016/j.biocon.2010.04.031

LaForgia ML, Spasojevic MJ, Case EJ, et al (2018) Seed banks of native forbs, but not exotic grasses, increase during extreme drought. Ecology 99:896–903. doi: 10.1002/ecy.2160

Landres PB, Morgan P, Swanson FJ (1999) OVERVIEW OF THE USE OF NATURAL VARIABILITY CONCEPTS IN MANAGING ECOLOGICAL SYSTEMS. Ecol Appl 9:1179–1188. doi: 10.1890/1051-0761(1999)009[1179:OOTUON]2.0.CO;2

Larson DL, Bright JB, Drobney P, et al (2013) Using prairie restoration to curtail invasion of Canada thistle: the importance of limiting similarity and seed mix richness. Biol Invasions 15:2049–2063. doi: 10.1007/s10530-013-0432-0

Lauterbach D, Nehring S (2013) Naturschutzfachliche Invasivitätsbewertung Lupinus polyphyllus - Vielblättrige Lupine. Bundesamt Für Naturschutz Bonn 2S Bundesamt für Naturschutz, Konstantinstrasse 110, 53179 Bonn; Phone: +492288491-0; www.bfn.de; neobiota@bfn.de:

Lazzaro L, Giuliani C, Fabiani A, et al (2014) Soil and plant changing after invasion: The case of Acacia dealbata in a Mediterranean ecosystem. Sci Total Environ 497–498:491–498. doi: 10.1016/j.scitotenv.2014.08.014

Lehner F, Coats S, Stocker TF, et al (2017) Projected drought risk in 1.5°C and 2°C warmer climates: Drought in 1.5°C and 2°C Warmer Climates. Geophys Res Lett 44:7419–7428. doi: 10.1002/2017GL074117

Lewis SL, Maslin MA (2015) Defining the Anthropocene. Nature 519:171–180. doi: 10.1038/nature14258

Liška J, Soldán Z (2004) Alien vascular plants recorded from the Barentsburg and Pyramiden settlements, Svalbard. Preslia 76:279–290

Liu Y, Oduor AMO, Zhang Z, et al (2017) Do invasive alien plants benefit more from global environmental change than native plants? Glob Change Biol 23:3363–3370. doi: 10.1111/gcb.13579

Löbel S, Dengler J, Hobohm C (2006) Species richness of vascular plants, bryophytes and lichens in dry grasslands: The effects of environment, landscape structure and competition. Folia Geobot 41:377–393. doi: 10.1007/BF02806555

Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141:269–281. doi: 10.1007/s00442-004-1570-y

Loreau M, de Mazancourt C (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol Lett 16:106–115. doi: 10.1111/ele.12073

MacArthur R (1970) Species packing and competitive equilibrium for many species. Theor Popul Biol 1:1–11. doi: 10.1016/0040-5809(70)90039-0

MacArthur R (1955) Fluctuations of Animal Populations and a Measure of Community Stability. Ecology 36:533. doi: 10.2307/1929601

Macarthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat 101:377–385. doi: 10.1086/282505

Mace GM (2019) The ecology of natural capital accounting. Oxf Rev Econ Policy 35:54–67. doi: 10.1093/oxrep/gry023

Magnusson B (2010) NOBANIS - Invasive Alien Species Fact Sheet - Lupinus nootkatensis

Magnusson B., Magnusson S.H., Sigurdsson B.D. (2008) Plant succession in areas colonized by the introduced Nootka Lupin in Iceland. In: Palta JA, Berger JD (eds) Lupins for health and wealth. International Lupin Association, Canterbury, New Zealand

McCabe GJ, Palecki MA, Betancourt JL (2004) Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. Proc Natl Acad Sci 101:4136–4141. doi: 10.1073/pnas.0306738101

McCauley DJ (2006) Selling out on nature. Nature 443:27–28. doi: 10.1038/443027a

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453. doi: 10.1016/S0169-5347(99)01679-1

McNaughton SJ (1977) Diversity and Stability of Ecological Communities: A Comment on the Role of Empiricism in Ecology. Am Nat 111:515–525. doi: 10.1086/283181

Meine C (2017) Restoration and “Novel Ecosystems”: Priority or Paradox? <sup/>. Ann Mo Bot Gard 102:217–226. doi: 10.3417/2016037

Morse NB, Pellissier PA, Cianciola EN, et al (2014) Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. Ecol Soc 19:art12. doi: 10.5751/ES-06192-190212

Murphy GEP, Romanuk TN (2014) A meta-analysis of declines in local species richness from human disturbances. Ecol Evol 4:91–103. doi: 10.1002/ece3.909

Naeem S (1998) Species Redundancy and Ecosystem Reliability. Conserv Biol 12:7

Nagy S (2009) Grasslands as a bird habitat. In: Veen P, Jefferson R, de Smidt J, van der Straaten J (eds) Grasslands in Europe of High Nature Value. KNNV Publishing, Zeist, pp 35–41

Otte A, Maul P (2005) Verbreitungsschwerpunkt und strukturelle Einnischung der Stauden-Lupine (Lupinus polyphyllus Lindl.) in Bergwiesen der Rhön. Tuexenia 25:151–182

Otte A, Obert S, Volz H, Weigand E (2002) Effekte von Beweidung auf Lupinus polyphyllus Lindl. in Bergwiesen des Biosphärenreservates Rhön. Neobiota 1:101–133

Panter KE, Taylor JB, Lee ST, et al (2017) Lupine Poisoning in Sheep on the USDA-ARS US Sheep Experiment Station (USSES), Dubois, Idaho. Int J Poisonous Plant Res 79

Papier CM, Poulos HM, Kusch A (2019) Invasive species and carbon flux: the case of invasive beavers (Castor canadensis) in riparian Nothofagus forests of Tierra del Fuego, Chile. Clim Change 153:219–234. doi: 10.1007/s10584-019-02377-x

Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. Ecol Lett 8:959–967. doi: 10.1111/j.1461-0248.2005.00799.x

Pauchard A, Meyerson LA, Bacher S, et al (2018) Biodiversity assessments: Origin matters. PLOS Biol 16:e2006686. doi: 10.1371/journal.pbio.2006686

Pearson DE, Ortega YK, Villarreal D, et al (2018) The fluctuating resource hypothesis explains invasibility, but not exotic advantage following disturbance. Ecology 99:1296–1305. doi: 10.1002/ecy.2235

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends Ecol Evol 24:497–504. doi: 10.1016/j.tree.2009.03.016

Petitpierre B, Kueffer C, Broennimann O, et al (2012) Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. Science 335:1344–1348. doi: 10.1126/science.1215933

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307:321–326

Pinto SM, Ortega YK (2016) Native species richness buffers invader impact in undisturbed but not disturbed grassland assemblages. Biol Invasions 18:3193–3204. doi: 10.1007/s10530-016-1208-0

Pyšek P, Chytrý M, Jarošík V (2010) Habitats and land use as determinants of plant invasions in the temperate zone of Europe. In: Perrings C, Mooney H, Williamson M (eds) Bioinvasions and Globalization. Ecology, Economics, Management, and Policy. Oxford University Press, Oxford, pp 66–79

Ramula S, Pihlaja K (2012) Plant communities and the reproductive success of native plants after the invasion of an ornamental herb. Biol Invasions 14:2079–2090. doi: 10.1007/s10530-012-0215-z

Ramula S, Sorvari J (2017) The invasive herb Lupinus polyphyllus attracts bumblebees but reduces total arthropod abundance. Arthropod-Plant Interact 11:911–918. doi: 10.1007/s11829-017-9547-z

Reichstein M, Bahn M, Ciais P, et al (2013) Climate extremes and the carbon cycle. Nature 500:287–295. doi: 10.1038/nature12350

Reynolds PL, Glanz J, Yang S, et al (2017) Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer. Ecosphere 8:e01711. doi: 10.1002/ecs2.1711

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431. doi: 10.1191/0309133306pp490pr

Richardson DM, Pyšek P, Rejmanek M, et al (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107

Riege DA (2008) The use of Lupinus nootkatensis in a revegetation and afforestation program in Southwest Iceland. In: Palta JA, Berger JD (eds) Lupins for health and wealth: 12th International Lupin Conference , Fremantle, Western Australia, 14-18 September 2008. International Lupin Association, Canterbury, New Zealand

Rilov G, Mant R, Lyons D, et al (2012) How strong is the effect of invasive ecosystem engineers on the distribution patterns of local species, the local and regional biodiversity and ecosystem functions? Environ Evid 1:10. doi: 10.1186/2047-2382-1-10

Robertson BA, Rehage JS, Sih A (2013) Ecological novelty and the emergence of evolutionary traps. Trends Ecol Evol 28:552–560. doi: 10.1016/j.tree.2013.04.004

Russell BD, Harley CDG, Wernberg T, et al (2012) Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. Biol Lett 8:164–166. doi: 10.1098/rsbl.2011.0779

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656

Schlaepfer MA, Sax DF, Olden JD (2011) The Potential Conservation Value of Non-Native Species: Conservation Value of Non-Native Species. Conserv Biol 25:428–437. doi: 10.1111/j.1523-1739.2010.01646.x

Seneviratne SI, Nicholls N, Easterling D, et al (2012) Changes in climate extremes and their impacts on the natural physical environment. Manag Risks Extreme Events Disasters Adv Clim Change Adapt 109–230

Sheppard C, Burns B, Stanley M (2016) Future-proofing weed management for the effects of climate change: is New Zealand underestimating the risk of increased plant invasions? N Z J Ecol 40:398–405. doi: 10.20417/nzjecol.40.45

Sheppard CS, Burns BR, Stanley MC (2014) Predicting plant invasions under climate change: are species distribution models validated by field trials? Glob Change Biol 20:2800–2814. doi: 10.1111/gcb.12531

Sigurdardottir H (2008) Earthworm activity in a lupin patch in Heidmörk, Southern Iceland. In: Palta JA, Berger JD (eds) Lupins for health and wealth: 12th International Lupin Conference , Fremantle, Western Australia, 14-18 September 2008. International Lupin Association, Canterbury, New Zealand

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change: Behaviour and evolution. Evol Appl 4:367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Simberloff D, Martin J-L, Genovesi P, et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66. doi: 10.1016/j.tree.2012.07.013

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Sousa R, Morais P, Dias E, Antunes C (2011) Biological invasions and ecosystem functioning: time to merge. Biol Invasions 13:1055–1058. doi: 10.1007/s10530-011-9947-4

Strayer DL (2012) Eight questions about invasions and ecosystem functioning. Ecol Lett 15:1199–1210. doi: 10.1111/j.1461-0248.2012.01817.x

Sutcliffe LME, Batáry P, Kormann U, et al (2015) Harnessing the biodiversity value of Central and Eastern European farmland. Divers Distrib 21:722–730. doi: 10.1111/ddi.12288

Takimoto G (2009) Early warning signals of demographic regime shifts in invading populations. Popul Ecol 51:419–426. doi: 10.1007/s10144-009-0148-2

Thiel D, Nagy L, Beierkuhnlein C, et al (2012) Uniform drought and warming responses in Pinus nigra provenances despite specific overall performances. For Ecol Manag 270:200–208. doi: 10.1016/j.foreco.2012.01.034

Thiele J, Isermann M, Otte A, Kollmann J (2010) Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. J Veg Sci 21:213–220. doi: 10.1111/j.1654-1103.2009.01139.x

Thomson DM, Kwok JW, Schultz EL (2018) Extreme drought alters growth and interactions with exotic grasses, but not survival, for a California annual forb. Plant Ecol 219:705–717. doi: 10.1007/s11258-018-0828-0

Thuiller W, Richardson DM, Midgley GF (2007) Will Climate Change Promote Alien Plant Invasions? In: Nentwig W (ed) Biological Invasions. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 197–211

Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proc Natl Acad Sci U S A 101:10854–10861

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and Ecosystem Functioning. Annu Rev Ecol Evol Syst 45:471–493. doi: 10.1146/annurev-ecolsys-120213-091917

Tilman D, Reich PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc Natl Acad Sci 109:10394–10397. doi: 10.1073/pnas.1208240109

Tinch R, Beaumont N, Sunderland T, et al (2019) Economic valuation of ecosystem goods and services: a review for decision makers. J Environ Econ Policy 1–20. doi: 10.1080/21606544.2019.1623083

Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realized niche shift during a global biological invasion. Proc Natl Acad Sci 111:10233–10238. doi: 10.1073/pnas.1405766111

Tippett MK, Lepore C, Cohen JE (2016) More tornadoes in the most extreme U.S. tornado outbreaks. Science 354:1419–1423. doi: 10.1126/science.aah7393

Török P, Janišová M, Kuzemko A, et al (2018) Grasslands, their Threats and Management in Eastern Europe. In: Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton, US, pp 64–88

Truitt AM, Granek EF, Duveneck MJ, et al (2015) What is Novel About Novel Ecosystems: Managing Change in an Ever-Changing World. Environ Manage 55:1217–1226. doi: 10.1007/s00267-015-0465-5

Tucker AJ, Williamson CE (2014) The invasion window for warmwater fish in clearwater lakes: the role of ultraviolet radiation and temperature. Divers Distrib 20:181–192. doi: 10.1111/ddi.12138

Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. Philos Trans R Soc B Biol Sci 372:20160135. doi: 10.1098/rstb.2016.0135

Vacchiano G, Barni E, Lonati M, et al (2013) Monitoring and modeling the invasion of the fast spreading alien *Senecio inaequidens* DC. in an alpine region. Plant Biosyst - Int J Deal Asp Plant Biol 147:1139–1147. doi: 10.1080/11263504.2013.861535

Valtonen A, Jantunen J, Saarinen K (2006) Flora and lepidoptera fauna adversely affected by invasive Lupinus polyphyllus along road verges. Biol Conserv 133:389–396. doi: 10.1016/j.biocon.2006.06.015

van Kleunen M, Dawson W, Maurel N (2015) Characteristics of successful alien plants. Mol Ecol 24:1954–1968. doi: 10.1111/mec.13013

Van Ruijven J, Berendse F (2010) Diversity enhances community recovery, but not resistance, after drought: Diversity promotes community recovery. J Ecol 98:81–86. doi: 10.1111/j.1365-2745.2009.01603.x

Vautard R, Gobiet A, Sobolowski S, et al (2014) The European climate under a 2 °C global warming. Environ Res Lett 9:034006. doi: 10.1088/1748-9326/9/3/034006

Vellend M, Baeten L, Myers-Smith IH, et al (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proc Natl Acad Sci 110:19456–19459. doi: 10.1073/pnas.1312779110

Vetter VMS, Tjaden NB, Jaeschke A, et al (2018) Invasion of a Legume Ecosystem Engineer in a Cold Biome Alters Plant Biodiversity. Front Plant Sci 9:. doi: 10.3389/fpls.2018.00715

Vilà M, Corbin JD, Dukes JS, et al (2007) Linking Plant Invasions to Global Environmental Change. In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 93–102

Vilà M, Espinar JL, Hejda M, et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems: Ecological impacts of invasive alien plants. Ecol Lett 14:702–708. doi: 10.1111/j.1461-0248.2011.01628.x

Vitousek PM, Walker LR (1989) Biological Invasion by Myrica Faya in Hawai'i: Plant Demography, Nitrogen Fixation, Ecosystem Effects. Ecol Monogr 59:247–265. doi: 10.2307/1942601

Vogel A, Scherer-Lorenzen M, Weigelt A (2012) Grassland Resistance and Resilience after Drought Depends on Management Intensity and Species Richness. PLoS ONE 7:e36992. doi: 10.1371/journal.pone.0036992

Volz H (2003) Ursachen und Auswirkungen der Ausbreitung von Lupinus polyphyllus Lindl. im Bergwiesenökosystem der Rhön und Maßnahmen zu seiner Regulierung. Justus-Liebig-Universität Gießen

Volz H, Otte A (2001) Occurrence and spreading ability of Lupinus polyphyllus Lindl. in the Hochrhoen area (central Germany). BfN-Skripten 32:97–98

Vrahnakis M, Janišová M, Rūsiņa S, et al (2013) The European Dry Grassland Group (EDGG): stewarding Europe's most diverse habitat type. In: Baumbach H, Pfützenreuter S (eds) Steppenlebensräume Europas: Gefährdung, Erhaltungsmaßnahmen und Schutz. Thüringer Ministerium für Landwirtschaft, Forsten, Umwelt und Naturschutz, Erfurt, p 18

Vuijk D (2016) NOOTKA LUPINE

WallisDeVries MF, van Swaay CAM (2009) Grasslands as habitats for butteflies in Europe. In: Veen P, Jefferson R, de Smidt J, van der Straaten J (eds) Grasslands in Europe of High Nature Value. KNNV Publishing, Zeist

Wang YF, Cui XY, Hao YB, et al (2011) The fluxes of CO2 from grazed and fenced temperate steppe during two drought years on the Inner Mongolia Plateau, China. Sci Total Environ 410–411:182–190. doi: 10.1016/j.scitotenv.2011.09.067

Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH (2011) Terrestrial Ecosystem Responses to Species Gains and Losses. Science 332:1273–1277. doi: 10.1126/science.1197479

Wasowicz P (2016) Non-native species in the vascular flora of highlands and mountains of Iceland. PeerJ 4:e1559. doi: 10.7717/peerj.1559

Wasowicz P, Pasierbiński A, Przedpelska-Wasowicz EM, Kristinsson H (2014) Distribution Patterns in the Native Vascular Flora of Iceland. PLoS ONE 9:e102916. doi: 10.1371/journal.pone.0102916

Wasowicz P, Przedpelska-Wasowicz EM, Kristinsson H (2013) Alien vascular plants in Iceland: Diversity, spatial patterns, temporal trends, and the impact of climate change. Flora - Morphol Distrib Funct Ecol Plants 208:648–673. doi: 10.1016/j.flora.2013.09.009

Weissmann H, Shnerb NM (2015) Predicting catastrophic shifts. ArXiv150603344 Cond-Mat Physicsnlin Q-Bio

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Front Ecol Environ 5:475–482. doi: 10.1890/070037

Wilsey BJ, Daneshgar PP, Hofmockel K, Polley HW (2014) Invaded grassland communities have altered stability-maintenance mechanisms but equal stability compared to native communities. Ecol Lett 17:92–100. doi: 10.1111/ele.12213

Wilson JB, Peet RK, Dengler J, Pärtel M (2012) Plant species richness: the world records. J Veg Sci 23:796–802. doi: 10.1111/j.1654-1103.2012.01400.x

Wolf KM, DiTomaso JM (2016) Management of blue gum eucalyptus in California requires region-specific consideration. Calif Agric 70:39–47. doi: 10.3733/ca.v070n01p39

Wolfe BT, Van Bloem SJ (2012) Subtropical dry forest regeneration in grass-invaded areas of Puerto Rico: Understanding why Leucaena leucocephala dominates and native species fail. For Ecol Manag 267:253–261. doi: 10.1016/j.foreco.2011.12.015

Wright JP, Jones CG (2006) The Concept of Organisms as Ecosystem Engineers Ten Years On: Progress, Limitations, and Challenges. BioScience 56:203. doi: 10.1641/0006-3568(2006)056[0203:TCOOAE]2.0.CO;2

Xie Q, Wang T, Zeng C, et al (2018) Predicting fluctuations-caused regime shifts in a time delayed dynamics of an invading species. Phys Stat Mech Its Appl 493:69–83. doi: 10.1016/j.physa.2017.10.036

Xu X, Wolfe L, Diez J, et al (2019) Differential germination strategies of native and introduced populations of the invasive species Plantago virginica. NeoBiota 43:101–118. doi: 10.3897/neobiota.43.30392

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc Natl Acad Sci 96:1463–1468. doi: 10.1073/pnas.96.4.1463

Zeiter M, Schärrer S, Zweifel R, et al (2016) Timing of extreme drought modifies reproductive output in semi-natural grassland. J Veg Sci 27:238–248. doi: 10.1111/jvs.12362

10 MANUSCRIPTS

Table 3: Overview of the manuscripts presented in this thesis and how each of them contributes to the overall storyline. Further information can be found in chapter 4 "Most important findings of manuscripts presented in this thesis" or in the respective chapter of the manuscripts below.

Manuscript 1	Crucial first steps
Author	second
Topic	Global analysis of the factors influencing seedling emergence of plant invaders
Key findings	• Warm, semi-arid and humid experimental climates are suitable for the germination of *Lupinus polyphyllus*, *Senecio inaequidens* and *Verbascum thapsus* • The species adaptation to its source region modifies its responses under different climates
Manuscript 2	Stress tolerance of the invader – (where) can they prevail after germination?
Author	first
Topic	Analysis of the abiotic and biotic stress tolerance of a globally invasive, nitrogen fixing ecosystem engineer
Key findings	• *L. polyphyllus* is co-limited by extreme weather events and competition • Extreme climatic events negatively affect native species more strongly than the invader • Reduced biotic resistance during phases of increased abiotic stress can open potential invasion windows for *L. polyphyllus*
Manuscript 3	Niche shift and propagation limits – how far will they come?
Author	first
Topic	Niche shift analysis and estimation of the propagation limits of an invasive ecosystem engineer on the European continent
Key findings	• Niche expansion of *L. polyphyllus* in the invasive range • Amount of suitable habitat of *L. polyphyllus* will increase under future climate conditions in the native and invasive range • But overall habitat suitability will decrease, especially in the invasive range • Targeted application of management measures in combination with extreme weather events
Manuscript 4	Impact of invader presence
Author	first
Topic	Impact of invader presence on the biodiversity-stability relationship of grassland ecosystems to extreme drought events
Key findings	• Biodiversity stabilizes community productivity by increasing the ability of native species to recover from extreme drought • Invader presences disturbs this stabilizing relationship and can even turn it into a negative relationship, depending on the invader • The negative invader impact is independent of the invaders own performance under increased stress
Manuscript 5	Another legume invader – impact and succession of an ecosystem engineer in a cold biome
Author	first
Topic	Impact/hazardous potential of a nitrogen fixing invasive plant species in a sub-polar oceanic climate
Key findings	• Invader presence leads to loss of species diversity and richness, changes in community composition • Climate change significantly increases the amount of suitable habitat for *Lupinus nootkatensis* • Acceleration of ecological change: additive effects of climate change and accelerated succession due to invader presence

10.1 Manuscript 1

plant biology

Plant Biology ISSN 1435-8603

RESEARCH PAPER

Factors influencing seedling emergence of three global invaders in greenhouses representing major eco-regions of the world

M. A. S. Arfin-Khan[1,2], V. M. S. Vetter[1,3], Z. A. Reshi[4], P. A. Dar[5] & A. Jentsch[1]

1 Disturbance Ecology, BayCEER, University of Bayreuth, Bayreuth, Germany
2 Department of Forestry and Environmental Science, Shahjalal University of Science and Technology, Sylhet, Bangladesh
3 Geoecology/Physical Geography, Institute for Environmental Science, University of Landau, Mainz, Germany
4 Department of Botany, University of Kashmir, Srinagar, India
5 Department of Botany, Amar Singh College, Srinagar, India

Keywords
Biological invasion; climate; cross-continental range expansion; ecosystem vulnerability; germination plasticity; local adaptation; provenance.

Correspondence
V. Vetter, Disturbance Ecology, BayCEER, University of Bayreuth, Germany.
E-mail: vanessa.vetter@uni-bayreuth.de

Editor
R. Bekker

Received: 28 March 2017; Accepted: 22 January 2018

doi:10.1111/plb.12710

ABSTRACT

- Successful germination and seedling emergence in new environments are crucial first steps in the life history of global plant invaders and thus play a key role in processes of range expansion.
- We examined the germination and seedling emergence success of three global plant invaders – *Lupinus polyphyllus*, *Senecio inaequidens* and *Verbascum thapsus* – in greenhouses and climate chambers under climate regimes corresponding to seven eco-regions. Seed materials were collected from one non-native population for *L. polyphyllus* and *S. inaequidens*, and from 12 populations for *V. thapsus* (six natives and six non-natives).
- Experimental climates had significant effects on species responses. No species germinated in the dry (humidity $\leq$ 50%) and cool ($\leq$ 5 °C) experimental climates. But all species germinated and emerged in two moderately cool (12–19 °C) and in three warm (24–27 °C) experimental climates. In general, *V. thapsus* showed higher fitness than *S. inaequidens* and *L. polyphyllus*. The climate of the seed source region influenced responses of native and non-native populations of *V. thapsus*. Non-native populations of *V. thapsus*, originating from the warmer seed source, showed higher performance in warm experimental climates and lower performance in moderately cool experimental climates compared to native populations. Responses of *V. thapsus* populations were also related to precipitation of the seed source region in moderately dry experimental climates.
- The warm, semi-arid and humid experimental climates are suitable for the crucial first steps of invasion success for *L. polyphyllus*, *S. inaequidens* and *V. thapsus*. The species adaptation to its source region modified the responses of our studied plants under different experimental climates representing major eco-regions of the world.

INTRODUCTION

Germination and seedling emergence are key traits in the life-history of plants, contributing to the invasion success in new habitats (Brändle *et al.* 2003; Hierro *et al.* 2009; Donohue *et al.* 2010; Beckmann *et al.* 2011; Hirsch *et al.* 2012; Luo & Cardina 2012; Gioria & Pyšek 2017). Plants introduced into new habitats often face different climates from that of their origin. Therefore, the ability to germinate under a wide range of climate conditions and adaptation to climatic stress during the seedling emergence stage is crucial for successful establishment (Cervera & Parra-Tabla 2009; Hou *et al.* 2014). Even after the establishment of an invader in a new environment, germination and seedling emergence success are important because they facilitate further range expansion processes (Theoharides & Dukes 2007). Moreover, the environmental conditions under which germination takes place determine the environmental conditions experienced in later life stages (Donohue *et al.* 2005).

Despite several previous studies on how global invaders respond to new environments (Ebeling *et al.* 2008; Alba & Hufbauer 2012; Kumschick *et al.* 2013), few have addressed the question of where and why they are able to germinate (Hou *et al.* 2014; Leiblein-Wild *et al.* 2014; Menge *et al.* 2016), grow and establish (Alexander *et al.* 2012). A quantification of their early stage performance would allow predictions on the future range expansion of global invaders (Parker *et al.* 2003; Bossdorf *et al.* 2005). The range expansion becomes more predictable if we know whether good early stage performance allows the species thrive in various climate conditions or if the species is not rapidly adapting, but instead filling its climate niches in new places.

Predicting the future range expansion and understanding the vulnerability of various eco-regions to plant invasions are two important ecological issues the world faces today. Exploring the climate thresholds for various life-history traits of global invader species can help when predicting their future range expansion (Beckmann *et al.* 2011; Alexander *et al.* 2012; Luo &

Cardina 2012). Width of germination niche alone can strongly influence ecological or geographic ranges of plant species (Grime *et al.* 1981; Brändle *et al.* 2003; Cervera & Parra-Tabla 2009; Hierro *et al.* 2009) as germination is frequently subjected to environmental filtering before other life-history traits are expressed (Donohue *et al.* 2005; Gioria & Pyšek 2017). Distributional patterns of plant species can also be affected by the environmental conditions essential for seedling emergence and establishment (Donohue *et al.* 2010). It would therefore be worthwhile to examine climate thresholds, explore the climate niche for germination and seedling emergence of global invaders, and help predict their possible future geographic range based on these results. There are few studies that have tested the climate thresholds of germination and seedling emergence success of global invaders across species under various contrasting environments (Hou *et al.* 2014; Hock *et al.* 2015).

Furthermore, studying germination and seedling emergence of native and non-native populations of a global invader can improve our understanding of the processes underlying range expansion (Donohue *et al.* 2010). Studies undertaken in few climatic conditions generally conclude that non-native populations have higher germination responses than native ones (Hierro *et al.* 2009; Beckmann *et al.* 2011; Hirsch *et al.* 2012), which might contribute to the establishment success of globally distributed invaders. The temperature and precipitation of the source region can influence the global invader establishment success because germination responses of native and non-native populations may differ along climate gradients such as temperature and precipitation (Eckhart *et al.* 2011; Hirsch *et al.* 2012). For more insight on the ongoing range expansions of widely distributed invaders it is therefore essential to examine germination and seedling emergence success of their native and non-native populations under different climate conditions (Hierro *et al.* 2009; Donohue *et al.* 2010; Beckmann *et al.* 2011).

Here, we tested germination and seedling emergence of three global invaders, *Verbascum thapsus, Lupinus polyphyllus* and *Senecio inaequidens*, under seven experimental climate conditions representing gradients in temperature and moisture availability of major eco-regions of the world. Furthermore, the performances of native *versus* non-native *V. thapsus* populations were investigated under those experimental climates. This kind of experiment will allow us to assess whether or not the germination and seedling emergence success of native and non-native populations are influenced by local adaptation. We hypothesise that the seedling emergence of the three global invaders will be climate-dependent. In addition, we hypothesise that the performance of native and non-native populations of *V. thapsus* will be determined by local adaptations. In this context, we expect that temperature and precipitation of the seed source regions will be related to responses of native and non-native populations of *V. thapsus* under experimental climates.

METHODS

Study species: invasive across continents

Lupinus polyphyllus (Fabaceae), the garden lupine, is native to the western parts of North America (California, Oregon, Washington, Montana, Idaho, Nevada) and Canada (British Columbia, Alberta; Beuthin 2012). Since the 1900s it has been introduced into the European countries of Austria, Denmark, Britain, Estonia, Finland, Germany, Italy, Latvia, Lithuania, Norway, Poland, Sweden and the central part of European Russia as an ornamental plant, soil improver and stabiliser and as fodder (Fremstad 2010).

Senecio inaequidens (Asteraceae), the South African ragwort, is native to South Africa and Lesotho but has been introduced in Europe, especially to Belgium, France, Germany, Italy, the Netherlands, Britain and Spain during the late 20th century. The species reaches the Mediterranean coast, and expansion continues towards the eastern Pyrenean region. *S. inaequidens* has also invaded many habitats in South America (Ernst 1998; Lachmuth *et al.* 2010).

Verbascum thapsus (Scrophulariaceae), the common mullein, is native to Eurasia. Its geographic distribution ranges from Western Europe to China, crossing to the east *via* Russia. It is also present in Turkey, where the *Verbascum* genus is currently composed of over 250 species (Sharifnia 2007; Alba & Hufbauer 2012). *V. thapsus* now also exists in Canada, in U.S. states, Australia, New Zealand and La Reunion (Ansari & Daehler 2010). It is considered as a noxious weed in Colorado, South Dakota and Hawaii (Alba & Hufbauer 2012), and is one of the most common species in mountain regions around the world (Seipel *et al.* 2012, 2015; Hock *et al.* 2015).

Climate of the seed source regions

Seeds of *L. polyphyllus* (northern Black Forest) and *S. inaequidens* (Bayreuth) were collected from their non-native range in Europe (Germany). Mean annual air temperature and precipitation of the northern Black Forest range from 5.5–6.5 °C and 750–2200 mm, respectively, depending on elevation and exposure (Ministry for the Environment, Climate and Energy Economics, Baden-Württemberg). Bayreuth has a mean annual air temperature of 8.2 °C, and mean annual precipitation of 724 mm (Foken 2007). Seeds of *V. thapsus* were collected from two native ranges, Europe and Asia, as well as from two non-native ranges, North America and Australia (Table 1). From each continent, populations of three distinct source regions (total 12 populations) were collected that differ in climate conditions. We focused on differences in mean annual temperature and precipitation of the source regions (Table 1) as it is evident that temperature and precipitation are important drivers of germination and establishment success of many invasive plant species (Monty & Mahy 2009; Wang *et al.* 2009; Beckmann *et al.* 2011; Elliott *et al.* 2011; Alexander *et al.* 2012; Kumschick *et al.* 2013; Menge *et al.* 2016). Overall, mean annual temperature of source regions was warmer for non-native than for native populations (Table 1). In contrast, the overall precipitation of the source regions was significantly higher for native than for non-native populations of *V. thapsus*. After the collection, all seeds were stored in a refrigerator at temperatures below 0 °C and weighed before the start of the experiment (*L. polyphyllus*, 24.45 ± 7.97 mg seed^{-1}; *S. inaequidens*, 0.21 ± 0.03 mg seed^{-1}; *V. thapsus*, 0.08 ± 0.03 mg seed^{-1}).

Germination trials in various experimental climates

Seeds were placed in Petri dishes (9.0-cm diameter, 20 seeds dish^{-1}, number of replications = five Petri dishes for each factorial combinations) containing Rotilabo round filter paper

Table 1. Geographic and climatic characteristics of six native and six non-native populations of *Verbascum thapsus*. Mean values of native *versus* non-native ranges are marked in bold. Climate data were retrieved from the Worldclim database to a resolution of 0.5°, reference period 1960–1990 (Hijmans *et al.* 2005).

Origin of populations	Population Code	Region of populations	Latitude	Longitude	Elevation m a.s.l	Annual mean temperature °C)	Annual precipitation (mm)
Native range					**1587.2**	**8.6**	**960.7**
Europe	CH5	Grischuns, Switzerland	46.679780	10.164628	1843	2.4	935
Europe	CH2	Haldenstein, Switzerland	46.869583	09.492533	1360	4.4	1211
Europe	CH3	Grischuns, Switzerland	46.700110	08.861860	1100	6.6	1353
Asia	KA3	Kashmir, India	34.250000	74.933330	1940	12.1	795
Asia	KA2	Kashmir, India	34.266670	74.816670	1680	12.3	782
Asia	KA1	Kashmir, India	34.216670	74.783330	1600	13.7	688
Non-native range					**760.3**	**10.5**	**672.8**
North America	MT2	Joebrown, Montana	45.168000	−110.851033	1547	6.5	388
North America	OR3	Wallowa, Oregon	45.282560	−117.769100	1079	6.5	478
North America	OR2	Wallowa, Oregon	45.409170	−117.891800	916	8.1	516
Australia	AU6	New South Wales	−35.316670	149.398600	820	11.6	756
Australia	AU3	New South Wales	−36.563920	149.795400	160	14.9	947
Australia	AU1	New South Wales	−36.539750	149.825300	40	15.3	952

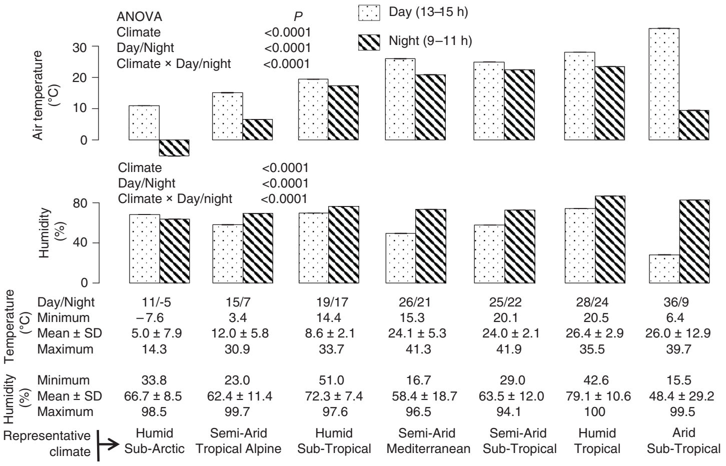


Fig. 1. Climate characteristics of seven experimental climates (five greenhouses and two climate chambers). Mean values and SE of day/night temperature (°C) and humidity (%) measured over 6 weeks are shown here. Temperature (°C) and humidity (%) are significantly different between seven experimental- climate conditions. Data were tested *via* LMEM and ANOVA. Significance level was set to $P < 0.05$.

(601A, cellulose, Ø membrane 90 mm). Petri dishes were initially sprayed once with fungicide (Previcur N Fungicide, diluted to 0.15% l^{-1}) to protect the seeds from fungal infection, and then placed in seven experimental climates. In the following days of the experiment, the dishes were watered daily between 09:00 and 11:00 h to keep the filter paper moist. We used the same water level (5 ml $dish^{-1}$ day^{-1}) and approximately the same photoperiod (13–15 h day/9–11 h night) in all experimental setups to disentangle the effects of experimental climates, mainly temperature and humidity, on germination and seedling emergence.

Experimental climates corresponding to seven eco-regions

We investigated seven experimental climates, five in greenhouse conditions and two in climate chambers. The facilities of the botanical garden at the University of Bayreuth were used as proxy for experimental climates representing the following eco-regions: Semiarid Tropical-alpine, Humid Subtropical, Semiarid Mediterranean, Semiarid Subtropical and Humid Tropical (see Figure S1). We follow these naming conventions in this study. Plants inside the greenhouses of the botanical garden are mostly grown in climate conditions similar to their natural eco-region. Two additional experimental climates investigated in climate chambers are termed: Humid Subarctic (= cool climate) and Arid Subtropical (= dry climate). Characteristics of the experimental climates regarding air temperature and humidity are described in Fig. 1. Temperature and humidity of all experimental setups were logged every 10 min with HOBO pro v2 onset data loggers (Fig. 1). The high differences in temperature and humidity among the target climates created different drying conditions inside the Petri dishes even though they were watered similarly in all seven experimental climates. We visually observed that Petri dishes in the Arid Subtropical climate dried out faster compared to other experimental climates.

Response variables

We observed first seed germination on day 3 of the experiment and thereafter continued data collection on each alternate day during the first 2 weeks, and then once a week during the weeks 3, 4, 5 and 6. At each sampling point, we recorded new germination and seedling emergence of the target species in all Petri dishes. We stopped collecting data after week 6 because no new germination or seedling emergence was observed after that sampling date. We then visually checked the viability of seeds that did not germinate. We considered the seeds viable if they did not show signs of fungal infection or rot, and if they were firm when squeezed with tweezers (Seipel *et al.* 2015). Finally, we added the total count and calculated the percentage of seedling emergence of all viable seeds. We defined ‘germination’ as the stage when the radicle began to emerge from a seed. The appearance of the full radicle marks the end of the ‘germination stage’ and the beginning of the ‘seedling emergence’ stage. We recorded the end of the seedling emergence stage when the first leaves began unfolding from the initial shoots.

Statistical analysis

Analyses were done using the statistical software R 3.0.2 (R Core Team 2013). A two-factorial ANOVA was performed using linear mixed effects models (LMEMs, due to the presence of random effects) to test the main and interaction effects of experimental climates and species. Number of replications ($n = 5$) was used as a random factor in this model. Germination strongly correlated ($r^2 = 0.99$) with the seedling emergence (see Figure S2), therefore only the seedling emergence data and analyses are shown. Since we had one non-native population each from *L. polyphyllus* and *S. inaequidens* (both from Europe), we used the average seedling emergence of non-native populations of *V. thapsus* from Australia for species comparison. From the two non-native continents, Australia and North America, we selected the Australian population as this is the most distant non-native continent from the species' native range. Furthermore, average outcomes of Australian populations mirror the overall responses of all non-native populations of *V. thapsus*.

Additionally, we analysed variation in seedling emergence among all investigated populations of *V. thapsus* under the different experimental climates. A factorial ANOVA was performed using LMEM (due to the presence of random effects) to test for significant differences. We tested seedling emergence against experimental climate, seed source region (native or non-native), mean annual temperature of seed source region, and annual precipitation of seed source region, taking into account all possible twofold interactions. Population and number of replications were used as random factor in this model. If the main effect or one or more interaction effects were significant, regression analysis for the seedling emergence of *V. thapsus* populations and their climate of the seed source region were conducted using linear least-squares regression (function ‘lm’).

Homogeneous groups of factor combinations were identified by means of Tukey's HSD *post-hoc* comparisons. Prior to statistical analysis, residuals were checked for their homogeneity of variances and also for their normality. All characteristics were tested by examining the residuals *versus* fitted plots, and the normal qq-plots of the linear models (Faraway 2005). The level of significance was set to $P < 0.05$. LMEMs were conducted with the R function ‘lme’ (Bates *et al.* 2014) and Tukey HSD *post-hoc* comparisons with the function ‘glht’ (Bretz *et al.* 2010). Three R packages, multcomp (Simultaneous Inference in General Parametric Models, version 1.3-2), lme4 (Linear mixed-effect models using Eigen and S4, version 1.0-6) and sciplot (Scientific Graphing Functions for Factorial Designs, version: 1.1-0) were used for analysis and graph preparation.

The performance variability index, ranging from zero to one, was calculated for seedling emergence success of all three species as well as for each population of *V. thapsus*. This performance variability index estimates the species fitness, defined as the outcome of the interaction of traits with the artificial environments. Calculation was used the following formula:

$$\begin{aligned}&\text{Performance variability index}\\&\quad=(\max_{\text{seedlingemergence}}\\&\qquad-\min_{\text{seedlingemergence}})/\max_{\text{seedlingemergence}}\end{aligned}$$

Here, max/min correspond to the mean maximum/minimum number of seedlings that emerged from their seeds in the Petri dishes while subject to different experimental climates. Means were calculated from responses under five out of seven experimental climates as no germination and seedling emergence were observed in the two climate chamber experiments.

RESULTS

Performances of three global plant invaders under seven experimental climates

The experimental climate conditions had significant effects on the seedling emergence of all species (for significant values see Table 2). No germination and seedling emergence occurred under 5 °C in the Humid Subarctic climate chamber nor under 48.4% humidity in the Arid Subtropical climate chamber. However, seedling emergence under the other five experimental climates was influenced by temperature and humidity gradients, being significantly lower in the two moderately cool experimental climates (Semiarid Tropical-alpine greenhouse, 41.7%; Humid Subtropical greenhouse, 53.5%) compared to the three warmer experimental climates (Humid Tropical, 76.0%; Semiarid Subtropical, 78.1%; and Semiarid Mediterranean, 79.0% greenhouses).

Species responded differently under the five experimental climate conditions inside the greenhouses (see Table 2 and Fig. 2). Seedling emergence rate of *V. thapsus* was climate-dependent. *L. polyphyllus* and *S. inaequidens* performed consistently, but *L. polyphyllus* had higher seedling emergence than *S. inaequidens* in all five experimental climates. *S. inaequidens* performed equally well compared to *V. thapsus* only in the experimental Semiarid tropical-alpine climate. However, in the Humid Subtropical, Semiarid Mediterranean, Semiarid Subtropical and Humid tropical experimental climates,

Table 2. Factors influencing the seedling emergence of three global invaders *Verbascum thapsus*, *Lupinus polyphyllus* and *Senecio inaequidens*. For *V. thapsus*, seeds of native and non-native populations were used, while in the other invasive species only seeds of non-native populations were tested. *F*- and *P*-values of a factorial ANOVA, performed with linear LMEM, are shown.

	Seedling emergence	
Factors	*F*	*P*
V. thapsus, L. polyphyllus and *S. inaequidens* from non-native ranges		
Experimental climate	361.8	<0.0001
Species	164.8	<0.0001
Experimental climate × Species	37.9	<0.0001
Populations of *V. thapsus* from native and non-native ranges		
Experimental climate (eco-region)	894.8	<0.0001
Range of populations (native or non-native)	1.3	0.3258
Temperature of seed source (Mean annual)	20.0	0.0111
Precipitation of seed source (Annual total)	3.5	0.1366
Experimental climate × Range	28.9	<0.0001
Experimental climate × Temperature	48.5	<0.0001
Range × Temperature	0.1	0.8202
Experimental climate × Precipitation	5.9	<0.0001
Range × Precipitation	0.2	0.6636
Temperature × Precipitation	1.7	0.2630

Table 3. Performance variability index for seedling emergence success of the three global invaders *Verbascum thapsus*, *Lupinus polyphyllus* and *Senecio inaequidens*. The index ranges from zero to one, with 0 = minimum and 1 = maximum fitness for seedling emergence. Here, fitness refers to the outcome of the interaction of traits with the artificial environments. For calculation, the seedling emergence of the five experimental climates is used.

Species or populations	Performance variability index
Species	
L. polyphyllus	0.25
S. inaequidens	0.43
V. thapsus	0.73
Populations of *V. thapsus*	
Native range (mean)	0.63
Asia	0.32
Europe	0.93
Non-native range (mean)	0.84
Australia	0.72
North America	0.95

S. inaequidens showed only about half the seedling emergence rate compared to *V. thapsus*. In comparison to *L. polyphyllus*, performance of *V. thapsus* was significantly lower in the Semiarid tropical-alpine and Humid Subtropical experimental climates, equally in the Semiarid Mediterranean and Humid Tropical climates, and higher in the Semiarid Subtropical experimental climate. The global germination niche maps, prepared based on the present study, suggest that *L. polyphyllus*, *S. inaequidens* and *V. thapsus* are able to germinate and emerge in places outside their current distributions (see Figure S3). Performance variability index for seedling emergence success was high in *V. thapsus* (0.73), moderate in *S. inaequidens* (0.43) and low in *L. polyphyllus* (0.25; Table 3).

Performances of *V. thapsus* populations under seven experimental climates

Seedling emergence of *V. thapsus* populations from native *versus* non-native ranges varied by experimental climates (Table 2). Seedling emergence was only observed in the five greenhouse experimental climates, but not in the cool and dry climate chamber experiments. In general, responses were significantly higher for non-native populations in the three warm experimental climates, and lower in the two moderately cool experimental climates when compared to native populations (Fig. 3, Figure S4). Within the native range, Asian populations surprisingly performed better in Semiarid Tropical-alpine and in Humid Subtropical experimental climates than European populations. Similarly, within the non-native range, Australian populations outperformed the North American populations in Semiarid Tropical-alpine and in Humid Subtropical experimental climates (Fig. 3).

Mean annual temperature of the seed source region had significant positive effects on seedling emergence of *V. thapsus* populations in two moderately cool experimental climate conditions (Fig. 4; Interaction effect: Table 2). No significant relationships between the temperature of seed source region and seedling emergence of *V. thapsus* populations were observed in the three warmer experimental climates. Precipitation of the seed source regions had negative effects in two warm and dry experimental climates, with populations from drier regions showing a higher performance than the populations from comparatively wet regions (Fig. 4; Interaction effect: Table 2).

The performance variability index for seedling emergence success of *V. thapsus* populations differed between native and non-native ranges and also within the same range (Table 3). Overall, the performance variability index was higher for non-native (0.84) than native (0.63) populations. Within the native

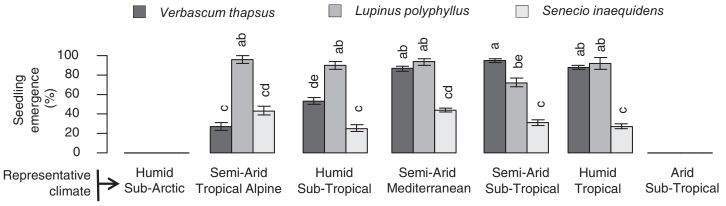


Fig. 2. Seedling emergence of the non-native ranges of the three global invaders *Verbascum thapsus* (Australia), *Lupinus polyphyllus* (Germany) and *Senecio inaequidens* (Germany) in response to climate characteristics. Experimental climates are representative of seven eco-regions defined by temperature (°C) and humidity (%) (see Fig. 1 for details). Mean values and SE of seedling emergence over 6 weeks are shown. Significant interaction effects between species and experimental climates were tested *via* a Tukey HSD test (function 'glht') at significance $P < 0.05$.

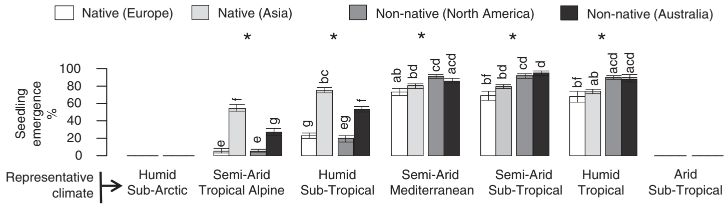


Fig. 3. Seedling emergence rates of *Verbascum thapsus* populations from two native (Europe, Asia) and two non-native (North America, Australia) continents tested in seven experimental climate conditions (see Fig. 1 for climatic details). Mean values and SE of three populations within a continent (range) are shown. Small letters indicate significantly different ($P < 0.05$) interaction effects between experimental climates and native *versus* non-native ranges tested with a Tukey HSD test (function 'glht'). Significant differences between native and non-native ranges indicated with asterisks.

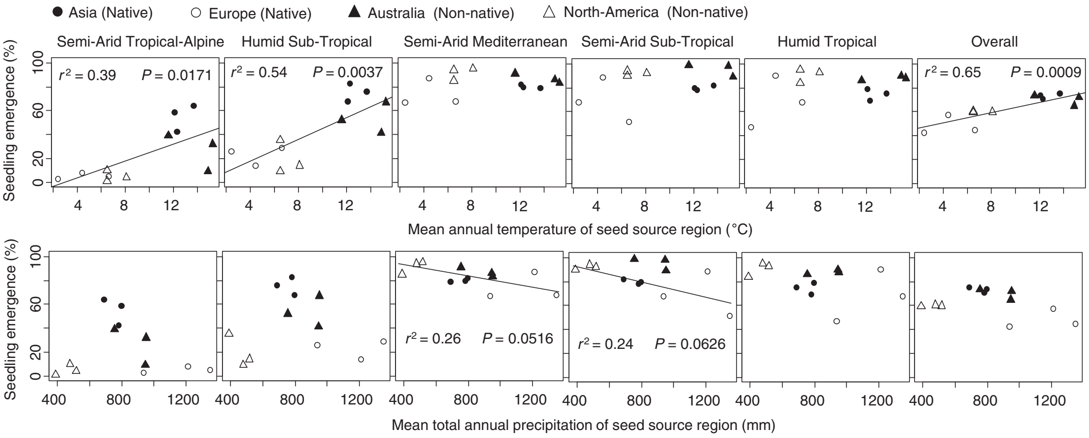


Fig. 4. Relationship between seedling emergence and mean annual temperature and annual precipitation of the seed source regions of *Verbascum thapsus* populations in five experimental climate conditions. Regression lines are shown only for (by trend) significant results. *P*- and r^2-values are derived by linear least-squares regression (function 'lm') at a significance of $P < 0.05$.

range, European populations (0.93) showed higher performance variability compared to Asian populations (0.32). Within the non-native range, North American populations (0.95) had higher performance variability than Australian populations (0.72).

DISCUSSION

Performances of three global plant invaders under seven experimental climates

Our central hypothesis, that seedling emergence of the three global invaders is climate-dependent, is supported. In the five experimental climates, seedling emergences of all three species were observed, indicating species are adapted to those climate conditions. It is evident that invasive species are able to germinate and establish under a wide range of temperatures. For instance, the optimal range for *V. thapsus* is between 20–35 °C (Ansari & Daehler 2000; Seipel *et al.* 2015). However, no germination occurred in Humid Subarctic and in Arid Subtropical experimental climates; implying that both low air temperature and low air humidity can limit seedling emergence of the three global invaders *V. thapsus*, *L. polyphyllus* and *S. inaequidens*. Evidently, the extreme climates with an average day/night temperature ≤5 °C (night temperatures <5 °C) in Humid Subarctic and an average humidity <50% in Arid Subtropical experimental climate filtered seedling emergence success.

Germination and seedling emergences were species-specific. Evidence suggests that seed size affects germination, seedling emergence and early stage establishment (Townsend 1992; Myint *et al.* 2010; Sõber & Ramula 2013). The differences in seed size could be one explanation for resource-driven germination and seedling emergence success in the present study. The large seeds of *L. polyphyllus* (24.45 ± 7.97 mg seed^{-1}) might enable them to germinate more efficiently than *S. inaequidens* (0.21 ± 0.03 mg seed^{-1}). However, the advantage of a larger seed size decreased with more favourable climate conditions, possibly explaining why seedling emergence success of the small *V. thapsus* seeds (0.08 ± 0.03 mg seed^{-1}) increased with temperature rise and even exceeded *L. polyphyllus*, at least in the Semiarid Subtropical experimental climate condition (temperature, 24 °C; humidity, 63.5%).

Performance of invasive species under different climate conditions in the later life stage can be influenced by phenotypic plasticity (Sultan 2000, 2001; Bossdorf *et al.* 2005; van Kleunen & Fischer 2005; Valladares *et al.* 2007; Nicotra *et al.* 2010). The present study shows that performance or fitness of three global invaders differs in their early life traits such as germination and seedling emergence success. Different responses of species in five out of seven experimental climate conditions and different performance variability index values suggest that the three global invaders followed different germination strategies under different experimental climates. *L. polyphyllus* followed the maximum germination strategy with low variability across all climates; *S. inaequidens* followed consistently lower germination strategy with moderate variability across all climates; and *V. thapsus* followed an opportunistic germination strategy with higher germination in optimal conditions and lower germination in stress conditions (*i.e.* high variability). The maximum germination strategy of *L. polyphyllus* and opportunistic germination strategy of *V. thapsus* enables them to establish within a broad geographic range. This is in line with the current distribution of our target species, showing larger distribution ranges of *L. polyphyllus* and *V. thapsus* compared to those of *S. inaequidens* (Ernst 1998; Sharifnia 2007; Fremstad 2010; Alba & Hufbauer 2012; Seipel *et al.* 2012, 2015). Lower germination across all climates might restrict *S. inaequidens* to a small geographic range.

Performances of native and non-native population of *V. thapsus* under seven experimental climates

Our data support the hypothesis that performances of populations from native and non-native ranges are determined by local adaptations to the climate of the corresponding seed source regions (temperature and precipitation). Indeed, non-native populations from warmer source regions had higher performances in warmer climates and lower performances in moderately cool experimental climates compared to native populations and *vice versa*. The overall mean annual temperature of the native seed source region was significantly colder than the seed source region of non-native populations. Thus, native populations probably were adapted to cooler climates while non-native populations were adapted to warmer climates. This is also supported by Seipel *et al.* (2015) who found that native *V. thapsus* populations from cooler seed source (Kashmir, India) germinated better at low temperatures compared to other non-native populations, indicating evidence of local adaptation.

Positive correlations between temperature of seed source region and responses of *V. thapsus* populations in two moderately cool experimental climates were due to higher performances of native Asian and non-native Australian populations. These positive correlations did not indicate that populations from the warmer region had higher performance in moderately cool experimental climates; rather they suggest better performance of populations under minimal temperature shifts (see Figure S5). In summary, seedling emergence of native and non-native populations depends on the similarities in temperature conditions between the climate of the seed source region and the experimental climate. Eckhart *et al.* (2011) found that germination of *Clarkia xantiana* populations is related to the temperature of their seed source region. However, temperature of the seed source region could not explain the seedling emergence of *V. thapsus* populations in three warmer experimental climates, possibly because local adaptation cannot influence germination and seedling emergence success under optimal conditions. Moreover, negative correlations (Fig. 4) between precipitation of the seed source regions and seedling emergence in two warm and moderately dry experimental climates indicate that precipitation of the seed source regions also shapes responses of populations. Similar findings were presented in a recent study of Hirsch *et al.* (2012), that precipitation of the seed source regions are negatively correlated with germination responses of plant populations. Our data are in accordance with other previous findings (Parker *et al.* 2003; Giménez-Benavides *et al.* 2007; Macel *et al.* 2007; Kim & Donohue 2013), suggesting that seedling recruitment, growth and reproduction of global invaders in new environments is often determined by local adaptation. The present study also showed that the responses of non-native populations are not always higher than native populations; rather they depend on the weather conditions under which they perform and on the adaptation of the populations to the climate at their respective seed source region.

A high performance variability index of the non-natives suggests that fitness of these populations (here germination or seedling emergence success) in the new environment is high compared to the populations of the native region. Surprisingly, we found significant differences in seedling emergence not only between but also within the same range, implying that performance variability exists both within native and non-native ranges. Previous studies regarding performance of native and non-native populations of *V. thapsus* have mainly worked with populations from the native European or the non-native American continent (Alba & Hufbauer 2012; Kumschick *et al.* 2013). The only exceptions are two recent studies, one by Seipel *et al.* (2015) that investigated performances of populations from Asia (native) and Australia (non-native) and one by Hock *et al.* (2015) in New Zealand (non-native). This could possibly explain why the seedling emergence patterns found here for *V. thapsus* populations are not present in most of the existing studies. It is also evident that performances of native *versus* non-native populations in later life stages vary due to genetic variations (Maron *et al.* 2004; Bossdorf *et al.* 2005; Lachmuth *et al.* 2010). Alexander *et al.* (2012) found different genetic clines in response to temperature among native and non-native populations of a global plant invader (*Plantago lanceolata*) in their later life stage. Therefore, we cannot exclude the possibility that responses of earlier life stages, *i.e.* germination and seedling emergence success of native versus non-native populations, varied in different climate conditions due to genetic variations. Genetic diversity within non-native populations is evident in several previous studies (Wu *et al.* 1987; Meyer & Allen 1999), however, not within their native populations. In the present study, we found significant response variations within native populations, which suggest that genetically based phenotypic differentiation may also exist within native populations.

ACKNOWLEDGEMENT

The results of the study have previously been published as part of the PhD thesis of M.A.S. Arfin-Khan, University of Bayreuth, Germany. We thank the German Academic Exchange Service (DAAD) for supporting the research stay of the first author and the Ecological-Botanical Garden of Bayreuth University for sharing greenhouse space for the experimental germination trial. Special thanks to Juergen Kreyling for helping to design the experiment and to Reinhold Stahlmann who helped to prepare the global germination niche maps. We also thank Jake M. Alexander, Tim Seipel, Keith McDougall and Christoph Kueffer for providing seed material.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Vegetation inside the five greenhouses of the botanical garden of the University of Bayreuth representing five eco-regions.

Figure S2. Germination and seedling emergence rates of three global invaders (*V. thapsus*, *L. polyphyllus*, *S. inaequidens*) from non-native continents under seven experimental climate conditions.

Figure S3. Global germination niche maps of three plant invaders: *L. polyphyllus, S. inaequidens* and *V. thapsus*.

Figure S4. Seedling emergence of *V. thapsus* populations (native *versus* non-native) under seven experimental climates.

Figure S5. Seedling emergence of *V. thapsus* populations under various temperature shifts (differences in mean temperature of climate of seed source region *versus* experimental climate).

REFERENCES

Alba C., Hufbauer R. (2012) Exploring the potential for climatic factors, herbivory, and co-occurring vegetation to shape performance in native and introduced populations of *Verbascum thapsus*. *Biological Invasions*, **14**, 2505–2518.

Alexander J.M., van Kleunen M., Ghezzi R., Edwards P.J. (2012) Different genetic clines in response to temperature across the native and introduced ranges of a global plant invader. *Journal of Ecology*, **100**, 771–781.

Ansari S., Daehler C.C. (2000) *Common Mullein (Verbascum thapsus): a literature review*. Pacific Cooperative Studies Unit, University of Hawaii at Manoa, Department of Botany, Honolulu (HI). PCSU Technical Report, 127.

Ansari S., Daehler C.C. (2010) Life history variation in a temperate plant invader, *Verbascum thapsus* along a tropical elevational gradient in Hawaii. *Biological Invasions*, **12**, 4033–4047.

Bates D., Maechler M., Bolker B., Walker S. (2014) Linear mixed-effects models using Eigen and S4.:1–74. URL: http://lme4.r-forge.r-project.org/

Beckmann M., Bruelheide H., Erfmeier A. (2011) Germination responses of three grassland species differ between native and invasive origins. *Ecological Research*, **26**, 763–771.

Beuthin M. (2012). *Plant guide for bigleaf lupine (Lupinus polyphyllus)*. USDA-Natural Resources Conservation Service, Plant Materials Center, Corvallis, OR, USA.

Bossdorf O., Auge H., Lafuma L., Rogers W.E., Siemann E., Prati D. (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.

Brändle M., Stadler J., Klotz S., Brandl R. (2003) Distributional range size of weedy plant species is correlated to germination patterns. *Ecology*, **84**, 136–144.

Bretz F., Hothorn T., Westfall P. (2010) *Multiple comparisons using R*. Chapman & Hall/CRC, Boca Raton, FL, USA.

Cervera J.C., Parra-Tabla V. (2009) Seed germination and seedling survival traits of invasive and non-invasive congeneric *Ruellia species* (Acanthaceae) in Yucatan, Mexico. *Plant Ecology*, **205**, 285–293.

Donohue K., Dorn L., Griffith C., Kim E., Anna A., Polisetty C., Schmitt J. (2005) The evolutionary ecology of seed germination of Arabidopsis thaliana : variable natural selection on germination timing. *Evolution*, **59**, 758–770.

Donohue K., Rubio de Casas R., Burghardt L., Kovach K., Willis C.G. (2010) Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 293–319.

Ebeling S.K., Hensen I., Auge H. (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. *Diversity and Distributions*, **14**, 225–233.

Eckhart V.M., Geber M.A., Morris W.F., Fabio E.S., Tiffin P., Moeller D.A. (2011) The geography of demography: long-term demographic studies and species distribution models reveal a species border limited by adaptation. *The American Naturalist*, **178**, S26–S43.

Elliott C.W., Fischer D.G., LeRoy C.J. (2011) Germination of three native *Lupinus* species in response to temperature. *Northwest Science*, **85**, 403–410.

Ernst W.H.O. (1998) Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in the Netherlands: from wool alien to railway and road alien. *Acta Botanica Neerlandica*, **47**, 131–151.

Faraway J.J. (2005) *Linear models with R*. Chapman & Hall/CRC, Boca Raton, FL, USA.

Foken T. (2007) Das Klima von Bayreuth: Status quo und Aufgaben für die Stadtplanung. *Standort*, **31**, 150–152.

Fremstad E. (2010) NOBANIS – invasive alien species fact sheet *Lupinus polyphyllus*. Online Database of the European Network on Invasive Alien Species – NOBANIS:1–11.

Giménez-Benavides L., Escudero A., Iriondo J.M. (2007) Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. *Annals of Botany*, **99**, 723–734.

Gioria M., Pyšek P. (2017) Early bird catches the worm: germination as a critical step in plant invasion. *Biological Invasions*, **19**, 1055–1080.

Grime J.P., Mason G., Curtis A. V, Rodman J., Band S.R., Mowforth M.A.G., Neal A.M., Shaw S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017–1059.

Hierro J.L., Eren Ö., Khetsuriani L., Diaconu A., Török K., Montesinos D., Andonian K., Kikodze D., Janoian L., Villarreal D., Estanga-Mollica M.E., Callaway R.M. (2009) Germination responses of an invasive species in native and non-native ranges. *Oikos*, **118**, 529–538.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hirsch H., Wypior C., Wehrden H., Von Wesche K., Renison D., Hensen I. (2012) Germination performance of native and non-native *Ulmus pumila* populations. *NeoBiota*, **68**, 53–68.

Hock M., Beckmann M., Hofmann R.R., Bruelheide H., Erfmeier A. (2015) Effects of UV-B radiation on germination characteristics in invasive plants in New Zealand. *NeoBiota*, **26**, 21–37.

Hou Q.-Q., Chen B.-M., Peng S.-L., Chen L.-Y. (2014) Effects of extreme temperature on seedling establishment of nonnative invasive plants. *Biological Invasions*, **16**, 2049–2061.

Kim E., Donohue K. (2013) Local adaptation and plasticity of *Erysimum capitatum* to altitude: its implications for responses to climate change. *Journal of Ecology*, **101**, 796–805.

van Kleunen M., Fischer M. (2005) Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist*, **166**, 49–60.

Kumschick S., Hufbauer R.A., Alba C., Blumenthal D.M. (2013) Evolution of fast-growing and more resistant phenotypes in introduced common mullein (*Verbascum thapsus*). *Journal of Ecology*, **101**, 378–387.

Lachmuth S., Durka W., Schurr F.M. (2010) The making of a rapid plant invader: genetic diversity and differentiation in the native and invaded range of *Senecio inaequidens*. *Molecular Ecology*, **19**, 3952–3967.

Leiblein-Wild M.C., Kaviani R., Tackenberg O. (2014) Germination and seedling frost tolerance differ between the native and invasive range in common ragweed. *Oecologia*, **174**, 739–750.

Luo J., Cardina J. (2012) Germination patterns and implications for invasiveness in three *Taraxacum* (Asteraceae) species. *Weed Research*, **52**, 112–121.

Macel M., Lawson C.S., Mortimer S.R., Smilauerova M., Bischoff A., Crémieux L., Dolezal J., Edwards A.R., Lanta V., Bezemer T.M., Van der Putten W.H., Igual J.M., Rodriguez-Barrueco C., Müller-Schärer H., Steinger T. (2007) Climate vs. soil factors in local adaptation of two common plant species. *Ecology*, **88**, 424–433.

Maron J.L., Vila M., Bommarco R., Elmendorf S., Beardsley P. (2004) Rapid evolution of an invasive plant. *Ecological Monographs*, **74**, 261–280.

Menge E.O., Bellairs S.M., Lawes M.J. (2016) Seed-germination responses of *Calotropis procera* (Asclepiadaceae) to temperature and water stress in northern Australia. *Australian Journal of Botany*, **64**, 441–450.

Meyer S.E., Allen P.S. (1999) Ecological genetics of seed germination regulation in *Bromus tectorum* L. *Oecologia*, **120**, 35–43.

Monty A., Mahy G. (2009) Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. *Oecologia*, **159**, 305–315.

Myint T., Chanprasert W., Srikul S. (2010) Effect of seed weight on germination potential of different oil palm (*Elaeis guineensis* Jacq.) crosses. *Seed Science and Technology*, **38**, 125–135.

Nicotra A.B., Atkin O.K., Bonser S.P., Davidson A.M., Finnegan E.J., Mathesius U., Poot P., Purugganan M.D., Richards C.L., Valladares F., van Kleunen M. (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, **15**, 684–692.

Parker I.M., Rodriguez J., Loik M.E. (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. *Conservation Biology*, **17**, 59–72.

R Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Seipel T., Kueffer C., Rew L.J., Daehler C.C., Pauchard A., Naylor B.J., Alexander J.M., Edwards P.J., Parks C.G., Arevalo J.R., Cavieres L.A., Dietz H., Jakobs G., McDougall K., Otto R., Walsh N. (2012) Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. *Global Ecology and Biogeography*, **21**, 236–246.

Seipel T., Alexander J.M., Daehler C.C., Rew L.J., Edwards P.J., Dar P.A., McDougall K., Naylor B., Parks C., Pollnac F.W., Reshi Z.A., Schroder M., Kueffer C. (2015) Performance of the herb *Verbascum thapsus* along environmental gradients in its native and non-native ranges. *Journal of Biogeography*, **42**, 132–143.

Sharifnia F. (2007) Notes on the distribution and taxonomy of *Verbascum* in Iran. *Iran Journal of Botany*, **13**, 30–32.

Sõber V., Ramula S. (2013) Seed number and environmental conditions do not explain seed size variability for the invasive herb *Lupinus polyphyllus*. *Plant Ecology*, **214**, 883–892.

Sultan S.E. (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, **5**, 537–542.

Sultan S.E. (2001) Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology*, **82**, 328–343.

Theoharides K.A., Dukes J.S. (2007) Plant invasion across space and time : factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256–273.

Townsend C.E. (1992) Seedling emergence of yellow-flowered alfalfa as influenced by seed weight and planting depth. *Agronomy Journal*, **84**, 821–826.

Valladares F., Gianoli E., Gómez J.M. (2007) Ecological limits to plant phenotypic plasticity. *New Phytologist*, **176**, 749–763.

Wang J., Ferrell J., MacDonald G., Sellers B. (2009) Factors affecting seed germination of Cadillo (*Urena lobata*). *Weed Science*, **57**, 31–35.

Wu L., Till-bottraud I., Torres A. (1987) Genetic differentiation in temperature-enforced seed dormancy among golf course populations of *Poa annua* L. *New Phytologist*, **107**, 623–631.

10.1.1 Supporting information Manuscript 1

Factors influencing seedling emergence of three global invaders in greenhouses representing major eco-regions of the world

Mohammed A. S. Arfin Khan[1,2],Vanessa M. S. Vetter[1,3,*], Zafer A. Reshi[4], Parvaiz A. Dar[5], Anke Jentsch[1]

*[1]Disturbance Ecology, BayCEER, University of Bayreuth, Germany (anke.jentsch@uni-bayreuth.de); [2]Department of Forestry and Environmental Science, Shahjalal University of Science and Technology, Sylhet-3114, Bangladesh (nobelarfin@yahoo.com); [3]Geoecology/Physical Geography, Institute for Environmental Science, University of Landau, Germany (vanessa.vetter@uni-bayreuth.de); [4]Department of Botany, University of Kashmir, Srinagar-190006, J&K, India (zreshi@yahoo.com); [5]Department of Botany, Amar Singh College Srinagar-19008, India (pervaizahmaddar@yahoo.com); *Corresponding author: Vanessa Vetter, vanessa.vetter@uni-bayreuth.de, Phone: +49 (0) 921 552188, Fax: +49 (0) 921552315.*

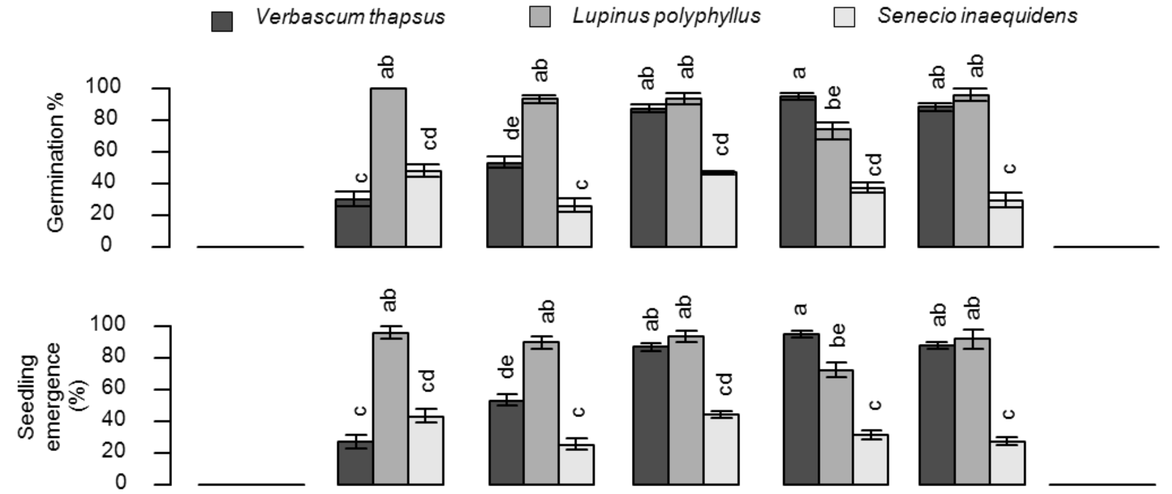
Fig. S1. Vegetation inside the five greenhouses of the botanical garden of the University of Bayreuth representative to five eco-regions: (a) Semi-Arid Tropical Alpine, (b) Humid Sub-Tropical, (c) Semi-Arid Mediterranean, (d) Semi-Arid Sub-Tropical and (e) Humid Tropical (Photos: A. Jentsch).

The Semi-Arid Mediterranean greenhouse is the home for trees and shrubs of the Mediterranean zone: Citrus-trees from the Mediterranean, Myrtle plants from Australia (Callistemon- or Eucalyptus species) or palms from Asia and North America. In the Semi-Arid Sub-Tropical greenhouse water storing (succulent) plants such as cacti and many representatives of the Euphorbiaceae and Apocynaceae families are extensively managed over the whole year. The Humid Sub-Tropical greenhouse environment is little colder and mistier, accommodating several endemic plant species of the laurel forests of the Canary Islands. The Semi-Arid

Tropical Alpine greenhouse accommodates plants growing in tropical high mountain regions. It is unique in its climatic features and the plants growing in it, such as the giant Ethiopian Lobelia (*Lobelia rhynchopetalum*). Some very important factors inside this greenhouse are: (i) an alternating day/night rhythm and the lowering of the night temperature down to the freezing point throughout the entire year, as well as (ii) a high light intensity with high fractions of UV and red light. The Humid Tropical greenhouse is rich in many types of trees, lianas and epiphytes. Bananas (Musa) and Cacao (Theobroma) are native to the tropics and are fruiting in this greenhouse.

Another two experimental climates, which we investigated in climate chambers, are termed: Humid Sub-Arctic (= cool climate) and Arid Sub-Tropical (= dry climate). In general, the Arid Sub-Tropical region is warmer during the day, cooler at night and drier during the whole year. The average daytime temperature of the Sahara, the largest hot desert of the Arid Sub-Tropical region, ranges from 30 to 45 °C, while at night the average temperature goes below 10 °C (Oliver, 2005). Therefore, we manipulated the Arid Sub-Tropical experimental climates in a climate chamber having day/night temperatures around 36/9 °C and mean humidity around 48%. On the other hand, the climate in the Humid Sub-Arctic eco-region is cool and humid. During the mid-growing season in July, average maximum temperatures of New Siberian Islands ranges from 8 to 11 °C and average minimum temperatures ranges from -3 to 1 °C (data: Climate Normals of the Kotel'nyj Island 1961 – 1990 retrieved from the NOAA's National Centers for Environmental Information, Center for Weather and Climate). We manipulated the Humid Sub-Arctic climatic conditions also in a climate chamber having day/night temperatures around 11/-5 °C and mean humidity around 67%.

Overall, the mean day/night temperature was cool in Humid Sub-Arctic climate (5 °C), moderately cool in the Semi-Arid Tropical-Alpine (12 °C) and Humid Sub-Tropical (18.6 °C) climates; and warm in the Semi-Arid Mediterranean (24.1 °C), Semi-Arid Sub-Tropical (24 °C), Humid Tropical (26.4 °C), and Arid Sub-tropical (26 °C) setups. Mean humidity of Arid Sub-tropical climate was exceptionally lower (mean < 50%) than in the other experimental setups (mean > 60%; except Semi-Arid Mediterranean = 58.4%, see Figure 1 for details).



Temp (ºC)	Day/Night	11/-5	15/7	19/17	26/21	25/22	28/24	36/9
	Minimum	-7.6	3.4	14.4	15.3	20.1	20.5	6.4
	Mean ± SD	5.0 ± 7.9	12.0 ± 5.8	18.6 ± 2.1	24.1 ± 5.3	24.0 ± 2.1	26.4 ± 2.9	26.0 ± 12.9
Humi (%)	Minimum	33.8	23.0	51.0	16.7	29.0	42.6	15.5
	Mean ± SD	66.7 ± 8.5	62.4 ± 11.4	72.3 ± 7.4	58.4 ± 18.7	63.5 ±12.0	79.1 ± 10.6	48.4 ± 29.2
Representative climate	→	Humid Sub-Arctic	Semi-Arid Tropical Alpine	Humid Sub-Tropical	Semi-Arid Mediterranean	Semi-Arid Sub-Tropical	Humid Tropical	Arid Sub-Tropical

Fig. S2. Germination and seedling emergence rates of three global invaders (*V. thapsus*, *L. polyphyllus*, *S. inaequidens*) from non-native continents under seven experimental-climate conditions. Climates here are representative to 7 eco-zones by temperature (ºC) and humidity (%). Mean values and standard errors are shown in the figure. Species responded differently under different climate conditions. Significant interaction effect between species and climates are indicated by different small letters ($p < 0.05$). Note: “Temp” = Temperature; “Humi” = Humidity.

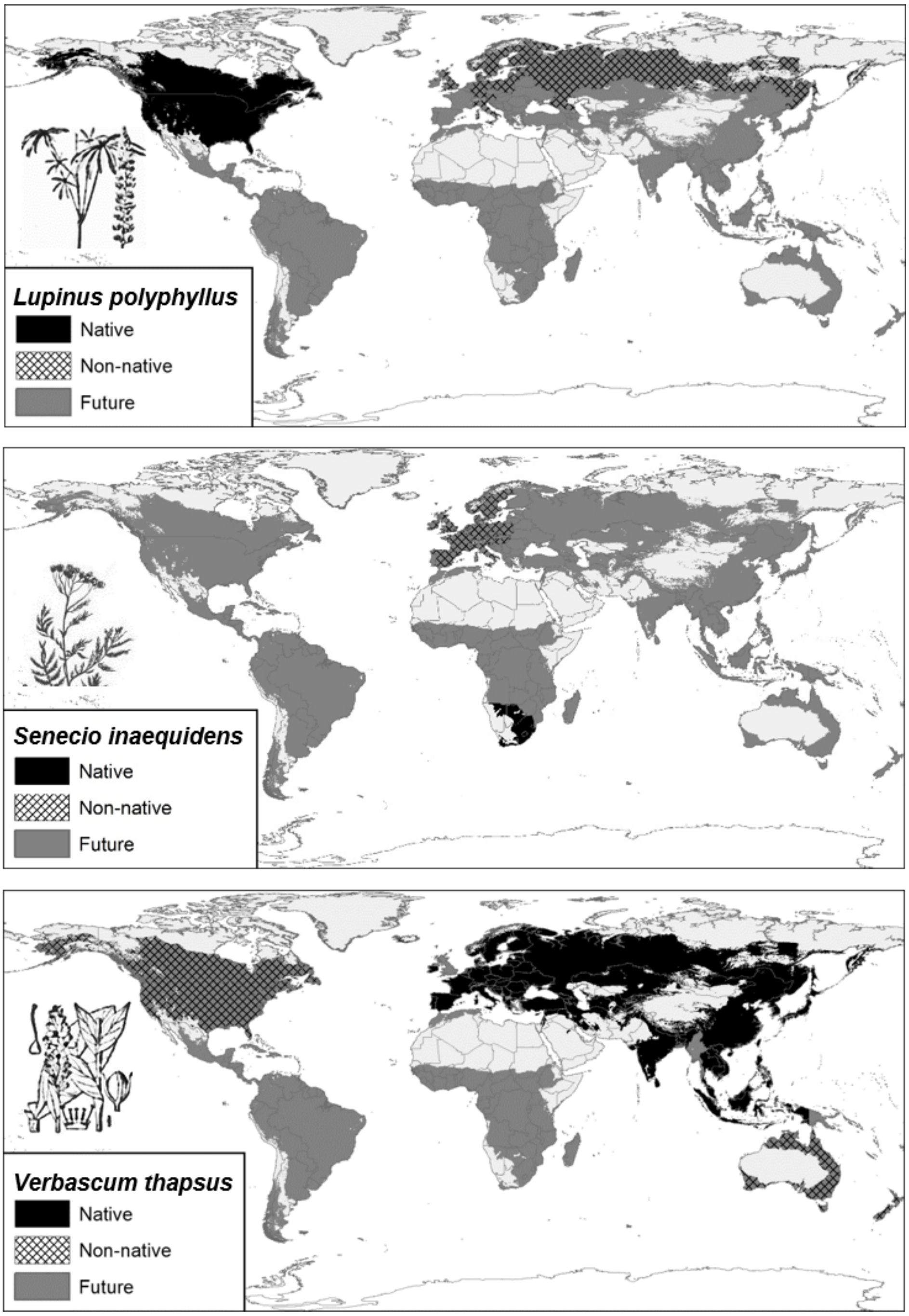
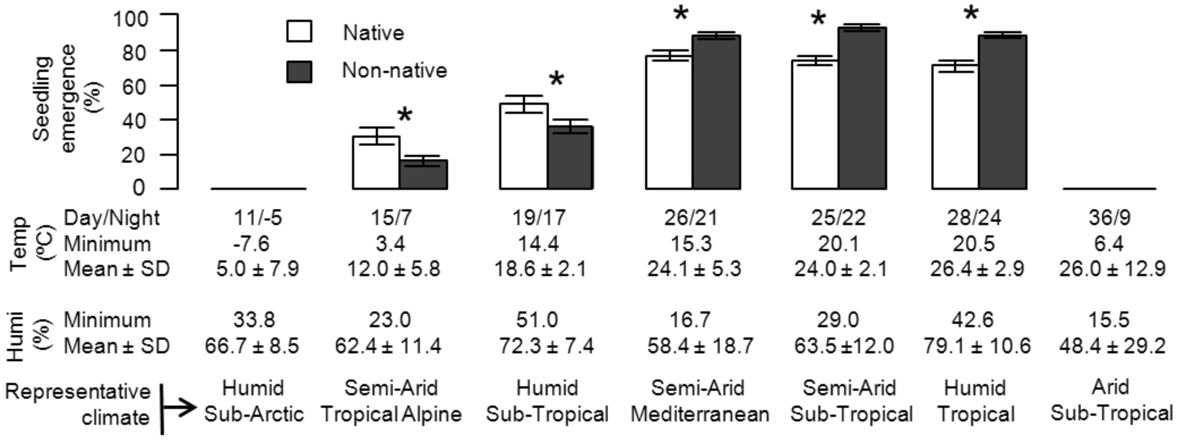


Fig. S3. Global germination niche maps of three plant invaders: *L. polyphyllus, S. inaequidens* and *V. thapsus*. Within the germination niche maps, native and non-native ranges of three global invaders were marked based on country specific presence absence data (see: Ernst 1998; Sharifnia 2007; Fremstad 2010; Ansari & Daehler 2010; Lachmuth *et al.* 2010; Alba & Hufbauer 2012; Seipel *et al.* 2012, 2015). Areas marked as future niches are climatically suitable habitats according to our germination experiment.

We developed global germination niche maps based on the climatic conditions under which the three global invaders can germinate and emerge. As germination and seedling emergence were observed at mean temperature above 5°C, we first selected all global areas which comply with this requirement. Precipitation and length of growing season are two other important abiotic factors for germination and seedling emergence in natural conditions. We followed the growing season criterion (mean monthly precipitation ≥ 2 x mean monthly temperature) to estimate how precipitation affects seedling emergence and germination. Mean monthly temperature and precipitation data were retrieved from the Worldclim database at a resolution of 2.5 arc-minutes, reference period 1959-2000 (Hijmans *et al.* 2005). Germination niche maps were produced to visualize climatic regions suitable for germination and establishment of the three invader species across the globe. All three global invader species need a minimum of four months growing seasons to germinate, establish, and produce viable seeds (Gross & Werner 1978; Ernst 1998; Elliott *et al.* 2011). Thus, we marked such areas in the global map where the above-mentioned temperature and precipitation conditions exist at least for four months. Finally, we crosschecked the global germination niche map to see whether it includes all areas of current distribution of the three global invaders. Afterwards species-specific niche maps for germination of the three global invaders were prepared by marking their respective native range and non-native range (country wise, within the projected germination niche) while the rest was indicated as future niche.

The global germination niche maps suggest that *L. polyphyllus*, *S. inaequidens*, and *V. thapsus* are able to germinate and emerge in places outside their current distributions. In general, warm and semi-arid to humid climates, such as tropical, sub-tropical, Mediterranean, and temperate eco-zones are vulnerable to the crucial first steps of invasion success by these three global invaders. However, micro-climatic conditions experienced by the seeds of the present study can be different from prevailing macro-climates in natural conditions. It is evident that macro-climate limits performance of invasive plants at later life stages (Alba & Hufbauer 2012; Hou *et al.* 2014). In addition, range predictions are difficult due to many factors such as climate, plant traits, local adaptation etc. as they are potentially influencing future ranges of species (Welk, 2004). This might explain why the predicted germination niches of these three species are larger than actual distributions of their later life stage, at least in their native range. Our results indicate that the Humid Sub-Arctic region may not be vulnerable to the establishment of the three invasive species due to the shorter (two months) growing season. The two month growing season can provide window only for germination and seedling emergence as temperatures remain above 5 °C but no time for flowering and seed production since the invaders require around four months of growing seasons to reach the seed production stage. In addition, the Arid Sub-Tropic eco-zone may also not be vulnerable to the establishment of the three invader species due to year round low humidity weather condition.



		Humid Sub-Arctic	Semi-Arid Tropical Alpine	Humid Sub-Tropical	Semi-Arid Mediterranean	Semi-Arid Sub-Tropical	Humid Tropical	Arid Sub-Tropical
Temp (°C)	Day/Night	11/-5	15/7	19/17	26/21	25/22	28/24	36/9
	Minimum	-7.6	3.4	14.4	15.3	20.1	20.5	6.4
	Mean ± SD	5.0 ± 7.9	12.0 ± 5.8	18.6 ± 2.1	24.1 ± 5.3	24.0 ± 2.1	26.4 ± 2.9	26.0 ± 12.9
Humi (%)	Minimum	33.8	23.0	51.0	16.7	29.0	42.6	15.5
	Mean ± SD	66.7 ± 8.5	62.4 ± 11.4	72.3 ± 7.4	58.4 ± 18.7	63.5 ±12.0	79.1 ± 10.6	48.4 ± 29.2
Representative climate	→	Humid Sub-Arctic	Semi-Arid Tropical Alpine	Humid Sub-Tropical	Semi-Arid Mediterranean	Semi-Arid Sub-Tropical	Humid Tropical	Arid Sub-Tropical

Fig. S4. Seedling emergence of *V. thapsus* populations (native vs. non-native) under seven experimental climates. Mean values and standard errors of seedling emergence over six weeks are shown in the figure. Significant differences between native vs. non-native populations were indicated by asterisk ($P < 0.05$). Note: “Temp” = Temperature (°C); “Humi” = Humidity (H %).

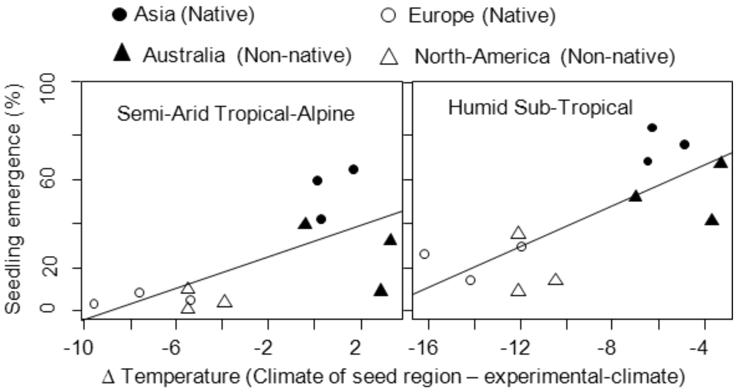


Fig. S5. Seedling emergence of *V. thapsus* populations under various temperature shifts (differences in mean temperature of climate of seed source region vs. experimental-climate).

References of supporting information

Alba C., Hufbauer R. (2012) Exploring the potential for climatic factors, herbivory, and co-occurring vegetation to shape performance in native and introduced populations of *Verbascum thapsus*. Biological Invasions **14**:2505–2518.

Ansari S., Daehler C.C. (2010) Life history variation in a temperate plant invader, *Verbascum thapsus* along a tropical elevational gradient in Hawaii. Biological Invasions **12**:4033–4047.

Elliott C.W., Fischer D.G., LeRoy C.J. (2011) Germination of three native Lupinus species in response to temperature. Northwest Science **85**:403–410.

Ernst W.H.O. (1998) Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in the Netherlands: from wool alien to railway and road alien. Acta Botanica Neerlandica **47**:131–151.

Fremstad E. (2010) NOBANIS – invasive alien species fact sheet *Lupinus polyphyllus*. Online Database of the European Network on Invasive Alien Species – NOBANIS:1–11.

Gross K.L., Werner P.A. (1978) The biology of Canadian weeds. 28. *Verbascum thapsus* L. and *V. blattaria* L. Can J Plant Sci **58**:401–413.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**:1965–1978.

Hou Q.-Q., Chen B.-M., Peng S.-L., Chen L.-Y. (2014) Effects of extreme temperature on seedling establishment of nonnative invasive plants. Biological Invasions 16:2049–2061.

Lachmuth S., Durka W., Schurr F.M. (2010) The making of a rapid plant invader: genetic diversity and differentiation in the native and invaded range of *Senecio inaequidens*. Molecular ecology **19**:3952–3967.

Oliver, J.E., 2005. Encyclopedia of World Climatology, Encyclopedia of Earth Sciences Series, Springer Science & Business Media, ISBN 9781402032646.

Sharifnia F. (2007) Notes on the distribution and taxonomy of Verbascum in Iran. Iran Journ Bot **13**:30–32.

Seipel T., Alexander J.M., Daehler C.C., Rew L.J., Edwards P.J., Dar P.A., McDougall K., Naylor B., Parks C., Pollnac F.W., Reshi Z.A., Schroder M., Kueffer C. (2015) Performance of the herb *Verbascum thapsus* along environmental gradients in its native and non-native ranges. Journal of Biogeography **42**:132–143.

Seipel T., Kueffer C., Rew L.J., Daehler C.C., Pauchard A., Naylor B.J., Alexander J.M., Edwards P.J., Parks C.G., Arevalo J.R., Cavieres L.A., Dietz H., Jakobs G., McDougall K., Otto R., Walsh N. (2012) Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. Global Ecology and Biogeography **21**:236–246.

Welk E., 2004. Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: Purple loosestrife (*Lythrum salicaria*) in North America. Ecological Modelling **179**:551-567.

10.2 Manuscript 2

plant biology

Plant Biology ISSN 1435-8603

RESEARCH PAPER

Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters

V. M. S. Vetter[1,2], J. Walter[1,3], P. A. Wilfahrt[1], C. Buhk[4], M. Braun[5], S. Clemens[5], E. Dinkel[6], M. Dubbert[6,7], A. Schramm[6], F. Wegener[6,7], C. Werner[6,7] & A. Jentsch[1]

1 Disturbance Ecology, BayCEER, University of Bayreuth, Bayreuth, Germany
2 Biogeography, BayCEER, University of Bayreuth, Bayreuth, Germany
3 Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany
4 Geoecology/Physical Geography, Institute for Environmental Science, University of Landau, Landau, Germany
5 Plant Physiology, BayCEER, University of Bayreuth, Bayreuth, Germany
6 BayCEER, University of Bayreuth, Bayreuth, Germany
7 Ecosystem Physiology, University of Freiburg, Freiburg, Germany

Keywords
Demographic dynamics; disturbance; ecological novelty; environmental change; flooding; habitat filtering; pulsed resources.

Correspondence
V. M. S. Vetter, Disturbance Ecology, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany.
E-mail: vanessa.vetter@uni-bayreuth.de

Editor
D. Byers

Received: 7 August 2018;
Accepted: 16 March 2019

doi:10.1111/plb.12987

ABSTRACT

- Successful alien plant invasion is influenced by both climate change and plant–plant interactions. We estimate the single and interactive effects of competition and extreme weather events on the performance of the global legume invader *Lupinus polyphyllus* (Lindl.).
- In three experimental studies we assessed (i) the stress tolerance of seedling and adult *L. polyphyllus* plants against extreme weather events (drought, fluctuating precipitation, late frost), (ii) the competitive effects of *L. polyphyllus* on native grassland species and *vice versa*, and (iii) the interactive effects of extreme weather events and competition on the performance of *L. polyphyllus*.
- Drought reduced growth and led to early senescence of *L. polyphyllus* but did not reduce adult survival. Fluctuating precipitation events and late frost reduced the length of inflorescences. Under control conditions, interspecific competition reduced photosynthetic activity and growth of *L. polyphyllus*. When subjected to competition during drought, *L. polyphyllus* conserved water while simultaneously maintaining high assimilation rates, demonstrating increased water use efficiency. Meanwhile, native species had reduced performance under drought.
- In summary, the invader gained an advantage under drought conditions through a smaller reduction in performance relative to its native competitors but was competitively inferior under control conditions. This provides evidence for a possible invasion window for this species. While regions of high elevation or latitude with regular severe late frost events might remain inaccessible for *L. polyphyllus,* further spread across Europe seems probable as the predicted increase in drought events may favour this non-native legume over native species.

INTRODUCTION

The establishment and spread of invasive species in their non-native ranges can alter ecosystem functions related to species diversity and abiotic processes (Sousa *et al.* 2011; Strayer 2012). However, their invasiveness is limited by their ability to establish populations while facing restraints of biotic and abiotic filters (Tilman 2004). Often, ecological research is temporally limited and examines static species responses, or ‘snapshots’, to environmental changes. As species must cope with temporal fluctuations in resource pools, research relying on such snapshots of a species’ life cycle may misjudge critical temporal dynamics (Ibanez *et al.* 2014). Moreover, the interaction of how abiotic filters such as extreme weather events (Seneviratne *et al.* 2012; Dai 2013; IPCC 2014) will alter biotic interactions like competition is little studied (Grant *et al.* 2014). The importance of understanding these dynamics is particularly relevant because climate change may further magnify the severity of these interactions, especially at the early establishment stage of species, which in turn will influence rates of spread. When combined into a holistic framework, examining multiple demographic stages (snapshots) under different biotic and abiotic conditions within and across multiple experiments can help to understand complex demographic dynamics (Ibanez *et al.* 2014) as well as interactions among drivers (Bradley *et al.* 2010).

Extreme weather events can facilitate the invasion processes by offering windows of opportunity during reduced community stability (Jentsch *et al.* 2007; Kreyling *et al.* 2008; Diez *et al.* 2012). Extreme events can affect plant invasions in two ways: (i) *via* pulsed resource changes, such as when drought and frost events reduce resource use of native species directly and indirectly through a decline in the overall or relative abundance of the native plant community (Kreyling *et al.* 2008; Diez *et al.*

2012; Caldeira *et al.* 2015); or (ii) *via* gradually fluctuating resources, such as moisture due to higher seasonal variation in precipitation (Davis *et al.* 2000). The probability and magnitude of extreme weather events, such as drought and heavy rainfall, are likely to increase in Europe as a result of climate change (IPCC 2014). Fluctuating precipitation, a short drought event followed by heavy rainfall, can be more stressful than a single extreme drought due to a hysteresis effect and opposing acclimatisation strategies (Gutschick & BassiriRad 2003). Similarly, increased temperature variation at key phenological stages may result in warmer winters accelerating plant emergence, thus increasing the susceptibility of plants to late frost events (Inouye 2008; Kreyling 2010; Kodra *et al.* 2011).

The globally invasive neophyte *Lupinus polyphyllus* (Lindl. 1827) is a leguminous, non-native species in Central Europe potentially benefitting from climate change (Fremstad 2010; Lauterbach & Nehring 2013). It has a high rate of reproduction and dispersal, and tends to monopolise resources (Lauterbach & Nehring 2013). However, there is still a crucial knowledge gap of how extreme weather events might influence the future spread of *L. polyphyllus* across Europe. In its North American native range *L. polyphyllus* usually occurs in both uplands and wetlands (Beuthin 2012). Given the similarity between the climate of its native range and the climate of its current European invasive range (Fremstad 2010), extreme drought events that are uncharacteristic for Central Europe but more common in the western USA (Loik *et al.* 2004; McCabe *et al.* 2004), could provide an invasion window for *L. polyphyllus* when it is less limited than competing native species. Although the invader historically occupies cool, subalpine habitats (Beuthin 2012), alpine environments may increasingly represent a potential invasion range as the climate warms; *L. polyphyllus* is already occasionally found above 2000 m a.s.l. in the Alps (Becker *et al.* 2005). Nonetheless, late frost might still be a barrier to the altitudinal and latitudinal maxima of *L. polyphyllus*' range expansion. *Lupinus polyphyllus* is a perennial plant that has high seedling mortality followed by a more stable adult phase. This is exemplified by seedlings being particularly sensitive to drought and water stress (Fenner 1987) because of their underdeveloped root system and vulnerability through transpiration (McDowell *et al.* 2008). Therefore, a bottleneck for *L. polyphyllus* establishment due to reduced water availability or cold temperatures is expected at the seedling stage.

After overcoming extrinsic processes (translocation filter and dispersal filter), the establishment of an invasive species requires overcoming abiotic and biotic filters that may suppress population growth (*sensu* Community Assembly Theory; Pearson *et al.* 2018). An important biotic filter is non-native plants being detrimental to native vegetation when they have higher competitive ability than the plants of the recipient community (Catford *et al.* 2009). So far, *L. polyphyllus* is mainly restricted to areas of high human development such as along roadways (Fremstad 2010; Lauterbach & Nehring 2013). Recently, the invader has started to decouple from this vector, spreading into new habitats without major human interference and now threatens large areas of species-rich mountain meadows (*e.g.* Volz 2003; Otte & Maul 2005; Hejda *et al.* 2009; Thiele *et al.* 2010). Thus, it is currently unclear whether and under which circumstances *L. polyphyllus* might be invasive in intact, natural resident plant communities. Competition can be measured directly (Markham & Chanway 1996; Weigelt & Jolliffe 2003) but also indirectly by monitoring ecophysiology of species, such as gas exchange, maintenance of photosynthetic active tissue and growth rates (Reich 2014), in the presence or absence of competing plants. Climate change alters the abiotic environment, which can in turn influence biotic filters. The strength of biotic interactions that an invading species experiences often differs from its native range, meaning the invasion process can be facilitated or hindered by the recipient community. Consequently, testing multiple filters independently and interactively through time provides critical insights into the dynamics of invasive species (Heckman *et al.* 2017).

Here, we combine the results of three experimental studies to demonstrate how abiotic and biotic drivers combine to influence an invasion window at multiple life stages of a non-native species. We use the globally invasive species, *L. polyphyllus*, in combination with two dominant Central European grassland species to assess: (i) stress tolerance to extreme weather events of seedling and adult *L. polyphyllus* plants, (ii) the interspecific competitive ability of *L. polyphyllus versus* native grassland species, and (iii) the combined effects of future extreme weather events and competition on the performance of *L. polyphyllus*. We combine these single snapshots to estimate the future invasion potential of *L. polyphyllus* as well as plant community shifts driven by the presence of non-native species. By using this three-fold approach, we draw conclusions on how *L. polyphyllus* is affected by resident communities under changing abiotic conditions. Additionally, we disentangle abiotic and biotic drivers of performance in the invader. We hypothesised that *L. polyphyllus*: (i) is less vulnerable to extreme events in its adult stage; (ii) compensates for high juvenile mortality by maintaining high resource allocation to reproduction under stressful abiotic conditions during the adult phase; and (iii) derives a competitive advantage over two co-occurring dominant species only during stressful abiotic conditions by maintaining relatively higher physiological performance, thus providing it with an invasion window.

MATERIAL AND METHODS

Species description

Lupinus polyphyllus (*Fabaceae*) is native to western parts of the United States and Canada (Beuthin 2012) but invasive globally, including many European countries, Chile, southern Australia and New Zealand (Fremstad 2010; Jauni & Ramula 2016; Ramula & Sorvari 2017). The species was originally introduced to Europe in the 1900s as a cover crop for soil amelioration, fodder and as an ornamental plant (Fremstad 2010), but it currently represents a threat to native plant communities, and is rapidly spreading across Europe (Fremstad 2010; Thiele *et al.* 2010; Starfinger & Kowarik 2011).

Seed source region and characteristics

For all three experiments, we obtained *L. polyphyllus* seeds from the IPK Gatersleben (Leibniz-Institute for Plant Genetics and Crop Plant Research, Germany), a non-native population in Central Europe. This source population of *L. polyphyllus* is in close proximity of the town of Unterkirchnach (008°21′50″ E, 48°04′44″ N) in the Black Forest of southwest Germany. *Lupinus polyphyllus* was introduced into this region in the 1980s for soil amelioration (personal communication Dr. Tobias Kühn, department head, Lower Forest Authority: Forestry Office of the city of Villingen-Schwenningen). The area of collection is situated at approximately 800 m a.s.l., has a mean annual air temperature of 7.66 °C and mean annual precipitation of 1141 mm (Fick & Hijmans 2017).

Study site

The experimental studies were conducted at the University of Bayreuth, Germany (49°55′19″ N, 11°34′55″ E). Bayreuth′s long-term mean annual air temperature (T_{air}) is 8.2 °C; with mean annual precipitation of 724 mm (1971–2000), distributed bi-modally with two major peaks in June/July and December/January (Foken 2007, German Weather Service).

Abiotic filter experiment: Impact of extreme weather events at two life cycle stages (hypothesis (i) and (ii))

The common garden experiment was set up below a rainout shelter (11 m × 7 m in size and 3.8 m in height), which consisted of a steel frame covered with transparent polyethylene foil (thickness 0.2 mm) allowing light transmission of approximately 90% of the photosynthetically active radiation (Thiele *et al.* 2010; Kreyling *et al.* 2012). To minimise heat increase due to greenhouse effects, air was allowed to circulate through 80-cm gaps between the ground and rainout shelter. The ground was covered with black polyethylene sheets to prevent weed growth.

In May 2012, 210 freshly germinated seeds were planted in 4-l pots filled with a sandy loam substrate and watered identically until they reached their target life cycle stages of (i) 4-week-old seedlings, which had one to three secondary leaves; and (ii) 12-month-old adults defined by the onset of flower production. As soon as the targeted life cycle stage was reached, plants were randomly assigned to the treatments imposing drought, fluctuating precipitation, frost and a control (natural weather conditions). Individuals of the seedling stage were used in the 2012 growing season of the experiment, and separate individuals of the adult stage were used in the 2013 growing season of the experiment. Treatments of the adult life-cycle stage were tested with a lower number of replicates due to increased mortality during the longer growth period.

Drought and fluctuating precipitation treatments ran for 44 days (28 June 2012 to 10 August 2012; 25 May 2013 to 8 July 2013) in both life cycle stages. We watered plants in the control ($n_{seedling} = 15$, $n_{adult} = 6$) and frost treatments twice a week, 250 ml at a time (equivalent to 8.33 mm of rainfall). The fluctuating precipitation treatment ($n_{seedling} = 15$, $n_{adult} = 6$) mimicked a combination of a short-term drought event of 2 weeks duration followed by a heavy rainfall event (1000 ml/33.33 mm). This was repeated three times during the period of 44 days. This is a typical level of rain fluctuation in the mesic temperate grasslands of the common garden region (Arfin Khan *et al.* 2014). The drought treatment ($n_{seedling} = 0$, $n_{adult} = 6$) was imposed by not watering the plants for 6 weeks. Drought duration was calculated based on the statistical 1000-year recurrence of consecutive days with <1 mm precipitation, corresponding to 42 days in Germany (Jentsch *et al.* 2011).

Weather conditions during the treatment phases of 2012 and 2013 are characterised by a mean temperature of 15.9 °C and 15.4 °C, mean precipitation sum of 318.1 and 322.9 mm, mean relative humidity of 71.5% and 73.5%, respectively (data: Micrometeorological basic data from the Ecological-Botanical Gardens of the University of Bayreuth 2015).

We treated potted plants of the seedling and adult stage with a simulated late frost event with temperatures as low as −10 °C. Using a refrigerated incubator (MIR-254 from SANYO), plants were subjected to a night frost simulation from 19:00 h until 10:00 or 11:00 h on the next day. Frost treatment of the seedlings ($n_{seedling} = 10$) was conducted on 17 July 2012 and between 5 and 18 July 2013 for adults ($n_{adult} = 12$). Starting at 18:00 h, the potted plants were transferred into the refrigerated incubator. This cooled the plants gradually, and after 1 h of frost treatment the refrigerated incubator slowly heated the plants to the preceding ambient temperatures. The frost scenarios of −10, −7 and −3 °C were chosen according to the absolute minimum temperatures in the alpine zone of Austria from 1961–1990 (data: Central Institute for Meteorology and Geodynamics Austria) to simulate late frost events of different magnitudes across altitudinal and latitudinal gradients.

We recorded three growth parameters every week: plant height, leaf width (measured as the longest distance across the leaf) and number of leaves. Furthermore, we recorded three fitness parameters: reproductive investment (length of inflorescences), senescence (percentage of necrotic/damaged plant material induced by abiotic stress) and survival of the plants. Plant vigour was assessed by estimating senescence weekly (0 = no senescence; 1 = <25% senescent; 2 = 25–50% senescent; 3 = 50–75% senescent; 4 = 75–99% senescent; 5 = plant dead, 100% senescent), thus senescence serves as a measure of plant stress. Every second day, survival was assessed. We recorded dead plants, as well as the day of death. As a proxy for resource allocation to reproduction, we recorded raceme length of adult plants every week. As seeds are borne from axillary stems along the entire inflorescence, longer racemes indicate increased seed production (personal observation, but see Norris 1992; Lauri 1996; Gellesch *et al.* 2017).

Biotic filter experiment: *L. polyphyllus* in competition with native species (hypothesis (iii))

In a controlled climate chamber experiment in 2013, we compared the competitive ability of *L. polyphyllus* against two widespread, native species of the region: the legume *Trifolium pratense* (L.) and the herb *Plantago lanceolata* (L.). From the local species pool, we selected two locally frequent, perennial, native species that naturally occur together with the invader on the local target substrate (Arfin Khan *et al.* 2014). We tested both intra- and interspecific competition. The chosen native species are common competitors of *L. polyphyllus* in temperate grassland communities. Three to 4-week-old seedlings were transplanted into 5-l pots containing potting soil. To test the intra- and interspecific competitive ability, we planted pots with four individuals as either *L. polyphyllus* monocultures or two *L. polyphyllus* individuals in competition with either two *P. lanceolata* or two *T. pratense* individuals. This approach controls for confounding density effects on plant competition. The control consisted of one individual planted in one pot per species. Each approach was replicated 12 times, leading to a total of 96 pots [36 single plant pots (3 species × 12 replicates) plus

36 monocultures (3 species × 12 replicates) plus 24 interspecific competition plots]. The plants grew for 10 weeks in a climate chamber under standardised laboratory conditions of 60% relative humidity (RH) and 20 °C. Artificial light was provided from 08:00 h until 18:00 h, with a photosynthetic photon flux density (PPFD) of 300–500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Pots were watered and rotated every second day to ensure equal light conditions.

After the end of the biotic filter experiment, we harvested the entire plant and separately measured the dry weight of leaves, shoots and roots. Aboveground biomass was calculated by summing the dry weight of leaves and shoots of the respective plant species. We calculated the relative neighbour effect (RNE) according to Markham & Chanway (1996) to quantify the competition effect upon the performance parameters: aboveground biomass and plant height (Weigelt & Jolliffe 2003).

$$\mathrm{RNE} = \frac{P_{\mathrm{control}} - P_{\mathrm{mix}}}{X}$$

with $X = P_{\mathrm{control}}$ if $P_{\mathrm{control}} > P_{\mathrm{mix}}$ and $X = P_{\mathrm{mix}}$ if $P_{\mathrm{mix}} > P_{\mathrm{control}}$

P is the performance per plant, while the subscripts 'control' and 'mix' designate a plant growing alone or in a mixture. P_{mix} plants were either growing in monocultures (intraspecific competition; for results see Appendix S1) or in mixture with native species (interspecific competition). Pairs for RNE calculation were selected on the basis of the randomly assigned plant numbers. RNE values range between −1 (maximum facilitation), 0 (no interaction) and +1 (maximum competition).

Leaf gas exchange parameters (transpiration rate, assimilation rate, stomatal conductance, internal CO_2 mole fraction, inherent water use efficiency (iWUE) and water potential) of *L. poyphyllus* and the competitor species were measured once a week using a portable gas exchange system (GSF-3100-C; Walz, Effeltrich, Germany) with the measuring head 3010-S. Measurements were conducted in the plant growth chamber at 23 °C cuvette temperature, 60% RH and 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD. Leaf water potentials were measured with a Scholander-type pressure chamber (PMS Instrument, Albany, OR, USA; Scholander *et al.* 1965).

Similar to the abiotic filter experiment, we again recorded plant height, leaf width, number of leaves, senescence and survival.

Combined filter experiment: *L. polyphyllus* in interspecific competition under extreme drought (hypothesis (iii))

The field experiment was set up in a natural, extensively managed grassland in the Ecological-Botanical Gardens of the University Bayreuth (Jentsch 2013). The grassland is mown twice per year in July and September and grows on a sandy loam soil. In May 2013, five *L. polyphyllus* seedlings were planted into matrix vegetation, yielding si × 0.5 m × 0.5 m plots each. Three of these plots were situated under three different rain-out shelters, 6 m × 7.5 m in size, simulating an extreme drought of 54 days from 29 May to 21 July 2013. Drought duration was calculated based on statistical 1000-year recurrence of consecutive days with <2.5 mm precipitation, which corresponds to 54 days in Germany (Jentsch 2013). The three control plots remained under natural conditions, except for an irrigation of 22.4 mm water once on 16 July to compensate for a lack of natural rainfall compared to the long-term average. We tested 30 planted *L. polyphyllus* individuals against the performance of two native species (30 *P. lanceolata* and 30 *T. pratense* individuals) that were already present in the matrix vegetation. The experiment ran for 8 weeks, starting on 29 May 2013. Drought was terminated by an artificial irrigation of 10 mm on 23 July (Jentsch 2013).

After the drought event, 20 leaf samples (one leaf randomly sub-sampled from ten plants in the drought treatment and ten plants in the control treatment) were taken to analyse the metabolite profiles of the drought-exposed plants *versus* control plants using gas chromatography mass spectrometry (GC-MS) to determine the content of osmoprotectants. Accumulation of compatible solutes represents a widespread strategy to acclimate to water deficit stress caused by drought. Methods, results and discussion of the GC-MS analyses can be found in Appendix S2.

Analogous to the biotic filter experiment, we again recorded gas exchange parameters and leaf water potentials of the study plants. Gas exchange measurements were conducted in the field (1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD) at natural levels of CO_2, soil moisture and temperature. We measured predawn leaf water potentials between 13:30 h and 16:00 h, and midday leaf water potentials between 11:00 h and 15:00 h.

Reproductive investment was not measured in the biotic and combined filter experiment as plants did not reach the adult stage within the experimental phase.

Statistical analyses

Analyses were done using the statistical software R 3.1.3 (R Core Team 2014). For the abiotic filter experiment, we tested the survival of the plants after 6 weeks of drought and after frost of varying magnitudes using logit regression models for binary data in combination with a one-way ANOVA to test dependence of survivorship upon treatment for each separate life cycle stage.

For the analysis of all three experiments, we used either linear models or generalised linear models (GLM), depending on whether the data were normally distributed, to test the treatment effects on senescence, growth, reproduction and gas exchange parameters, as well as water potentials. The experiments were tested individually. We accounted for non-normality by fitting the distribution of the data *via* the GLM family (Gaussian link 'identity'; gamma link 'inverse' or Poisson link 'log'). Pair-wise differences in the response parameters between the single treatments were analysed with an ANOVA and *post-hoc* Tukey test, or, in the case of non-normality and heterogeneous variances, with heteroscedasticity-consistent covariance estimations (Zeileis 2004; Hothorn *et al.* 2008).

The effect of treatment on the size of the inflorescence was tested using data from the final week of treatment. The normal distribution of the residuals as well as the homogeneity of variance was tested graphically (Crawley 2007). We used likelihood ratio tests in combination with a Wald Test for Model Coefficients (Lesnoff & Lancelot 2012) for validation of all models (Zuur *et al.* 2013).

RESULTS

Abiotic filter experiment: Impact of extreme weather events at two life cycle stages (hypothesis (i) and (ii))

Fluctuating precipitation did not affect *L. polyphyllus* survival in any of the life-cycle stages. The 6-week drought treatment significantly reduced the survival probability of seedlings (−28.6%) but not adults (Fig. 1). At the seedling stage in August 2012, after 6 weeks of drought, growth of drought-treated plants was significantly reduced relative to control plants, as measured by plant height (−44%), number of leaves (−37%) and leaf diameter (−42%). Plants of the fluctuating precipitation treatment (precip.; Fig. 2a) did not significantly differ from control plants (Appendix S1 in Table A.2). Senescence of drought-treated plants increased relative to both fluctuating precipitation (+45.4%) and control conditions (+46.6%; Fig. 2a, Appendix S1 in Table A.1).

Adult drought-treated plants in the second year (2013) showed a 50% increase in senescence and completely dropped all leaves (100% reduction relative to controls) in July after 6 weeks of drought, although the natural conditions in that year were moderately but slightly wetter compared to the previous year. Adult plant height, however, was not affected by drought (Fig. 2b, Appendix S1 in Table A.2). From 3 July onwards, leaves of the adult plants desiccated and did not rejuvenate after the end of the drought (8 July 2013). The fluctuating precipitation treatment increased senescence by 36.7% in adult plants while growth parameters were not significantly affected (Fig. 2b, Appendix S1 in Table A.2). Fluctuating precipitation significantly reduced length of inflorescences of adult plants (−35%; Fig. 3). Drought had no significant effect on the length of inflorescences.

Late frost effects of −10 °C caused significant reductions in survival of all life cycle stages (seedling: −100%, adult: −50%; Fig. 1), with the most pronounced effect at the seedling stage (no survivors). The survival of adult *L. polyphyllus* was not affected by late frost temperatures of −3 °C. Late frost significantly reduced length of inflorescence (−10 °C: −63.9%, −7 °C: −41%; −3 °C: 64.3%; Fig. 3).

Biotic filter experiment: *L. polyphyllus* in competition with native species (hypothesis (iii))

All plants survived the competition treatment. All species showed clear interspecific competition effects, as evidenced by significantly positive mean RNE values of aboveground biomass and plant height (Fig. 4a and b, Appendix S1 in Table A.3). However, the only significant difference in competitive strength between any pair of species was *L. polyphyllus* growing in interspecific competition with *T. pratense*. Here, there was a significant reduction in height of *L. polyphyllus* when grown in competition with *T. pratense* compared with *L. polyphyllus* growing in monoculture ($P_{\text{height}} < 0.01$). Root biomass of all species showed clear interspecific competition effects, as evidenced by their significantly positive RNE values (Fig. 4c). However, while root biomass of the native species indicated competitive suppression in the presence of the invader (Appendix S1 in Table A.3), *L. polyphyllus* roots were significantly less adversely affected by competition of native species (Fig. 4c). This suggests a relative competitive advantage for *L. polyphyllus*.

Under interspecific competition, assimilation rates ($P < 0.001$; Fig. 5a), transpiration rates and stomatal conductance (Appendix S1 in Table A.4) of *L. polyphyllus* were significantly lower than those of both native species. In the presence of native competitors, the invader maintained high water potentials, which were significantly less negative compared to *T. pratense* ($P < 0.001$) but statistically indistinguishable from *P. lanceolata* ($P = 0.998$; Fig. 5b). Competition did not reduce the assimilation rates of the native species *P. lanceolata* and *T. pratense* (Fig. 5a). In contrast, interspecific competition significantly reduced the assimilation rate of *L. polyphyllus*, an effect not observed under intraspecific competition (Fig. 5a). Leaf water potential in *P. lanceolata* increased when growing with the invader (Fig. 5b), particularly compared to the effects of a single *P. lanceolata* individual growing alone. Competition had no significant effect on the water potentials of *L. polyphyllus* and *T. pratense*.

The native species grew significantly taller when growing under intraspecific competition than when growing under interspecific competition with the invader. However, natives showed significantly reduced root biomass when growing in interspecific competition with the invader, suggesting differing resource allocation strategies depending on the identity of the competitor. *L. polyphyllus* showed no significant difference in aboveground biomass, plant height or root biomass under with intra- or interspecific competition (Appendix S1 in Figure A4).

Combined filter experiment: *L. polyphyllus* in interspecific competition under extreme drought (hypothesis (iii))

All plants survived the combined competition and drought treatment in a natural grassland site, conducted during 6 weeks

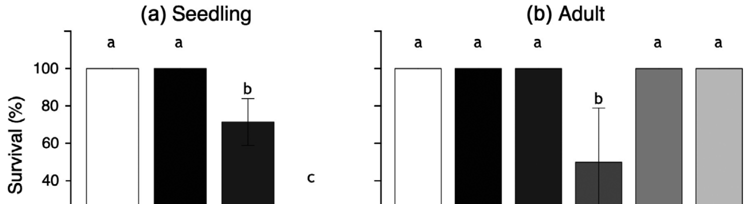


Fig. 1. Proportion of surviving *L. polyphyllus* individuals in the abiotic filter experiment under differing water regimes and late frost intensity along a gradient of growth over two field seasons (2012–2013). Data shown are the ± SE. Small letters represent significant differences between treatments at the significance level of 5% (Tukey HSD test). Precip., fluctuating precipitation.

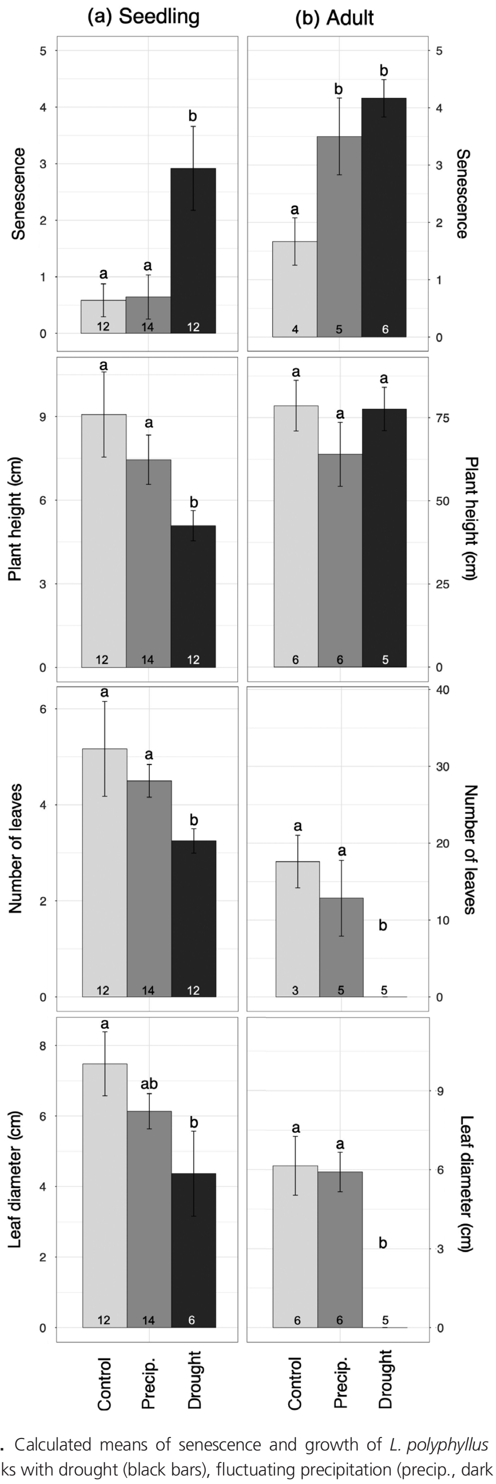


Fig. 2. Calculated means of senescence and growth of *L. polyphyllus* after 6 weeks with drought (black bars), fluctuating precipitation (precip., dark grey bars) or control (light grey bars) in the abiotic filter experiment. We used linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3) to check for differences between treatments at a significance level of 5%. Letters indicate a significant difference between treatments.

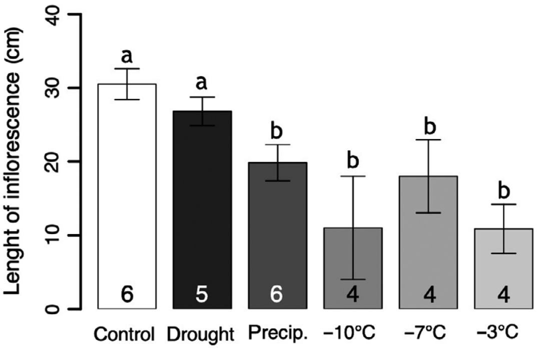


Fig. 3. Length of inflorescence of adult *L. polyphyllus* under different weather extremes, *e.g.* drought and fluctuating precipitation (precip.), as well as late frost at three intensity levels of the abiotic filter experiment. Letters represent significant differences in length of inflorescence between observed treatments at the significance level of 5% (Tukey HSD test).

in late spring and early summer 2013. Species, but not treatment effects or their interaction, had a significant effect upon assimilation rate ($P < 0.001$) and midday water potential ($P < 0.001$). Under natural conditions, native and invasive species showed similar assimilation rates (Fig. 6a). However, after 54 days of drought treatment at the end of July, the assimilation rates of *L. polyphyllus* were still significantly higher than those of the native competitors (Fig. 6a, Appendix S1 in Table A.5). Drought showed a trend in reducing the assimilation rates of the native species – which were substantially lower than under the controlled climate chamber conditions in the previous experiment – while *L. polyphyllus* was able to maintain high assimilation rates; however, these effects were not statistically significant. Predawn and midday water potentials of native plants in the control treatment were significantly more negative compared to those of *L. polyphyllus*; these differences disappeared under drought treatment (Fig. 6b and c).

DISCUSSION

Our results provide evidence that *L. polyphyllus* is co-limited by abiotic and biotic filters, but extreme climate events might negatively affect native species more strongly than the invader, thus reducing biotic resistance and opening a potential invasion window (Diez *et al.* 2012). In particular, *L. polyphyllus* was sensitive towards extreme weather events at both life stages, but seedlings were more strongly affected, pointing to an abiotic filter at this life stage (Melbourne *et al.* 2007; Catford *et al.* 2009). *Lupinus polyphyllus* showed reduced growth in competition with two native species under typical climate conditions, and these species were relatively less constrained by competitive interactions with *L. polyphyllus*, pointing to a biotic filter effect (*sensu* biotic resistance hypothesis; Levine *et al.* 2004). When combining abiotic (drought) and biotic (competition) filters, however, we found that *L. polyphyllus* was less limited than native species, pointing to a potential invasion window (*sensu* Diez *et al.* 2012) for establishment and population growth. Thus, our results showed that testing single filters/single invasion theories in isolation might lead to misleading conclusions concerning the ability of exotic species to establish themselves

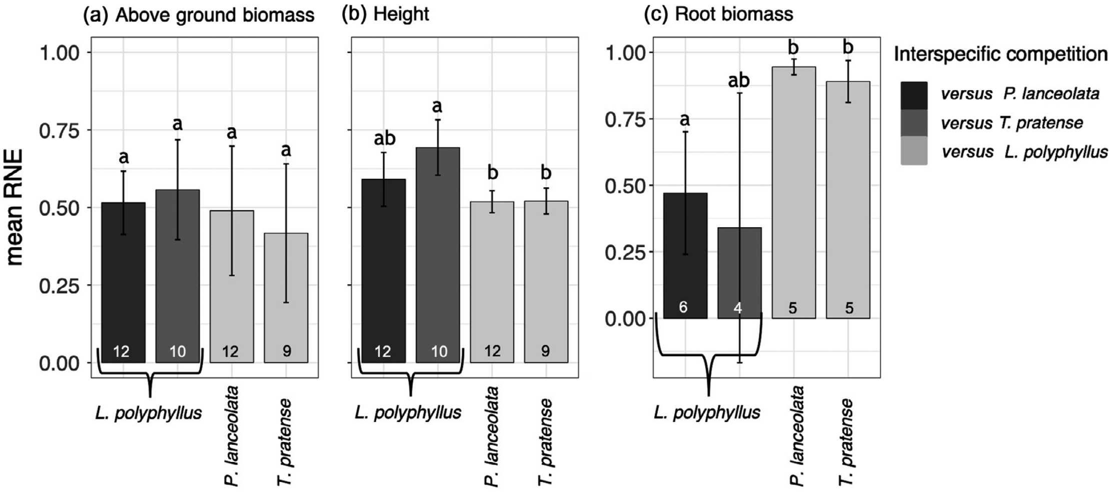


Fig. 4. Comparison of the relative neighbour effect (RNE) of *L. polyphyllus versus P. lanceolata* and *T. pratense* in controlled conditions of the biotic filter experiment. The target species is shown on the *x*-axis, while the respective interspecific competitior is indicated by the colour of the bars. RNE values of +1 indicate maximum competition, while values of −1 indicate maximum facilitation. No interaction is indicated by RNE values close to zero. Small letters represent significant differences between the observed species growing in interspecific competition. All differences are marked at the significance level of 5% using linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3).

in the recipient community (Tilman 2004; Ibanez *et al.* 2014; Pearson *et al.* 2018). Additionally, our results showed that a change in one factor, *e.g.* climate change altering the abiotic filter, can lead to changes in how those filters act together to shape species interactions (Pearson *et al.* 2018), resulting in synergistic effects of climate extremes and invasive species on physiological processes (Caldeira *et al.* 2015). Collectively, our results indicate that drier future climate conditions (IPCC 2014) could possibly lead to a slowing of the *L. polyphyllus* invasion process at the dispersal and establishment stage, while simultaneously providing advantages for extant populations relative to their native neighbours.

Abiotic filter experiment: Impact of extreme weather events at two life-cycle stages (hypothesis (i) and (ii))

Extreme abiotic events can reduce performance of *L. polyphyllus*, especially at the seedling stage. Our predictions were mostly confirmed by our abiotic filter experiment, as *L. polyphyllus* was sensitive to drought and extreme late frost, and seedlings were more vulnerable than the adult stage. Interestingly, adult invader plants survived the extreme drought event despite severe signs of stress. This shows a high potential for resistance to drought extremes (Bechtold 2018). Length of inflorescences did not change due to drought, suggesting that reproduction might be maintained even under increased levels of abiotic stress (Gellesch *et al.* 2017). These findings point to a possible fitness homeostasis in the invader, which would be conducive to the invasion success of *L. polyphyllus* by maintaining high reproductive output even under a dry future climate (Richards *et al.* 2006). While our experiment did not measure reproductive fitness *per se* of any species, these results nonetheless point to a potentially important avenue of research for understanding the invasion potential of *L. polyphyllus*.

Growth reduction of seedlings during drought has been linked to reallocation of resources to root production (Mokany *et al.* 2006). However, we did not see signs of regeneration of seedlings following the drought, suggesting insufficient carbon allocation to allow regrowth. Overall, this potential bottleneck of population growth in *L. polyphyllus* could potentially be mitigated given that mature plants were able to maintain allocation of resources to reproduction during the drought.

Adult *L. polyphyllus* seemed to acclimate to an extreme drought by reducing growth and leaf area while maintaining reproductive investments; a phenomenon which was not visible under fluctuating precipitation. In contrast to the severe drought, several short drought events might have had an additive effect, leading to reduced reproductive biomass at the end of the growing season (early senescence and reduced inflorescence length).

Severe frost increased mortality, especially in the seedling stage. This is in accordance with the findings of Bourion *et al.* (2003), stating that frost tolerance of pea seedlings is mainly dependent upon cold acclimation. When cold acclimatisation, *via* low non-freezing temperatures and light intensities, was prevented, even winter pea seedlings showed a high frost sensitivity (Bourion *et al.* 2003). However, Maqbool *et al.* (2010) state that legume plants are most frost-sensitive after initiation of the inflorescence. Sensitivity of *L. polyphyllus* during the flowering stage was not observed in terms of mortality, but rather *via* severe limitations for allocation of resources to reproduction in that year. This could indicate a potential range limit for the species, as sink populations could be maintained where frequent late frosts occur, although the species could struggle to reproduce locally.

Biotic filter experiment: *L. polyphyllus* in competition with native species (hypothesis (iii))

Our results are in line with the biotic resistance hypothesis (Levine *et al.* 2004; Parker & Hay 2005; Catford *et al.* 2009) that suggests competition with native species leads to

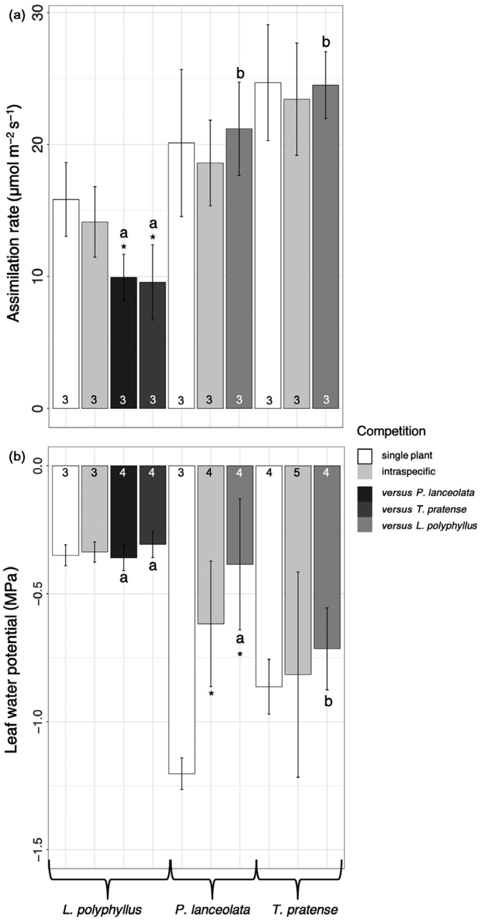


Fig. 5. Assimilation rate and leaf water potential of *L. polyphyllus, P. lanceolata* and *T. pratense* growing alone, in intraspecific or interspecific competition under controlled conditions of the biotic filter experiment. The target species is shown on the *x*-axis, while the competitive relationship and the respective interspecific competitior is indicated by the colour of the bars. We used linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3) to check for differences between treatments at the significance level of 5%. Small letters represent significant differences between interspecific competition treatments of all species, while stars indicate significant differences from the control (single plant growing alone in one pot).

community resistance against invasion. Both native plants and the invader, *L. polyphyllus*, were limited by competition. *Lupinus polyphyllus* seedlings did not show a superior competitive ability over native plant species. Rather, competition reduced the ecophysiological performance of the invader while the photosynthetic efficiency of the native plants remained higher than those of the invader. *Lupinus polyphyllus* suffered from competition with other species, showing lower primary production, while the primary production of the native species was equally or less adversely affected by interspecific competition with the invader. This might be due to the nitrogen fixation ability of *L. polyphyllus*, which increases the resource availability in the top soil of invaded ecosystems (Falinski 1998; Fremstad 2010; Lauterbach & Nehring 2013). Declines in native root biomass in the presence of the invader might indicate a shift in resource allocation in the native species, as increased nitrogen availability can cause competition to shift from belowground to aboveground biomass production (Hautier *et al.* 2009). While plant height of *L. polyphyllus* decreased due to competition, the roots of the invader were less affected compared to those of the native species. As long as the rhizomes of *L. polyphyllus* are not impacted by competition, its survivability and competitiveness remain high due to resprouting capacity and vegetative dispersal by polycormons of up to 0.2 m·year^{-1} (Volz & Otte 2001; Volz 2003). In competition with other species *L. polyphyllus* saved water and down-regulated primary production, resulting in reduced biomass production. Previous work on *L. polyphyllus* has demonstrated that native vegetation is unable to competitively exclude adult plants (Volz 2003; Valtonen *et al.* 2006; Thiele *et al.* 2010; Lauterbach & Nehring 2013) but we demonstrate here that young *L. polyphyllus* plants are still susceptible to asymmetric competition from established native vegetation.

As invasion is likely to be limited by the strongest competitors (May & Arthur 1972; Case 1990; Maron & Vilà 2001; Levine *et al.* 2004), we tested *L. polyphyllus* performance against two dominant grassland species of Central Europe. Both chosen native species, *P. lanceolata* and *T. pratense*, are themselves cosmopolitan weeds, which are invasive in the native regions of *L. polyphyllus* (Van der Aart & Vulto 1992; St. John & Ogle 2008; Hanley 2012). The similarity of preferred habitats around the world strengthens the likelihood that these two species are important competitors for *L. polyphyllus* in our study region, although the competitive ability of other co-occurring species remains untested.

Combined filter experiment: *L. polyphyllus* in interspecific competition under extreme drought (hypothesis (iii))

In contrast to the weak competitive ability of *L. polyphyllus* under control conditions, the performance of the invader improved under drought conditions relative to the interacting native species in a natural grassland site. After 54 days of drought, *L. polyphyllus* still showed high water use efficiency relative to other species, as evidenced by a high predawn and midday water potential and superior assimilation rate in *L. polyphyllus*. The invader was most efficient at assimilation in drought conditions in July. The invader might be able to partly avoid dehydration, thus explaining *L. polyphyllus* survival despite severe signs of stress in the abiotic filter experiment (Bechtold 2018). This potentially enabled high photosynthetic rates of the invader in a period where the water potentials of the interacting native species decreased relative to their respective controls and assimilation rates of the native species decreased relative to *L polyphyllus* in drought conditions. *L. polyphyllus* seems to possess the ability to partially compensate for water stress *via* accumulation of compatible solutes to retain cell turgor (Hsiao 1973). Our data imply that *L. polyphyllus* acclimates to drought stress through the accumulation of glutamic acid (1.5-fold increase in drought-stressed leaves; Appendix S2 in Fig. B.1), a metabolite found to increase upon dehydration in *Selaginella* and the resurrection plant *Sporobolus stapfianus* (Oliver *et al.* 2011; Yobi *et al.* 2013). Consequently, *L. polyphyllus* may obtain an indirect competitive advantage

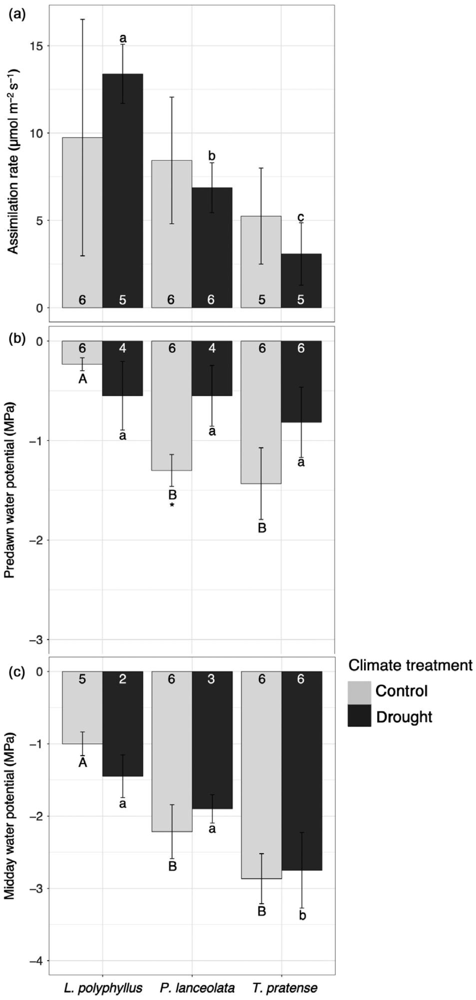


Fig. 6. Comparison of the response parameters leaf water potential and assimilation rate of *L. polyphyllus versus P. lanceolata* and *T. pratense* after 54 days of drought (21 July 2013) in the combined drought and competition filter experiment. Here, the plants grew in natural grasslands with and without rainout shelters. We used linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3) to check for differences between treatments at the significance level of 5%. Small letters represent significant differences across drought treatments of all species. Capital letters represent significant differences across the control treatment of all species. *Control plants differ significantly from drought-treated plants within one species. More detailed information on significance levels are given in Appendix S1 in Table A.5.

during periods of water stress by being less negatively impacted than its competitors. This would indicate a pathway for *L. polyphyllus* to utilise so-called 'invasion windows' (Catford *et al.* 2009; Diez *et al.* 2012), where the competitive ability of the native community is reduced by extreme abiotic stress such as drought. An 'invasion window' can be used by an invading species through superior abiotic stress tolerance (Diez *et al.* 2012), for which we found evidence in our study. Our results suggest that *L. polyphyllus* may be favoured under climate change scenarios due to superior competitive performance in simulated drought environments.

Limitation to *L. polyphyllus* invasion in the future

Across several ecosystems, it has been shown that extreme weather events can have positive and negative effects on invasive species competitiveness and performance and thus on native plant community structure and species loss (*e.g.* Bradley *et al.* 2009; Paudel *et al.* 2017, 2018; LaForgia *et al.* 2018). Invasive species do not necessarily benefit from climate change. On the contrary, previous studies have shown that if the conditions become climatically unsuitable, extreme weather events could significantly curtail the spread of non-native species and limit non-native plant abundance or prevent non-native plants from establishing and outcompeting native species (Bradley *et al.* 2009; Sorte *et al.* 2013; Laube *et al.* 2015; Paudel *et al.* 2018). Consequently, depending on the behaviour of the invasive species, extreme abiotic stress may therefore lead to an increased risk of invasion or opportunities for restoration/management (Bradley *et al.* 2009; Borgnis & Boyer 2016; Paudel *et al.* 2018). Both life cycle stages of *L. polyphyllus* suffered from extreme drought conditions. Therefore, from a purely abiotic perspective, one might conclude that *L. polyphyllus* might decline in its spread due to climate change. However *L. polyphyllus* may gain a (small) performance advantage under drought through higher survival, reproductive output and growth rates relative to its competitors, enabling the invader to outcompete native species during periods of stress (Davis *et al.* 2000; Paudel *et al.* 2018). Frost led to a critical reduction in length of the inflorescence, suggesting that *L. polyphyllus* persistence might be considerably limited by late and early frost events. Regions of high elevation or latitude with regular late frost events of at least −10 °C might remain inaccessible for the invader. Our results show that with a consistent (Kodra *et al.* 2011) or increasing magnitude (Inouye 2000) of frost events under future climate change, *L. polyphyllus* might be limited in its proliferation by late frost events, even at medium or low altitudes, due to both reduced reproductive allocation in the adult stage and reduced seedling survival. It should be noted, however, that we only used the seeds from one locality of the *L. polyphyllus* invasive range in Germany for our experiments. Thus, the frost limitation might be due to the limitations of this single population, as *L. polyphyllus* occurs up to 2900 m a.s.l. in its native range (Starfinger & Kowarik 2011), is already occasionally found above 2000 m a.s.l. in the Alps (Becker *et al.* 2005), and also occurs in Iceland and other parts of Scandinavia (Fremstad 2010; Ramula & Pihlaja 2012).

Similar to the frost treatment, fluctuating precipitation might also limit the spread of *L. polyphyllus* due to reduced survival (seedlings) and reproductive output (adults). In contrast to previous studies in which invasive species showed strong reproduction losses under drought conditions (Hild *et al.* 2001; LaForgia *et al.* 2018) *L. polyphyllus* retains its high reproductive output and is able to germinate in large areas across the world, apart from arid sub-tropical and humid sub-arctic regions (Arfin-Khan *et al.* 2018). Thus, *L. polyphyllus* appears to be a stress-tolerant species with buffered population dynamics even under extreme abiotic conditions (LaForgia *et al.* 2018; Thomson *et al.* 2018). However, given only a small advantage in the combined drought and competition experiment, it is questionable whether *L. polyphyllus* will be able to competitively exclude the native species (Cleland *et al.* 2015; Thomson *et al.* 2018).

Collectively, we showed that jointly studying abiotic and biotic filters reveals complex and interacting influences on *L. polyphyllus* performance. The single effect of drought had strong negative implications for *L. polyphyllus* aboveground biomass within our study, while the single effect of competition revealed an equal or even higher competitive ability of the native species. However, in combined drought and competition, *L. polyphyllus* showed a performance advantage over native species.

CONCLUSION

Our study revealed a higher susceptibility of *L. polyphyllus* seedlings to extreme weather events, such as drought and frost, and a relatively low competitive ability under controlled climate conditions. However, under drought, *L. polyphyllus* gained a performance advantage over native forbs, which were shown to be competitively superior under non-stressed conditions. Thus, we show that the filters driving invasion (here, abiotic and biotic characteristics) do not act in isolation but their synergistic effects may determine invasion success. Our results emphasise the importance of integrated assessments, testing multiple drivers of invasion individually and in combination. Based on our results, it is inconclusive whether the invasion of *L. polyphyllus* will be limited by a drier, future climate or whether its small performance advantage under combined drought and competition will be sufficient for it to benefit from climate change. Nonetheless, the invader demonstrates the potential to benefit from a drier climate relative to the native species. Therefore, it is advisable to monitor *L. polyphyllus* occurrences, in particular with regard to future climate scenarios, and, if necessary, to take management measures. Given the fact that *L. polyphyllus* seedlings are more susceptible to extreme weather events than adult plants, management actions might be especially effective at the seedling stage as well as shortly after extreme weather events. Snapshots at single time points of the demographic process might miss important dynamics, thus future invasion studies should combine demographic aspects with potential abiotic and biotic invasion filters.

ACKNOWLEDGEMENTS

The authors thank Prof. Dr. Thomas Foken, head of the Department for Micrometeorology of the University of Bayreuth, as well as the Bayreuth Centre of Ecology and Environmental Research (BayCEER) for the provision of climate data. We thank Kerstin Grant and all our student assistants, who helped so diligently in the data recording of the experiments. For their skillful technical assistance, we want to thank Ilse Thaufelder, Christine Pilsl and Eva Strätz. Additionally, we would also like to thank the reviewers for their thoughtful recommendations, which helped to further improve our manuscript, as well as Carmela Falzone for language editing. The combined filter experiment is part of the project SIGNAL (Jentsch 2013), which is funded by the ERA-Net BiodivERsA (http://www.biodiversa.org; Funding ID 01LC1201), with the national funders: Belgian Federal Science Policy Office (BELSPO), German Federal Ministry of Education and Research (BMBF), Bulgarian Science Fund and Ministère de l'Écologie, du Développement durable et de l'Énergie (France) as part of the 2011–2012 BiodivERsA call for research proposals. Research on extreme weather events and biotic filter experiments did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Additional results (*e.g.* mean values and significance levels, deviation from control) of the abiotic, biotic and combined filter experiments.

Appendix S2. GC-MS analysis.

REFERENCES

Arfin Khan M.A.S., Grant K., Beierkuhnlein C., Kreyling J., Jentsch A. (2014) Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland. *Plant and Soil*, **379**, 161–175.

Arfin-Khan M.A.S., Vetter V.M.S., Reshi Z.A., Dar P.A., Jentsch A. (2018) Factors influencing seedling emergence of three global invaders in greenhouses representing major eco-regions of the world (R. Bekker, Ed.). *Plant Biology*, **20**, 610–618.

Bechtold U. (2018) Plant life in extreme environments: how do you improve drought tolerance? *Frontiers in Plant Science* **9** [online] Available from http://journal.frontiersin.org/article/10.3389/fpls.2018.00543/full (accessed 7 August 2018).

Becker T., Dietz H., Billeter R., Buschmann H., Edwards P.J. (2005) Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 173–183.

Beuthin M. (2012) *Plant guide for bigleaf lupine (Lupinus polyphyllus)*. USDA-Natural Resources Conservation Service, Plant Materials Center, Corvallis, OR, USA.

Borgnis E., Boyer K.E. (2016) Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the upper San Francisco Estuary. *Estuaries and Coasts*, **39**, 707–717.

Bourion V., Lejeune-Hénaut I., Munier-Jolain N., Salon C. (2003) Cold acclimation of winter and spring peas: carbon partitioning as affected by light intensity. *European Journal of Agronomy*, **19**, 535–548.

Bradley B.A., Oppenheimer M., Wilcove D.S. (2009) Climate change and plant invasions: restoration opportunities ahead? *Global Change Biology*, **15**, 1511–1521.

Bradley B.A., Blumenthal D.M., Wilcove D.S., Ziska L.H. (2010) Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, **25**, 310–318.

Caldeira M.C., Lecomte X., David T.S., Pinto J.G., Bugalho M.N., Werner C. (2015) Synergy of extreme drought and shrub invasion reduce ecosystem functioning and resilience in water-limited climates. *Scientific Reports*, **5**, 15110.

Case T.J. (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of the United States of America*, **87**, 9610–9614.

Catford J.A., Jansson R., Nilsson C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22–40.

Central Institute for Meteorology and Geodynamics Austria. Climate normals of Austria 1961– 1990. (Zentralanstalt für Meteorologie und Geodynamik Österreich, ZAMG. Klimanormalwerte Österreich 1961–1990). Available from http://www.zamg.ac.at/cms/de/dokumente/klima/dok_klimauebersichten/klimanormalwerte-oesterreich-1961-1990/view (accessed 27 July 2015).

Cleland E.E., Esch E., McKinney J. (2015) Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. *Oikos*, **124**, 33–40.

Crawley M.J. (2007) *The R book*. Wiley, Chichester, UK.

Dai A. (2013) Increasing drought under global warming in observations and models. *Nature Climate Change*, **3**, 52–58.

Davis M.A., Grime J.P., Thompson K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

Diez J.M., D'Antonio C.M., Dukes J.S., Grosholz E.D., Olden J.D., Sorte C.J., Blumenthal D.M., Bradley B.A., Early R., Ibáñez I., Jones S.J., Lawler J.J., Miller L.P. (2012) Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment*, **10**, 249–257.

Falinski J.B. (1998) Invasive alien plants and vegetation dynamics. In: Tokarska-Guzik B., Brock J.H., Brundu G., Child L. (Eds), *Plant invasions, ecological mechanisms and human responses*. Backhuys, Leiden, The Netherlands, pp 3–21.

Fenner M. (1987) Seedlings. *New Phytologist*, **106**, 35–47.

Fick S.E., Hijmans R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas: new Climate Surfaces for Global Land Areas. *International Journal of Climatology*, **37**, 4302–4315.

Foken T. (2007) Das Klima von Bayreuth: status quo und Aufgaben für die Stadtplanung. *Standort*, **31**, 150–152.

Fremstad E. (2010) NOBANIS – Invasive Alien Species Fact Sheet – *Lupinus polyphyllus*. Available from https://www.nobanis.org/.../speciesinfo/l/lupinus-polyphyllus/lupinus-polyphyllus.pdf (accessed 24 May 2012).

Gellesch E., Arfin Khan M.A.S., Jentsch A., Beierkuhnlein C. (2017) Grassland experiments under climatic extremes: reproductive fitness versus biomass. *Environmental and Experimental Botany*, **144**, 68–75.

German Weather Service. Available from http://www.dwd.de/bvbw/appmanager/bvbw/dwdwwwDesktop/?_nfpb=true&switchLang=en&_pageLabel=_dwdwww_klima_umwelt_datenzentren_gsnmc (accessed 11 January 2012).

Grant K., Kreyling J., Heilmeier H., Beierkuhnlein C., Jentsch A. (2014) Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecological Research*, **29**, 991–1001.

Gutschick V.P., BassiriRad H. (2003) Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences: Tansley review. *New Phytologist*, **160**, 21–42.

Hanley M.E. (2012) Seedling defoliation, plant growth and flowering potential in native- and invasive-range *Plantago lanceolata* populations: seedling tolerance in native and introduced ranges. *Weed Research*, **52**, 252–259.

Hautier Y., Niklaus P.A., Hector A. (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science*, **324**, 636–638.

Heckman R.W., Halliday F.W., Wilfahrt P.A., Mitchell C.E. (2017) Effects of native diversity, soil nutrients, and natural enemies on exotic invasion in experimental plant communities. *Ecology*, **98**, 1409–1418.

Hejda M., Pyšek P., Jarošík V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**, 393–403.

Hild A.L., Karl M.G., Haferkamp M.R., Heitschmidt R.K. (2001) Drought and grazing III: root dynamics and germinable seed bank. *Journal of Range Management*, **54**, 292–298.

Hothorn T., Bretz F., Westfall P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Hsiao T.C. (1973) Plant responses to water stress. *Annual Review Plant Physiology*, **24**, 519–570.

Ibanez I., Diez J.M., Miller L.P., Olden J.D., Sorte C.J., Blumenthal D.M., Bradley B.A., D'Antonio C.M., Dukes J.S., Early R.I., Grosholz E.D., Lawler J.J. (2014) Integrated assessment of biological invasions. *Ecological Applications*, **24**, 25–37.

Inouye D.W. (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, **3**, 457–463.

Inouye D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, **89**, 353–362.

IPCC (2014) Climate change 2014: impacts, adaptation, and vulnerability. In: Barros V.R., Field C.B., Dokken D.J., Mastrandrea M.D., Mach K.J., Bilir T.E., Chatterjee M., Ebi K.L., Estrada Y.O., Genova R.C., Girma B., Kissel E.S., Levy A.N., MacCracken S., Mastrandrea P.R., White L.L. (Eds), *Part B: Regional Aspects*. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK: 688 pp.

Jauni M., Ramula S. (2016) Demographic mechanisms of disturbance and plant diversity promoting the establishment of invasive *Lupinus polyphyllus*. *Journal of Plant Ecology*, **10**, 510–517.

Jentsch A. (2013) Sending a SIGNAL – the mechanisms of grassland resilience. *Research Media* EU: 21–23.

Jentsch A., Kreyling J., Beierkuhnlein C. (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, **5**, 365–374.

Jentsch A., Kreyling J., Elmer M., Gellesch E., Glaser B., Grant K., Hein R., Lara M., Mirzae H., Nadler S.E., Nagy L., Otieno D., Pritsch K., Rascher U., Schädler M., Schloter M., Singh B.K., Stadler J., Walter J., Wellstein C., Wöllecke J., Beierkuhnlein C. (2011) Climate extremes initiate ecosystem-regulating functions while maintaining productivity: drought effect on multiple ecosystem services. *Journal of Ecology*, **99**, 689–702.

Kodra E., Steinhaeuser K., Ganguly A.R. (2011) Persisting cold extremes under 21st-century warming scenarios: global warming and cold extremes. *Geophysical Research Letters*, **38**, L08705.

Kreyling J. (2010) Winter climate change: a critical factor for temperate vegetation performance. *Ecology*, **91**, 1939–1948.

Kreyling J., Beierkuhnlein C., Ellis L., Jentsch A. (2008) Invasibility of grassland and heath communities exposed to extreme weather events – additive effects of diversity resistance and fluctuating physical environment. *Oikos*, **117**, 1542–1554.

Kreyling J., Thiel D., Nagy L., Jentsch A., Huber G., Konnert M., Beierkuhnlein C. (2012) Late frost sensitivity of juvenile *Fagus sylvatica* L. differs between southern Germany and Bulgaria and depends on preceding air temperature. *European Journal of Forest Research*, **131**, 717–725.

LaForgia M.L., Spasojevic M.J., Case E.J., Latimer A.M., Harrison S.P. (2018) Seed banks of native forbs, but not exotic grasses, increase during extreme drought. *Ecology*, **99**, 896–903.

Laube J., Ziegler K., Sparks T.H., Estrella N., Menzel A. (2015) Tolerance of alien plant species to extreme events is comparable to that of their native relatives. *Preslia*, **87**, 31–53.

Lauri P. (1996) Quantitative analysis of relationships between inflorescence size, bearing-axis size and fruit-set – an apple tree case study. *Annals of Botany*, **77**, 277–286.

Lauterbach D., Nehring S. (2013) *Naturschutzfachliche Invasivitätsbewertung Lupinus polyphyllus – Vielblättrige Lupine*. Bundesamt für Naturschutz Bonn, Bonn, Germany.

Lesnoff M., Lancelot R. (2012) aod: Analysis of Overdispersed Data. R package version 1.3 [online] Available from http://cran.r-project.org/package=aod.

Levine J.M., Adler P.B., Yelenik S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions: biotic resistance to plant invasion. *Ecology Letters*, **7**, 975–989.

Loik M.E., Breshears D.D., Lauenroth W.K., Belnap J. (2004) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia*, **141**, 269–281.

Maqbool A., Shafiq S., Lake L. (2010) Radiant frost tolerance in pulse crops – a review. *Euphytica*, **172**, 1–12.

Markham J.H., Chanway C.P. (1996) Measuring plant neighbour effects. *Functional Ecology*, **10**, 548–549.

Maron J.L., Vilà M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, **95**, 361–373.

May R.M., Arthur R.H.M. (1972) Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences of the United States of America*, **69**, 1109–1113.

McCabe G.J., Palecki M.A., Betancourt J.L. (2004) Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 4136–4141.

McDowell N., Pockman W.T., Allen C.D., Breshears D.D., Cobb N., Kolb T., Plaut J., Sperry J., West A., Williams D.G., Yepez E.A. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.

Melbourne B.A., Cornell H.V., Davies K.F., Dugaw C.J., Elmendorf S., Freestone A.L., Hall R.J., Harrison S., Hastings A., Holland M., Holyoak M., Lambrinos J., Moore K., Yokomizo H. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover?: Invasion in a heterogeneous world. *Ecology Letters*, **10**, 77–94.

Mokany K., Raison R.J., Prokushkin A.S. (2006) Critical analysis of root : shoot ratios in terrestrial biomes. *Global Change Biology*, **12**, 84–96.

Norris R.F. (1992) Relationship between inflorescence size and seed production in Barnyardgrass (*Echinochloa crus-galli*). *Weed Science*, **40**, 74–78.

Oliver M.J., Guo L., Alexander D.C., Ryals J.A., Wone B.W.M., Cushman J.C. (2011) A sister group contrast using untargeted global metabolomic analysis delineates the biochemical regulation underlying desiccation tolerance in *Sporobolus stapfianus*. *The Plant Cell*, **23**, 1231–1248.

Otte A., Maul P. (2005) Verbreitungsschwerpunkt und strukturelle Einnischung der Stauden-Lupine (*Lupinus polyphyllus* Lindl.) in Bergwiesen der Rhön. *Tuexenia*, **25**, 151–182.

Parker J.D., Hay M.E. (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters*, **8**, 959–967.

Paudel S., Benavides J.C., MacDonald B., Longcore T., Wilson G.W.T., Loss S.R. (2017) Determinants of native and non-native plant community structure on an oceanic island. *Ecosphere*, **8**, e01927.

Paudel S., Milleville A., Battaglia L.L. (2018) Responses of Native and Invasive Floating Aquatic Plant Communities to Salinity and Desiccation Stress in the Southeastern US Coastal Floodplain Forests. Estuaries and Coasts [online] Available from http://link.springer.com/10.1007/s12237-018-0419-2 (accessed 26 August 2018).

Pearson D.E., Ortega Y.K., Eren Ö., Hierro J.L. (2018) Community assembly theory as a framework for biological invasions. *Trends in Ecology & Evolution*, **33**, 313–325.

R Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria [online]. https://www.R-project.org/

Ramula S., Pihlaja K. (2012) Plant communities and the reproductive success of native plants after the invasion of an ornamental herb. *Biological Invasions*, **14**, 2079–2090.

Ramula S., Sorvari J. (2017) The invasive herb *Lupinus polyphyllus* attracts bumblebees but reduces total arthropod abundance. *Arthropod-Plant Interactions*, **11**, 911–918.

Reich P.B. (2014) The world-wide 'fas–slow' plant economics spectrum: a traits manifesto (H. Cornelissen, Ed.). *Journal of Ecology*, **102**, 275–301.

Richards C.L., Bossdorf O., Muth N.Z., Gurevitch J., Pigliucci M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**, 981–993.

Scholander P.F., Hammel H.T., Bradstreet E.D., Hemmingsen E.A. (1965) Sap pressure in vascular plants – negative hydrostatic pressure can be measured in plants. *Science*, **148**, 339–346.

Seneviratne S.I., Nicholls N., Easterling D., Goodess C.M., Kanae S., Kossin J., Luo Y., Marengo J., McInnes K., Rahimi M., Reichstein M., Sorteberg A., Vera C., Zhang X. (2012) Changes in climate extremes and their impacts on the natural physical environment. In: Barros F.V., Stocker T.F., Qin D., Dokken D.J., Ebi K.L., Mastrandrea M.D., Mach K.J., Plattner G.-K., Allen S.K., Tignor M., Midgley P.M. (Eds), *Chapter 3, Managing the risks of extreme events and disasters to advance climate change adaptation (SREX)*. Cambridge University Press, Cambridge, UK, pp 109–230.

Sorte C.J.B., Ibáñez I., Blumenthal D.M., Molinari N.A., Miller L.P., Grosholz E.D., Diez J.M., D'Antonio C.M., Olden J.D., Jones S.J., Dukes J.S. (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance (K. Suding, Ed.). *Ecology Letters*, **16**, 261–270.

Sousa R., Morais P., Dias E., Antunes C. (2011) Biological invasions and ecosystem functioning: time to merge. *Biological Invasions*, **13**, 1055–1058.

St. John L., Ogle D. (2008) *Plant guide for red clover (Trifolium pratense L.)*. USDA-Natural Resources Conservation Service, Plant Materials Center, Corvallis, OR, USA [online] Available from https://plants.usda.gov/plantguide/pdf/pg_trpr2.pdf (accessed 2 August 2018).

Starfinger U., Kowarik I. (2011) *Lupinus polyphyllus* Lindl. (Fabaceae), Vielblättrige Lupine. Neobiota.de Gebietsfremde und invasive Arten Deutschland. Available from http://www.neobiota.de/12637.html (accessed 6 January 2015).

Strayer D.L. (2012) Eight questions about invasions and ecosystem functioning (H. Hillebrand, Ed.). *Ecology Letters*, **15**, 1199–1210.

Thiele J., Isermann M., Otte A., Kollmann J. (2010) Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *Journal of Vegetation Science*, **21**, 213–220.

Thomson D.M., Kwok J.W., Schultz E.L. (2018) Extreme drought alters growth and interactions with exotic grasses, but not survival, for a California annual forb. *Plant Ecology*, **219**, 705–717.

Tilman D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 10854–10861.

Valtonen A., Jantunen J., Saarinen K. (2006) Flora and lepidoptera fauna adversely affected by invasive *Lupinus polyphyllus* along road verges. *Biological Conservation*, **133**, 389–396.

Van der Aart P., Vulto J. (1992) Biogeography and human effects. In: Kuiper P., Bos M. (Eds), *Plantago: a multidisciplinary study*. Springer, Berlin, Germany.

Volz H. (2003) *Ursachen und Auswirkungen der Ausbreitung von Lupinus polyphyllus Lindl. im Bergwiesenökosystem der Rhön und Maßnahmen zu seiner Regulierung*. Justus-Liebig-Universität Gießen, Gießen, Germany.

Volz H., Otte A. (2001) Occurrence and spreading ability of *Lupinus polyphyllus* Lindl. in the Hochrhoen area (central Germany). *BfN-Skripten*, **32**, 97–98.

Weigelt A., Jolliffe P. (2003) Indices of plant competition. *Journal of Ecology*, **91**, 707–720.

Yobi A., Wone B.W.M., Xu W., Alexander D.C., Guo L., Ryals J.A., Oliver M.J., Cushman J.C. (2013) Metabolomic profiling in *Selaginella lepidophylla* at various hydration states provides new insights into the mechanistic basis of desiccation tolerance. *Molecular Plant*, **6**, 369–385.

Zeileis A. (2004) Econometric computing with HC and HAC covariance matrix estimators. *Journal of Statistical Software*, **11**, 1–17.

Zuur A.F., Hilbe J.M., Ieno E.N. (2013) *A beginner's guide to GLM and GLMM with R*. Highland Statistics Ltd., Newburgh, UK.

10.2.1 Erratum Manuscript 2 Figure 1

plant biology

Plant Biology ISSN 1435-8603

ERRATUM

In our manuscript “Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters” an error concerning the labelling of Figure 1 occurred. The labels “Drought” and “Precip.” were swapped for both, the adult and seedling plant life-cycle stages. However, results are given and discussed correctly in the results and discussion section of this paper.

This is the corrected version of Figure 1:

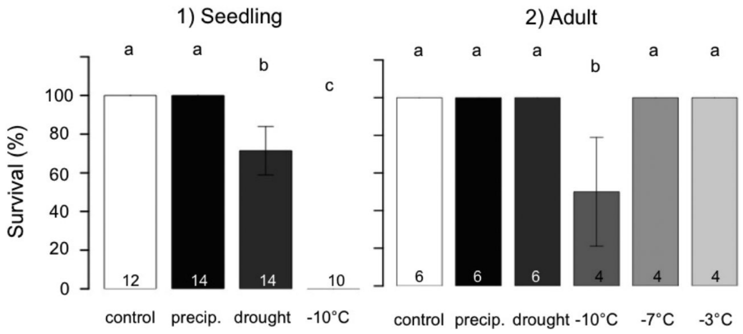


Fig. 1. Proportion of surviving *L. polyphyllus* individuals in the abiotic filter experiment under differing water regimes and late frost intensity along a gradient of growth over two field seasons (2012–2013). Data shown are the ±SE. Small letters represent significant differences between treatments at the significance level of 5% (Tukey HSD test). Precip., fluctuating precipitation.

10.2.2 Supporting information Manuscript 2

Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters

Vanessa Vetter[1], Julia Walter, Peter A. Wilfahrt, Constanze Buhk, Manuel Braun, Stephan Clemens, Eva Dinkel, Maren Dubbert, Alexander Schramm, Frederik Wegener, Christiane Werner, Anke Jentsch

[1]Disturbance Ecology, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany, vanessa.vetter@uni-bayreuth.de

Additional results (e.g. mean values and significance levels, deviation from control) of the abiotic, biotic and combined filter experiments

Originally, we tested three life cycle stages in the abiotic filter experiment: seedling, juvenile and adult plants of *L. polyphyllus*. We defined "seedling" as the plant life cycle stage, in which the plants had 1-3 secondary leaves (developmental age: 4 weeks). In the "juvenile" life cycle stage, plants had 6 – 11 leaves and showed progressive shoot growth, but no flower bud formation (developmental age: 14 weeks). The experiments for both life cycle stages took place in 2012. Experiments of the "adult" life cycle stage took place in the second year of the abiotic filter experiment in 2013. We defined plants as "adult" as soon as flower initiation started (developmental age: 12 months).
Seedlings suffered a drought period of 44 days (28-June- to 11-Aug-2012) and juveniles of 21 days (3-Sept- to 23-Sept-2012). At the end of September we had to stop treatments of the abiotic filter experiment because first night frosts occurred. For adult plants, the drought period was chosen to be similar to that of the seedlings and was set to 44 days (25-May- to 8-July-2013). According to soil moisture measurements, soil moisture of the juvenile pots of all treatments was very low before treatments started, due to very hot and dry outside weather conditions and despite regular watering. Therefore, the juveniles possibly suffered from a permanent drought since their seedling stage. For these two reasons, we decided to remove the data set of juvenile plants from the main manuscript. But here, results for all three life cycle stages are shown whenever possible.
See Figure A.1 for a more detailed description of the procedure of the abiotic filter experiment with all life cycle stages.

In the biotic and combined filter experiment we tested only the seedling life cycle stage.

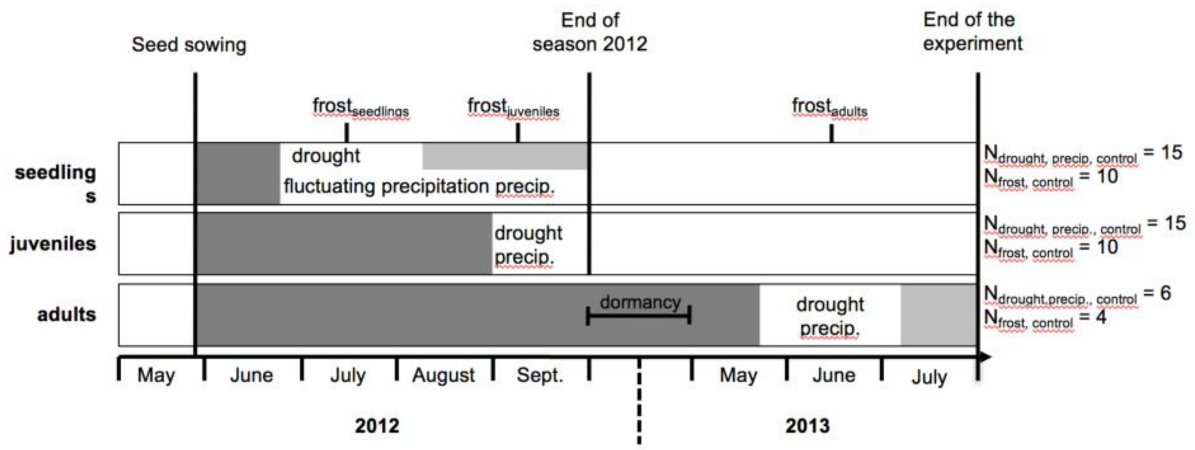


Figure A.1: Timeline of the abiotic filter experiment. Dark grey bars indicate the duration of the growth period until the plants reached the desired life cycle stage. Light grey bars indicate periods of normal watering, according to the control, after termination of treatment. Experimental duration: seedlings 28-June- to 28-Sept-2012; juveniles 3-Sept- to 28-Sept-2012; adults 25-May- to 31-July-2013.

Table A.1: The abiotic filter experiment – Table of mean values and standard deviations of all parameters across all weeks and stages tested for *Lupinus polyphyllus*. We used Tukey HSD test, verified with linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3) to test for significant difference between treatments drought, fluctuating precipitation and control ($p < 0.05$). Drought duration: seedling 28-June- to 11-Aug-2012; juvenile 3-Sept- to 23-Sept-2012; adult 25-May- to 8-July-2013. Duration of fluctuating precipitation (precip.): seedling 28-June- to 28-Sept-2012; juvenile 3-Sept- to 28-Sept-2012; adult 25-May- to 8-July-2013. (see also Figure A.1)

stage	treatment	date [DOY]	days in treat-ment		mean senescence (± STDV)	p (adj) value	mean shoot height [cm] (± STDV)	p (adj) value	mean number of leaves (± STDV)	p (adj) value	mean leaf diameter [cm]	p (adj) value
seedling	drought	11.07.12	14	drought vs. control	0,29 (± 1,07)	0.5129103	3,62 (± 1,69)	0.8785554	1,79 (±0,58)	0.9885603	3,33 (± 0,98)	0.7122256
seedling	fluctuating precipitation	11.07.12	14	precip. vs. drought	0,07 (± 0,27)	0.6635751	3,47 (± 1,30)	0.9646201	2,00 (± 0,55)	0.6422648	3,20 (± 0,78)	0.9127348
seedling	control	11.07.12	14	control vs. precip.	0,00 (± 0,00)	0.9583468	3,33 (± 1,65)	0.968807	1,75 (± 0,75)	0.5744399	3,60 (± 0,70)	0.4658883
seedling	drought	25.07.12	28	drought vs. control	0,77 (± 0,60)	0.0094864 **	5,47 (± 0,97)	0.0319814 *	3,23 (± 0,60)	0.9137513	3,68 (± 1,17)	0.0005308 ***
seedling	fluctuating precipitation	25.07.12	28	precip. vs. drought	0,21 (± 0,43)	0.0133756 *	5,81 (± 1,28)	0.6932971	3,43 (± 0,51)	0.6981578	4,76 (± 0,83)	0.0262032 *
seedling	control	25.07.12	28	control vs. precip.	0,17 (± 0,39)	0.9657346	6,64 (± 1,45)	0.1583527	3,33 (± 0,78)	0.9226018	5,40 (± 1,09)	0.2696500
seedling	drought	08.08.12	42	drought vs. control	2,92 (± 1,31)	0.000001 ***	5,08 (± 0,96)	0.0000332 ***	3,25 (± 0,45)	0.0003572 ***	4,37 (± 1,51)	0.0001822 ***
seedling	fluctuating precipitation	08.08.12	42	precip. vs. drought	0,64 (± 0,74)	0.0000008 ***	7,45 (± 1,69)	0.009196 *	4,50 (± 0,65)	0.0163162 *	6,14 (± 0,95)	0.0285271 *
seedling	control	08.08.12	42	control vs. precip.	0,58 (± 0,51)	0.984914	9,08 (± 2,70)	0.0923529 .	5,17 (± 1,75)	0.2771343	7,48 (± 1,60)	0.0407721 *
seedling	drought	22.08.12	56	drought vs. control	1,60 (± 0,89)	0.0259352 *	6,30 (± 1,36)	0.0001801 ***	4,40 (± 0,55)	0.0106374 *	5,58 (± 1,81)	0.0047315 **
seedling	fluctuating precipitation	22.08.12	56	precip. vs. drought	0,64 (± 0,74)	0.0329873 *	8,46 (± 1,76)	0.1429321	5,79 (± 0,97)	0.0454006 *	7,26 (± 1,28)	0.1485372
seedling	control	22.08.12	56	control vs. precip.	0,58 (± 0,51)	0.9738646	11,63 (± 2,68)	0.0021354 **	6,17 (± 1,27)	0.6342645	8,66 (± 2,00)	0.1011518
seedling	drought	05.09.12	70	drought vs. control	0,40 (± 0,55)	0.8919911	7,52 (± 1,78)	0.0033847 **	6,60 (± 1,14)	0.1357691	6,92 (± 1,41)	0.0220403 *

seedling	fluctuating precipitation	05.09.12	70	precip. vs. drought	0,50 (± 0,65)	0.9436162	8,26 (± 1,61)	0.8031276	7,79 (± 1,31)	0.2495757	7,78 (± 1,45)	0.6748694
seedling	control	05.09.12	70	control vs. precip.	0,55 (± 0,52)	0.9801202	11,87 (± 2,97)	0.0011915 **	8,09 (± 1,58)	0.8506871	9,89 (± 2,56)	0.0301631 *
juvenile	drought	05.09.12	3	drought vs. control	1,00 (± 0,00)	1.0000000	12,91 (± 1,68)	0.9406599	7,93 (± 0,80)	0.2093929	9,04 (± 1,26)	0.2910040
juvenile	fluctuating precipitation	05.09.12	3	precip. vs. drought	1,00 (± 0,38)	1.0000000	11,59 (± 2,00)	0.1397436	8,27 (± 1,16)	0.7158880	9,32 (± 1,77)	0.8488589
juvenile	control	05.09.12	3	control vs. precip.	1,00 (± 0,53)	1.0000000	12,68 (± 1,90)	0.2534769	8,67 (± 1,45)	0.6191808	9,82 (± 1,10)	0.5960599
juvenile	drought	12.09.12	10	drought vs. control	1,67 (± 0,62)	0.0014903 **	12,90 (± 1,71)	0.99568	8,40 (± 1,06)	0.0642640 .	8,56 (± 1,28)	0.0029889 **
juvenile	fluctuating precipitation	12.09.12	10	precip. vs. drought	1,87 (± 0,64)	0.5656368	11,79 (± 1,95)	0.2386483	9,00 (± 1,13)	0.4442215	8,22 (± 1,36)	0.7286649
juvenile	control	12.09.12	10	control vs. precip.	0,93 (± 0,26)	0.0000630 ***	12,96 (± 1,89)	0.2050108	9,53 (± 1,73)	0.5251287	10,15 (± 1,05)	0.0003084 ***
seedling	drought	19.09.12	84	drought vs. control	1,00 (± 0,71)	1,0000000	7,60 (± 1,94)	0.0009490 ***	7,20 (± 0,45)	0.3817628	6,87 (± 0,97)	0.0117224 *
seedling	fluctuating precipitation	19.09.12	84	precip. vs. drought	1,07 (± 0,27)	0.9092172	8,06 (± 1,89)	0.905309	8,29 (± 1,49)	0.4589305	7,51 (± 1,39)	0.7938357
seedling	control	19.09.12	84	control vs. precip.	1,00 (± 0,00)	0.853243	12,16 (± 2,31)	0.0001021 ***	8,45 (± 2,25)	0.9680496	10,05 (± 2,60)	0.0069580 **
juvenile	drought	19.09.12	17	drought vs. control	2,60 (± 0,74)	0.0000000 ***	13,09 (± 1,67)	0.6511132	8,67 (± 1,23)	0.0104707 *	8,53 (± 1,32)	0.0035651 **
juvenile	fluctuating precipitation	19.09.12	17	precip. vs. drought	1,87 (± 0,52)	0.0010795 **	11,61 (± 2,03)	0.0762581 .	9,00 (± 1,13)	0.8486716	9,74 (± 1,34)	0.0301955 *
juvenile	control	19.09.12	17	control vs. precip.	1,00 (± 0,00)	0.0001241 ***	12,51 (± 1,71)	0.3753811	10,53 (± 2,36)	0.0410286 *	10,11 (± 1,07)	0.6984754
juvenile	drought	26.09.12	24	drought vs. control	2,67 (± 0,71)	0.0000000 ***	13,27 (± 1,84)	0.9916393	9,00 (± 1,41)	0.0827753 .	9,66 (± 1,04)	0.2226325

juvenile	fluctuating precipitation	26.09.12	24	precip. vs. drought	2,13 (± 0,52)	0.0257978 *	11,70 (± 2,08)	0.1798438	9,67 (± 1,45)	0.5783979	10,01 (± 1,45)	0.7667650
juvenile	control	26.09.12	24	control vs. precip.	1,00 (± 0,00)	0.0000002 ***	13,16 (± 2,13)	0.1393599	10,47 (± 1,77)	0.3552096	10,52 (± 1,05)	0.4919197
adult	drought	24.05.13	0	drought vs. control	0,83 (± 0,41)	0.8234901	75,33 (± 9,35)	0.0175125 *	30,83 (± 4,83)	0.1638512	8,53 (± 1,41)	0.8766790
adult	fluctuating precipitation	24.05.13	0	precip. vs. drought	0,67 (± 0,52)	0.8234901	51,42 (± 10,08)	0.0007973 ***	21,83 (± 7,25)	0.0430718 *	9,55 (± 1,98)	0.5233366
adult	control	24.05.13	0	control vs. precip.	0,67 (± 0,52)	1,0000000	59,33 (± 6,70)	0.2957355	24,33 (± 5,09)	0.7421192	8,98 (± 1,30)	0.8125477
adult	drought	06.06.13	13	drought vs. control	1,00 (± 0,00)	0.6690874	80,33 (± 5,56)	0.5108924	32,33 (± 7,74)	0.9989893	9,28 (± 1,03)	0.9251567
adult	fluctuating precipitation	06.06.13	13	precip. vs. drought	1,00 (± 0,00)	0.6690874	65,50 (± 13,08)	0.0369261 *	27,33 (± 7,09)	0.4247747	9,22 (± 1,80)	0.9961456
adult	control	06.06.13	13	control vs. precip.	1,00 (± 0,00)	1,0000000	74,25 (± 7,65)	0.2656149	32,17 (± 5,12)	0.4479309	8,98 (± 1,18)	0.9539329
adult	drought	19.06.13	26	drought vs. control	4,17 (± 0,41)	0.000007 ***	77,60 (± 7,44)	0.924907	11,20 (± 3,42)	0.0081357 **	6,48 (± 0,66)	0.9042617
adult	fluctuating precipitation	19.06.13	26	Precip. vs. drought	2,50 (± 0,55)	0.0000344 ***	64,67 (± 11,60)	0.1242913	13,00 NA	0.8338309	4,25 (± 1,92)	0.0651056 .
adult	control	19.06.13	26	control vs. precip.	2,00 (± 0,00)	0.19913	79,92 (± 10,43)	0.0510947 .	18,60 (± 2,07)	0.2276716	6,87 (± 1,47)	0.0223533 *
adult	drought	03.07.13	40	drought vs. control	4,17 (± 0,41)	0.0000086 ***	77,60 (± 7,44)	0.9578283	0,00 (± 0,00)	0.0049042 **	0,00 (± 0,00)	0.0000001 ***
adult	fluctuating precipitation	03.07.13	40	precip. vs. drought	2,40 (± 0,55)	0.0000350 ***	64,58 (± 11,74)	0.1042647	14,00 (± 8,28)	0.0059709 **	4,36 (± 0,96)	0.0000206 ***
adult	control	03.07.13	40	control vs. precip.	2,00 (± 0,00)	0.3486085	79,25 (± 9,10)	0.0506334 .	16,67 (± 3,51)	0.7866188	6,73 (± 1,46)	0.0039945 **
adult	drought	08.07.13	44	drought vs. control	4,17 (± 0,41)	<1e-04 ***	77,60 (± 7,44)	0.9834	0,00 (± 0,00)	<1e-04 ***	0,00 (± 0,00)	<1e-05 ***

adult	fluctuating precipitation	08.07.13	44	precip. vs. drought	3,50 (± 0,84)	0.24	64,00 (± 12,02)	0.0931 .	12,83 (± 6,15)	<1e-04 ***	5,92 (± 0,94)	<1e-05 ***
adult	control	08.07.13	44	control vs. precip.	1,67 (± 0,52)	<1e-04 ***	78,58 (± 9,54)	0.0841 .	17,60 (± 3,91)	0.371	6,15 (± 1,39)	0.945
adult	drought	17.07.13	53	drought vs. control	4,17 (± 0,41)	0.0000112 ***	77,60 (± 7,44)	0.9857644	0,00 (± 0,00)	0.0000708 ***	0,00 (± 0,00)	0.0000000 ***
adult	fluctuating precipitation	17.07.13	53	precip. vs. drought	3,50 (± 0,84)	0.1790431	64,08 (± 12,18)	0.1026579	12,83 (± 6,15)	0.0008883 ***	5,75 (± 0,67)	0.0000060 ***
adult	control	17.07.13	53	control vs. precip.	1,67 (± 0,52)	0.0003189 ***	78,58 (± 9,54)	0.0625539 .	17,60 (± 3,91)	0.2096981	8,83 (± 1,95)	0.0018766 **
adult	drought	31.07.13	67	drought vs. control	4,17 (± 0,41)	0.0000799 ***	77,60 (± 7,44)	0.9472000	0,00 (± 0,00)	0.0000010 ***	0,00 (± 0,00)	0.0000000 ***
adult	fluctuating precipitation	31.07.13	67	precip. vs. drought	2,67 (± 0,52)	0.0002876 ***	64,67 (± 12,42)	0.1369302	9,67 (± 4,93)	0.0008907 ***	3,85 (± 0,90)	0.0000106 ***
adult	control	31.07.13	67	control vs. precip.	2,25 (± 0,50)	0.3877246	79,58 (± 10,27)	0.0644058 .	18,40 (± 1,82)	0.0018739 **	6,25 (± 1,14)	0.0007896 ***

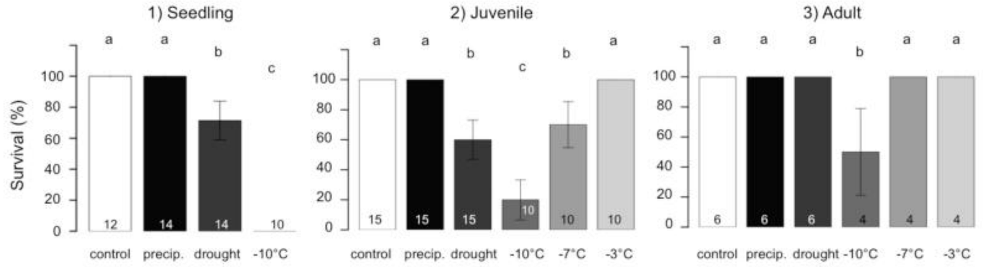


Figure A.2: Proportion of surviving 1) seedling, 2) juvenile, and 3) adult *L. polyphyllus* individuals in control, and under the extreme weather events fluctuating precipitation (precip.), drought and late frost of different intensities (mean ± SE). Small letters indicate significant differences between weather treatments for a given life cycle stage ($p < 0.05$). Sample sizes are shown inside bars. In the seedling stage, three control plants, one drought and one plant of the fluctuating precipitation treatment were excluded from the analyses due to fatal herbivore damage. The individual time points of data acquisition can be found in Fig. A.1.

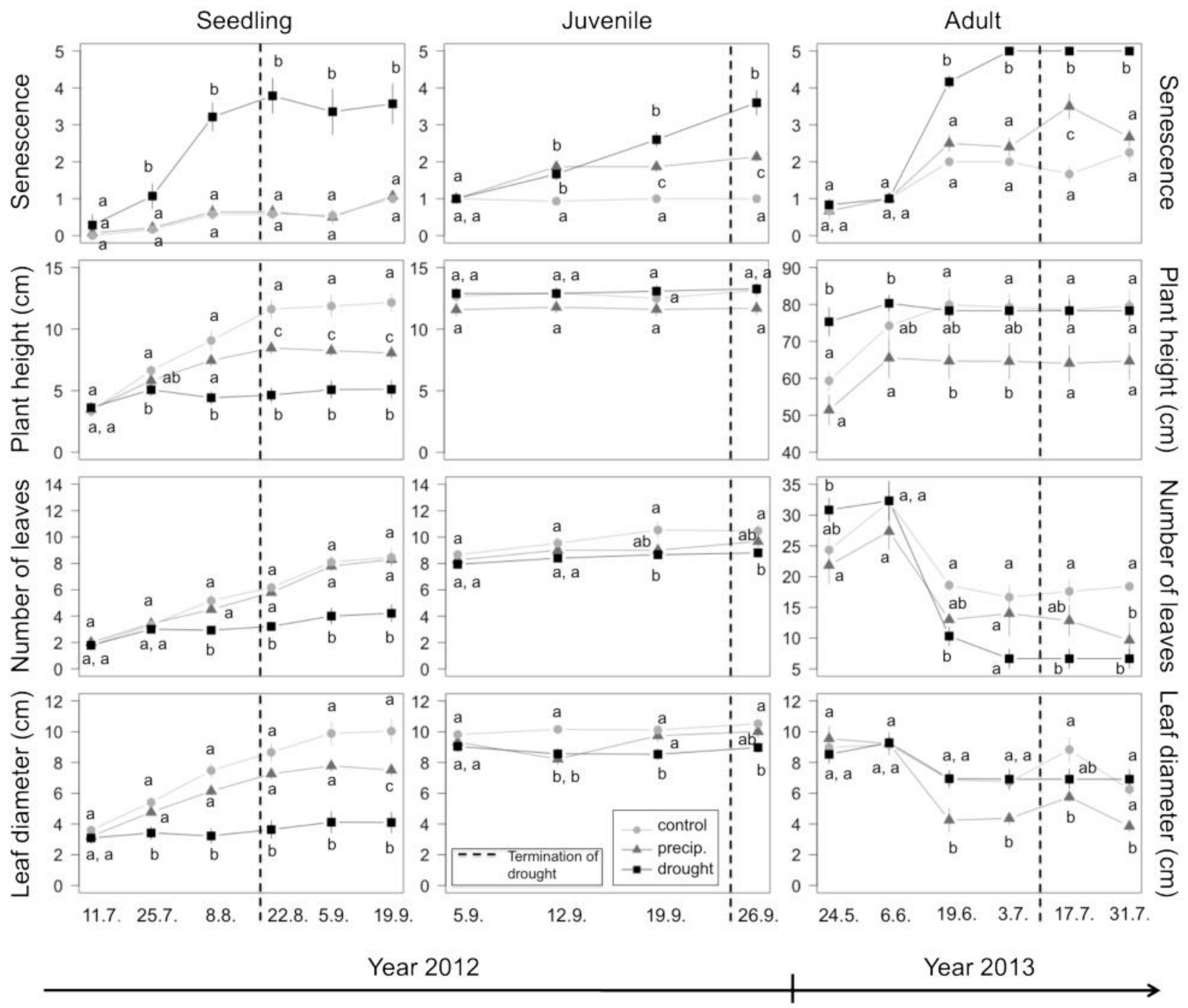


Figure A.3: Temporal dynamics of senescense and growth of seedling, juvenile and adult *L. polyphyllus* under progressing drought (black squares) and subsequent recovery from drought (from the dashed line onwards), as well as in fluctuating precipitation (precip., greay traingels) and control (grey circles). Seedlings: $n_{control} = 12$, $n_{drought} = 14$, $n_{precip.} = 14$; juveniles: $n_{control} = 15$, $n_{drought} = 15$, $n_{precip.} = 15$; adults: $n_{control} = 6$, $n_{drought} = 6$, $n_{precip.} = 6$. Small letters indicate significant differences between weather treatments for a given life cycle stage ($p < 0.05$). In case any part of the plant (e.g. leaves) completely desiccated, the last value prior to the loss was kept throughout the remaining measurement period. Please note that the adult stage has a separate y-axis with a different scaling.

Table A.2: The abiotic filter experiment – Table of the percentage deviation of the treatments drought and fluctuating precipitation from control.

stage	treatment	date [DOY]	weeks in treatment	senescence [%]	senescence minus control [%]	plant height [%]	number of leaves [%]	leaf diameter [%]
seedling	drought	18.07.2012	3	0,0	0,0	97,0	114,6	80,4
seedling	fluctuating precipitation	18.07.2012	3	1,4	1,4	93,5	109,4	83,8
seedling	control	18.07.2012	3	0,0	0,0	100,0	100,0	100,0
seedling	drought	08.08.2012	6	58,3	46,7	56,0	62,9	58,4
seedling	fluctuating precipitation	08.08.2012	6	12,9	1,2	82,1	87,1	82,0
seedling	control	08.08.2012	6	11,7	0,0	100,0	100,0	100,0
adult	drought	13.06.2013	3	80,0	56,7	100,2	96,9	78,8
adult	fluctuating precipitation	13.06.2013	3	53,3	30,0	81,8	76,4	52,9
adult	control	13.06.2013	3	23,3	0,0	100,0	100,0	100,0
adult	drought	08.07.2013	6	83,3	50,0	98,7	0,0	0,0
adult	fluctuating precipitation	08.07.2013	6	70,0	36,7	81,4	72,9	96,2
adult	control	08.07.2013	6	33,3	0,0	100,0	100,0	100,0

Table A.3: The biotic filter experiment - Impact of interspecific competition upon aboveground biomass, plant height and root growth of the native species *Trifolium pratense* and *Plantago lanceolata* in comparison to the invader *Lupinus polyphyllus*. We used Tukey HSD tests, verified with linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3) to test for significant difference between the species ($p < 0.05$). Abrevations: inter = interspecific competition.

Species	Interaction	RNE above ground biomass	p (adj) value Pr(>|z|)	RNE plant height	p (adj) value Pr(>|z|)	RNE root (± STDV)	p (adj) value Pr(>|z|)	mean root dry weight [g] (± STDV)	p (adj) value Pr(>|z|)
T. pratense	inter - Lupinus	0,42 (± 0,34)	0,776	0,52 (± 0,06)	0,00585 **	0,86 (± 0,15)	0,02628 *	0,49 (± 0,59)	0,34946
L. polyphyllus	inter - Trifolium	0,56 (± 0,26)		0,69 (± 0,14)		0,09 (± 0,47)		1,30 (± 0,71)	
P. lanceolata	inter - Lupinus	0,49 (± 0,37)	0,997	0,52 (± 0,06)	0,45752	0,95 (± 0,02)	0,03969 *	0,35 (± 0,23)	0,00435 **
L. polyphyllus	inter - Plantago	0,52 (± 0,18)		0,59 (± 0,15)		0,35 (± 0,52)		0,86 (± 0,23)	

Table A.4: The biotic filter experiment – Table of mean values and standard deviations of all gas-exchange parameters tested. We used Tukey HSD tests, verified with linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3) to test for significant difference between treatments ($p < 0.05$). Abbrevations: mono = one single plant growing without competition, intra = intraspecific competition: measured plant growing in competition with conspecifics, inter = interspecific competition: measured plant growing in competition with LP = *Lupinus polyphyllus* / PL = *Plantago langeolata* / TP = *Trifolium pratense*. In the main manuscript only the assimilation rate and water potential data for the interspecific competition effect is shown.

Variables		***T. pratense*** **(± STDV)**	**p (adj) value Pr(>|z|)**	***P. lanceolata*** **(± STDV)**	**p (adj) value Pr(>|z|)**	***L. polyphyllus*** **(± STDV)**	**p (adj) value Pr(>|z|)**
Transpiration rate	mono	3,60 (± 0,55)		3,49 (± 1,26)		2,29 (± 0,08)	
	intra	4,08 (± 0,58)		3,85 (± 0,44)		2,32 (± 0,95)	
	inter - LP	3,86 (± 0,59)	<0,001 ***	3,73 (± 0,91)	0,00178 **	-	
	inter - PL	-	-	-	-	1,39 (± 0,14)	0,99999
	inter - TP	-	-	-	-	1,38 (± 0,64)	
Assimilation rate	mono	24,69 (± 3,88)		20,12 (± 4,92)		15,84 (± 2,47)	
	intra	23,44 (± 3,76)		18,60 (± 2,87)		14,14 (± 2,36)	
	inter - LP	24,50 (± 2,24)	< 1e-04 ***	21,19 (± 3,13)	< 1e-04 ***	-	
	inter - PL	-	-	-	-	9,93 (± 1,55)	0,997918
	inter - TP	-	-	-	-	9,56 (± 2,51)	
Stomatal water vapour conductance	mono	289,18 (± 40,99)		292,65 (± 123,10)		176,39 (± 15,70)	
	intra	365,21 (±75,04)		336,44 (± 50,83)		154,39 (± 58,35)	
	inter - LP	310,36 (± 36,55)	<0,001 ***	329,14 (± 112,35)	0,0158 *	-	
	inter - PL	-	-	-	-	97,15 (± 8,64)	1,0000
	inter - TP	-	-	-	-	98,24 (± 50,54)	
Vapour pressure deficit	mono	12,45 (± 0,47)		12,20 (± 1,20)		13,06 (± 0,85)	
	intra	11,28 (± 0,82)		11,50 (± 0,58)		14,95 (± 0,93)	
	inter - LP	12,46 (± 1,76)	0,5092	11,57 (± 1,04)	0,0452 *	-	
	inter - PL	-	-	-	-	14,35 (± 1,11)	0,9998
	inter - TP	-	-	-	-	14,28 (± 0,68)	
Internal CO_2 mole fraction	mono	289,43 (± 30,07)		306,26 (± 65,90)		283,77 (± 17,95)	
	intra	310,07 (± 35,21)		341,83 (± 7,58)		280,08 (± 62,84)	
	inter - LP	321,92 (± 1,18)	0,359	350,88 (± 43,92)	0,643	-	
	inter - PL	-	-	-	-	306,08 (± 34,34)	0,924
	inter - TP	-	-	-	-	286,15 (± 31,76)	
iWUE	mono	86,97 (± 22,01)		74,23 (± 19,95)		90,44 (± 18,40)	
	intra	64,64 (± 3,46)		56,84 (± 17,10)		96,21 (± 19,81)	
	inter - LP	79,97 (± 14,23)	0,530	67,48 (± 15,43)	0,144	-	
	inter - PL	-	-	-	-	102,64 (± 17,61)	1,0000
	inter - TP	-	-	-	-	104,81 (± 21,87)	
Water potential	mono	0,86 (± 0,09)		1,20 (± 0,06)		0,35 (± 0,04)	
	intra	0,82 (± 0,46)		0,62 (± 0,25)		0,34 (± 0,04)	
	inter - LP	0,72 (± 0,16)	0,00017 ***	0,39 (± 0,26)	0,99824	-	
	inter - PL	-	-	-	-	0,36 (± 0,05)	0,56735
	inter - TP	-	-	-	-	0,31 (± 0,05)	

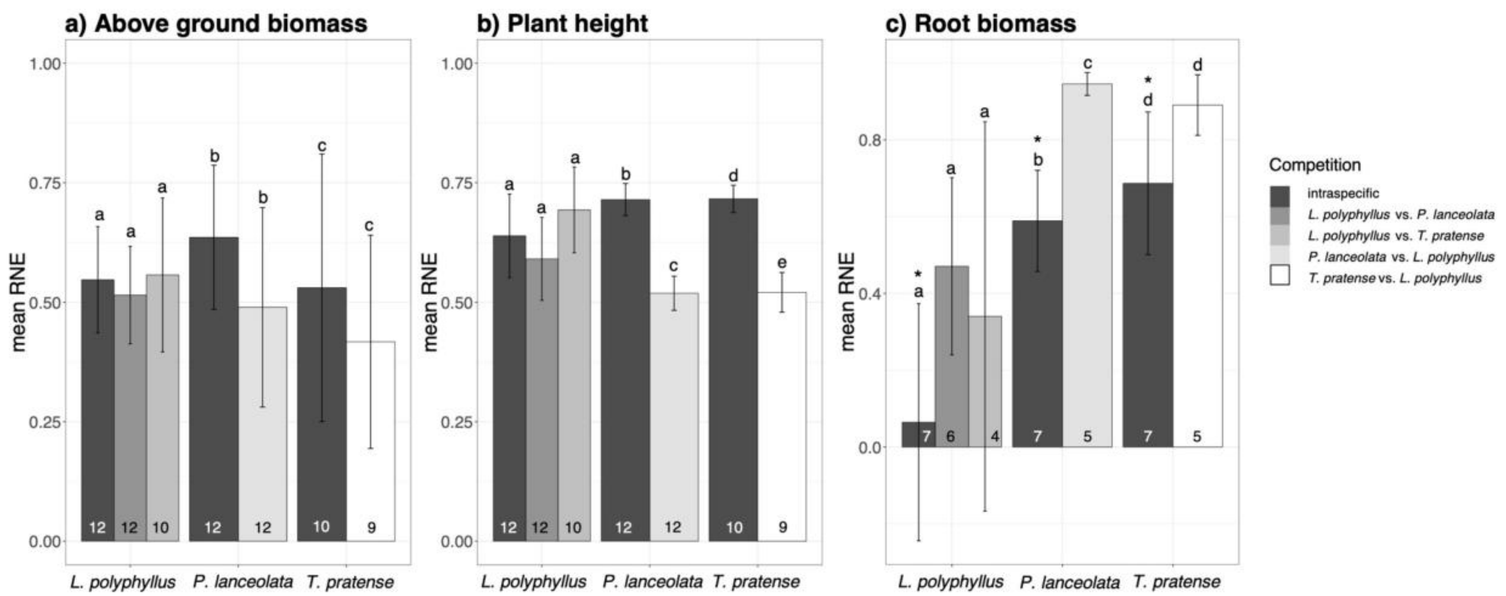


Figure A4: Comparison of the relative neighbor effect (RNE) of *L. polyphyllus* versus *P. lanceolata* and *T. pratense* in controlled conditions of the biotic filter experiment. The target species is shown on the x-axis, while the respective competition treatment is indicated by the color of the bars.
Small letters represent significant differences between the observed competition treatments within one species. Stars mark significant differences between the intraspecific competition treatment of the invader compared to the native species. Please note, that stars do not indicate significant differences between the intraspecific competition treatment of the native species. All differences are marked at the significance level of 5% using linear regressions in combination with a heteroskedasticity-consistent covariance estimation (HC3).
RNE values of +1 indicate maximum competition, while values of -1 indicate maximum facilitation. No interaction is indicated by RNE values close to zero.

Mean RNE values of aboveground biomass, plant height and root biomass of all species showed clear intraspecific competition effects. All species clearly suffered from the competition induced by their conspecifics. In intraspecific competition, *L. polyphyllus* shows significantly less root biomass than the native species.

GC-MS Analysis

This Appendix S2 contains information about the GC-MS analysis performed within the combined filter experiment of the manuscript.

Metabolic profiling

At the end of the combined filter experiment 20 leaf samples (one leaf randomly sub-sampled from 10 plants in the drought treatment and 10 plants in the control treatment) were taken to conduct metabolic profiling using GC-MS analysis. The extraction of polar leaf compounds was carried out according to (Strehmel *et al.* 2014), with the following modifications: frozen leaf material of the 17 samples was homogenized for one minute using a ball mill (Retsch, MM2, Hahn, Germany) at full speed. For the extraction, 600 µl of cooled 80% methanol with 0.05 mg/ml ribitol (internal standard) was added to 16.5 – 75 mg of the homogenized material. After the thermomixing at 37 °C for 5 min 300 µl chloroform was added to the samples. Following a second thermomixing, 600 µl H_2O bidest was added and the samples were centrifugated for 10 min at 14000 rpm. The supernatant was than stored at -20 °C for further analysis. For the analysis 10 µl of the supernatant was transferred to glass vial inserts and then dried under vacuum in a Speed-Vac (Mettler Toledo, Germany). The gas chromatography mass spectrometry (GC-MS) setup consisted of a Gerstel MPS autosampler, an Agilent 7890A GC system and a 5975C inert MSD (Gerstel GmbH, Mülheim/Ruhr, Germany). Chromatographic separation was performed on a Zebron Guardian ZB-5 (40 m x 0.25 mm, 25 µm, 10 m integrated precolumn, Phenomenex Aschaffenburg, Germany). Freeze dried extracts were derivatized for 90 min at 40 °C and 1000 rpm in the Gerstel MPS thermocycler, using 10 µl of methoxyamine hydrochloride (20mg/ml MeOx in pyridine with 0.02 % n-alkane retention time standard mix (C10-C32)) per sample. This was followed by trimethylsilylation with 20 µl N-methyl-N-trimethylsilyltrifluoroacetamide for 45 min at 40 °C and 1000 rpm. Prior to the injection 30 µl hexane was added to the derivatized samples and 1 µl of the sample was injected into the GC-MS. Chromatography was performed as described (Strehmel *et al.* 2014) with the exception, that the injector temperature was set to 250 °C and an initial oven temperature adjusted to 60 °C (1 min hold) with 10 °C heating steps to 300 °C where the temperature was held for 5 min. The resulting chromatograms of the GC-MS of the leaf samples were baseline corrected with the help of MetAlign (Lommen 2009) and imported into Tagfinder (Luedemann *et al.* 2008). Tagfinder was then used for retention index (RI) calculation, mass spectral tag – alignment and identification of these mass spectral tags based on the "GOLM Metabolome Database" (Kopka *et al.* 2005) using RI-Values which were adjusted to our system. For the tag assignment we used the following settings: time scan width: 1.7, gliding median group count: 1, min fragment intensity: 500, Tag-clustering was carried out using a Pearson correlation with a maximum tag distance of 0.4. Every resulting cluster with a size bigger than three was used for the forward identification with the GOLM library based on the cluster spectrum. The resulting maximum tag intensities of the identified compounds were normalized to the tag intensities of the internal standard ribitol and to the corresponding dry weight.

Statistical Analysis

In the combined filter experiment, GC-MS data for annotated signals were tested after log10 transformation using a Mann-Whitney U-test. The data was visualized with a Whiskers Box-Plot performed with GraphPad Prism5 (http://www.graphpad.com/).

Results

The GC-MS-based metabolite profiling of leaves harvested from *L. polyphyllus* plants of the combined filter experiment resulted in the detection of 233 mass tag clusters. Out of these, 36 metabolites could be annotated using the GOLM Database (http://gmd.mpimp-golm.mpg.de/; Kopka et al., 2005) and one metabolite, lupanine, a typical metabolite of lupines, was annotated using the NIST-library (NIST05, National Institute of Standards and Technology, Gaithersburg, MD, USA; http://www.nist.gov/srd/mslist.htm). We identified organic acids (e. g. citric acid, malic acid), amino acids (e.g. glutamic acid, aspartic acid), sugars and sugar alcohols (e.g. xylitol, fructose), fatty acids (e.g. erythronic acid) and cyclitols (e. g. D-pinitol and myo-Inositol) in the metabolite profiles. The list of annotated signals can be found in Fig. B2. Only one metabolite, glutamic acid, accumulated more strongly (about 1.5 fold) in the drought-stressed leaves (Fig. B.1). All the others showed no significant differences between ambient and drought treated plants.

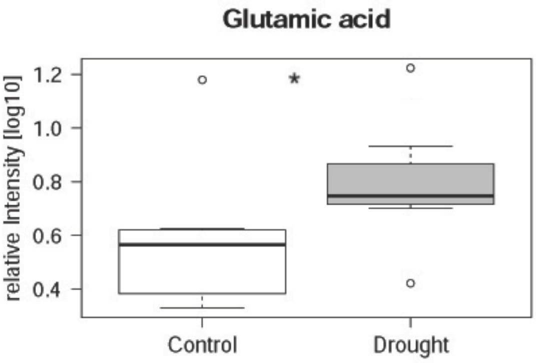
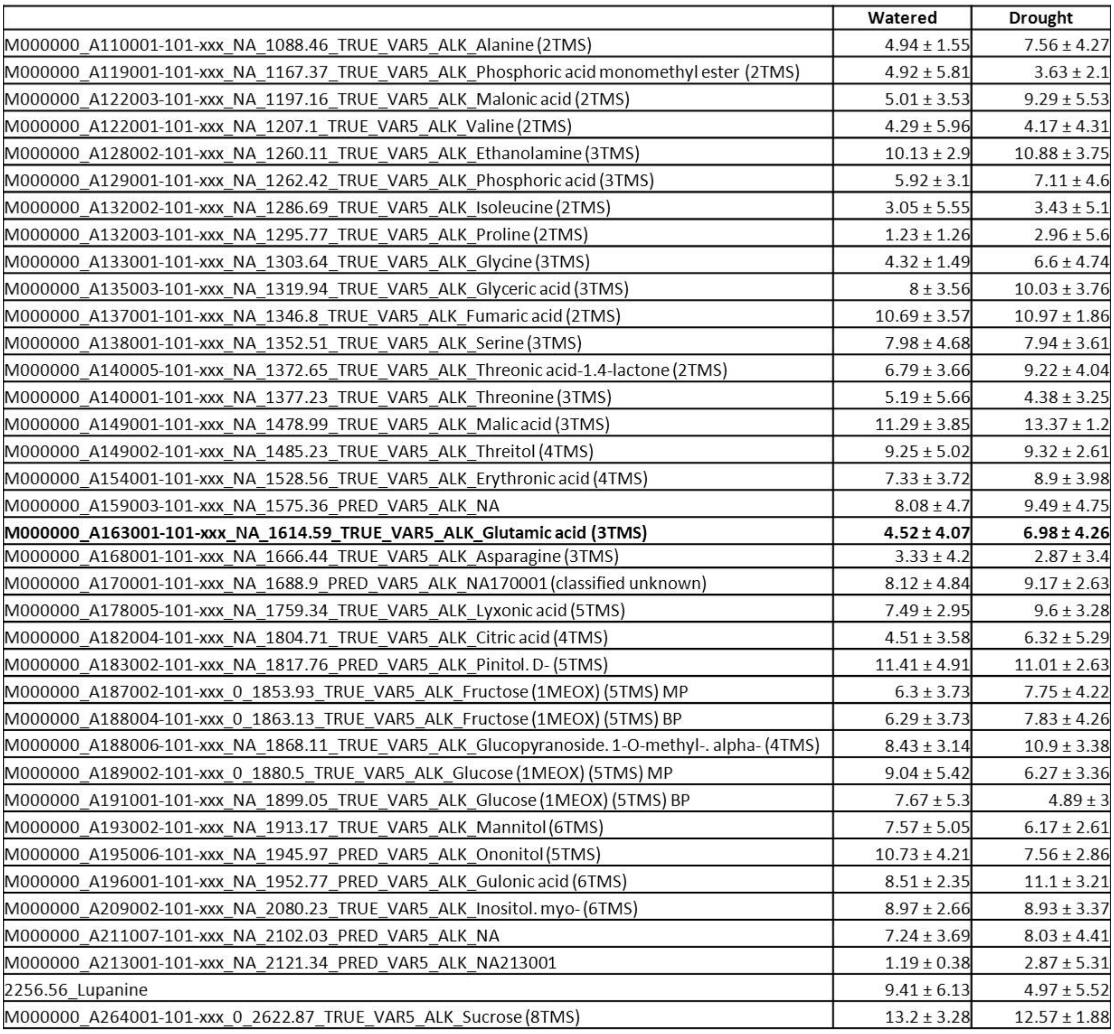


Fig. B.1: Glutamic acid relative intensity in drought stressed (n=8) versus control plants (n=10). The star visualizes significant differences (Mann-Whitney U test, $p<0.05$) in the relative intensity of the metabolite between the tested groups.

Discussion

One possible explanation for the high drought resistance of adult *L. polyphyllus* is that they possess the ability to partially compensate water stress via accumulation of compatible solutes to keep up cell turgor (Hsiao 1973). This is also in agreement with relatively high water potentials under natural conditions compared to native species. Our data implies that *L. polyphyllus* reacts to drought stress with the accumulation of glutamic acid. This metabolite might play a role in drought stress acclimation of *L. polyphyllus*. Glutamic acid was found to increase upon dehydration in Selaginella and the resurrection plant *Sporobolus stapfianus* (Oliver *et al.* 2011; Yobi *et al.* 2013) in previous studies. Whether this increase has a physiological importance with respect to drought tolerance in *L. polyphyllus*, which of course is phylogenetically distant from Selaginella and *S. stapfianus*, will have to be addressed in more detailed analyses.



	Watered	**Drought**
M000000_A110001-101-xxx_NA_1088.46_TRUE_VAR5_ALK_Alanine (2TMS)	4.94 ± 1.55	7.56 ± 4.27
M000000_A119001-101-xxx_NA_1167.37_TRUE_VAR5_ALK_Phosphoric acid monomethyl ester (2TMS)	4.92 ± 5.81	3.63 ± 2.1
M000000_A122003-101-xxx_NA_1197.16_TRUE_VAR5_ALK_Malonic acid (2TMS)	5.01 ± 3.53	9.29 ± 5.53
M000000_A122001-101-xxx_NA_1207.1_TRUE_VAR5_ALK_Valine (2TMS)	4.29 ± 5.96	4.17 ± 4.31
M000000_A128002-101-xxx_NA_1260.11_TRUE_VAR5_ALK_Ethanolamine (3TMS)	10.13 ± 2.9	10.88 ± 3.75
M000000_A129001-101-xxx_NA_1262.42_TRUE_VAR5_ALK_Phosphoric acid (3TMS)	5.92 ± 3.1	7.11 ± 4.6
M000000_A132002-101-xxx_NA_1286.69_TRUE_VAR5_ALK_Isoleucine (2TMS)	3.05 ± 5.55	3.43 ± 5.1
M000000_A132003-101-xxx_NA_1295.77_TRUE_VAR5_ALK_Proline (2TMS)	1.23 ± 1.26	2.96 ± 5.6
M000000_A133001-101-xxx_NA_1303.64_TRUE_VAR5_ALK_Glycine (3TMS)	4.32 ± 1.49	6.6 ± 4.74
M000000_A135003-101-xxx_NA_1319.94_TRUE_VAR5_ALK_Glyceric acid (3TMS)	8 ± 3.56	10.03 ± 3.76
M000000_A137001-101-xxx_NA_1346.8_TRUE_VAR5_ALK_Fumaric acid (2TMS)	10.69 ± 3.57	10.97 ± 1.86
M000000_A138001-101-xxx_NA_1352.51_TRUE_VAR5_ALK_Serine (3TMS)	7.98 ± 4.68	7.94 ± 3.61
M000000_A140005-101-xxx_NA_1372.65_TRUE_VAR5_ALK_Threonic acid-1.4-lactone (2TMS)	6.79 ± 3.66	9.22 ± 4.04
M000000_A140001-101-xxx_NA_1377.23_TRUE_VAR5_ALK_Threonine (3TMS)	5.19 ± 5.66	4.38 ± 3.25
M000000_A149001-101-xxx_NA_1478.99_TRUE_VAR5_ALK_Malic acid (3TMS)	11.29 ± 3.85	13.37 ± 1.2
M000000_A149002-101-xxx_NA_1485.23_TRUE_VAR5_ALK_Threitol (4TMS)	9.25 ± 5.02	9.32 ± 2.61
M000000_A154001-101-xxx_NA_1528.56_TRUE_VAR5_ALK_Erythronic acid (4TMS)	7.33 ± 3.72	8.9 ± 3.98
M000000_A159003-101-xxx_NA_1575.36_PRED_VAR5_ALK_NA	8.08 ± 4.7	9.49 ± 4.75
M000000_A163001-101-xxx_NA_1614.59_TRUE_VAR5_ALK_Glutamic acid (3TMS)	**4.52 ± 4.07**	**6.98 ± 4.26**
M000000_A168001-101-xxx_NA_1666.44_TRUE_VAR5_ALK_Asparagine (3TMS)	3.33 ± 4.2	2.87 ± 3.4
M000000_A170001-101-xxx_NA_1688.9_PRED_VAR5_ALK_NA170001 (classified unknown)	8.12 ± 4.84	9.17 ± 2.63
M000000_A178005-101-xxx_NA_1759.34_TRUE_VAR5_ALK_Lyxonic acid (5TMS)	7.49 ± 2.95	9.6 ± 3.28
M000000_A182004-101-xxx_NA_1804.71_TRUE_VAR5_ALK_Citric acid (4TMS)	4.51 ± 3.58	6.32 ± 5.29
M000000_A183002-101-xxx_NA_1817.76_PRED_VAR5_ALK_Pinitol. D- (5TMS)	11.41 ± 4.91	11.01 ± 2.63
M000000_A187002-101-xxx_0_1853.93_TRUE_VAR5_ALK_Fructose (1MEOX) (5TMS) MP	6.3 ± 3.73	7.75 ± 4.22
M000000_A188004-101-xxx_0_1863.13_TRUE_VAR5_ALK_Fructose (1MEOX) (5TMS) BP	6.29 ± 3.73	7.83 ± 4.26
M000000_A188006-101-xxx_NA_1868.11_TRUE_VAR5_ALK_Glucopyranoside. 1-O-methyl-. alpha- (4TMS)	8.43 ± 3.14	10.9 ± 3.38
M000000_A189002-101-xxx_0_1880.5_TRUE_VAR5_ALK_Glucose (1MEOX) (5TMS) MP	9.04 ± 5.42	6.27 ± 3.36
M000000_A191001-101-xxx_NA_1899.05_TRUE_VAR5_ALK_Glucose (1MEOX) (5TMS) BP	7.67 ± 5.3	4.89 ± 3
M000000_A193002-101-xxx_NA_1913.17_TRUE_VAR5_ALK_Mannitol (6TMS)	7.57 ± 5.05	6.17 ± 2.61
M000000_A195006-101-xxx_NA_1945.97_PRED_VAR5_ALK_Ononitol (5TMS)	10.73 ± 4.21	7.56 ± 2.86
M000000_A196001-101-xxx_NA_1952.77_PRED_VAR5_ALK_Gulonic acid (6TMS)	8.51 ± 2.35	11.1 ± 3.21
M000000_A209002-101-xxx_NA_2080.23_TRUE_VAR5_ALK_Inositol. myo- (6TMS)	8.97 ± 2.66	8.93 ± 3.37
M000000_A211007-101-xxx_NA_2102.03_PRED_VAR5_ALK_NA	7.24 ± 3.69	8.03 ± 4.41
M000000_A213001-101-xxx_NA_2121.34_PRED_VAR5_ALK_NA213001	1.19 ± 0.38	2.87 ± 5.31
2256.56_Lupanine	9.41 ± 6.13	4.97 ± 5.52
M000000_A264001-101-xxx_0_2622.87_TRUE_VAR5_ALK_Sucrose (8TMS)	13.2 ± 3.28	12.57 ± 1.88

Fig. B.2: Annotated signals of the metabolic profiling. Table without normalised Glucopyranose signal.

References

Hsiao T.C. (1973) Plant responses to water stress. Annual Review Plant Physiology:519–570.

Kopka J., Schauer N., Krueger S., Birkemeyer C., Usadel B., Bergmuller E., Dormann P., Weckwerth W., Gibon Y., Stitt M., Willmitzer L., Fernie A.R., Steinhauser D. (2005) GMD@CSB.DB: the Golm Metabolome Database. Bioinformatics **21**:1635–1638.

Lommen A. (2009) MetAlign: Interface-Driven, Versatile Metabolomics Tool for Hyphenated Full-Scan Mass Spectrometry Data Preprocessing. Analytical Chemistry **81**:3079–3086.

Luedemann A., Strassburg K., Erban A., Kopka J. (2008) TagFinder for the quantitative analysis of gas chromatography--mass spectrometry (GC-MS)-based metabolite profiling experiments. Bioinformatics **24**:732–737.

Oliver M.J., Guo L., Alexander D.C., Ryals J.A., Wone B.W.M., Cushman J.C. (2011) A Sister Group Contrast Using Untargeted Global Metabolomic Analysis Delineates the Biochemical Regulation Underlying Desiccation Tolerance in Sporobolus stapfianus. The Plant Cell **23**:1231–1248.

Strehmel N., Kopka J., Scheel D., Böttcher C. (2014) Annotating unknown components from GC/EI-MS-based metabolite profiling experiments using GC/APCI(+)-QTOFMS. Metabolomics **10** [online] URL: http://link.springer.com/10.1007/s11306-013-0569-y (accessed 16 December 2015).

Yobi A., Wone B.W.M., Xu W., Alexander D.C., Guo L., Ryals J.A., Oliver M.J., Cushman J.C. (2013) Metabolomic Profiling in Selaginella lepidophylla at Various Hydration States Provides New Insights into the Mechanistic Basis of Desiccation Tolerance. Molecular Plant **6**:369–385.

10.3 Manuscript 3

Niche conservatism or niche shift? Implications for the management of a legume invader

in prep. for re-submission

Vanessa M.S. Vetter[1,2], Anja Jaeschke[3], Constanze Buhk[2], Anke Jentsch[1]

[1]Disturbance Ecology, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

[2]Geoecology/Physical Geography, University of Landau, Fortstr. 7, 76829 Landau, Germany

[3]Biogeography, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

Corresponding author: Vanessa Vetter, vanessa.vetter@uni-bayreuth.de, phone: 0049 (0) 921552305

ABSTRACT

Plant ecosystem engineers modulate limiting abiotic and biotic resources of other species. By changing the habitat conditions to their needs, those plant species become highly effective invaders, and also show major impact on the affected ecosystems. Here, we analyze the niche dynamics of the globally invasive, nitrogen fixing ecosystem engineer *Lupinus polyphyllus* across North America (native) and the European continent (invasive). Additionally, we are estimating the maximum amount of suitable habitat under current and future climate conditions, as well as invader impact.

We calculated the niche dynamics of *L. polyphyllus* by testing for a shift of the niche centroid, and estimating niche stability, unfilling and expansion of the native and invasive range. Based on the niche calculations, we fitted species distribution models (SDM) using an ensemble modelling approach to relate the species occurrences of *L. polyphyllus* to climate and soil variables across the large spatial scales of the two continents, North America and Europe.

Niche stability between the native and invasive niche of *L. polyphyllus* was 79.61% and niche unfilling 1.24%. In addition, we observed a shift in the niche centroid (Euclidean distance = 3.452) and a niche expansion (20.39%) in the invasive range. This points to a niche shift of the legume ecosystem engineer in its invasive range of Europe.

Central Europe shows a very high habitat suitability for *L. polyphyllus* under current climate conditions, alongside with the coastal areas and mountainous regions of northern, southern and eastern Europe. In its native range, *L. polyphyllus* preferably covers mountainous regions and the coastal areas of the US West Coast. The invader’s amount of suitable habitat is projected to increase in the course of climate change in both ranges. At the same time, the habitat suitability is projected to decrease, especially for the invasive range albeit remaining overall suitable for the invader.

Lupinus polyphyllus has not yet reached its niche saturation in its invasive range of Europe and the amount of suitable habitat is projected to increase due to climate change. Consequently, it is highly probable that its invasion process will continue to progress albeit the general decrease in habitat suitability.

Keywords: alien species, biological invasions, biomod, climate change, ensemble model, environmental niche model, terrestrial plant invader, niche dynamics, niche shift, non-native species, range shift, transformer species.

INTRODUCTION

Ecosystem engineers (Jones et al., 1994) are often intentionally introduced to new environments by humans e.g. for soil and water conservation, soil improvement or to restore degraded ecosystems (Ayanu et al., 2015; Vetter et al., 2018). They generally possess traits that can positively influence soil stability, nutrient and hydrological cycling, and light infiltration (Ayanu et al., 2015) and show protective characteristics, e.g. reduced erosion (Fei et al., 2014; Vetter et al., 2018). However, if they become invasive, those positive traits of the respective alien ecosystem engineer can have negative and long-lasting effects on native communities and ecosystem properties (Catford et al., 2012; Fei et al., 2014; Richardson et al., 2000) that often extend far beyond its life span and/or presence (Ehrenfeld, 2003, 2010; Richardson et al., 2000). Especially invasive ecosystem engineers can strongly influence native ecosystems by altering energy, water and/or nutrient fluxes (e.g. *Myrica faya* a nitrogen fixing tree invasive in Hawaii: Vitousek et al. 1987; or *L. nootkatensis* a nitrogen fixing invasive legume in Iceland: Vetter et al. 2018). While the general threat imposed by non-native species is discussed controversial (Boltovskoy et al., 2018; Goodenough, 2010), it is highly likely that invasive ecosystem engineers will cause shifts in the ecosystem functions of the affected habitat and thus, might subsequently lead to biodiversity loss (Bellard et al., 2016; Simberloff et al., 2013), large scale homogenization and reduced ecosystem (multi-) functioning (Buhk and Jungkunst, 2019; Ehrenfeld, 2010).

The globally invasive neophyte *Lupinus polyphyllus* (Lindley 1827) (Fremstad, 2010; Vetter et al., 2019), a perennial forb, potentially profits from climate change (Lauterbach and Nehring, 2013). In general, climate change (IPCC, 2014) might favor biological invasions directly by warmer temperatures, prolonged growing seasons or elevated CO_2 (Liu et al., 2017), as well as by indirect effects like the enhanced establishment and spread of plants after disturbances and land-use change (Hulme, 2017). Hence, large areas might become increasingly accessible to invasive species. *Lupinus polyphyllus* is additionally promoted by human activities, has a high potential of reproduction and dispersal, tends to monopolize resources (Lauterbach and Nehring, 2013) and acts as an ecosystem engineer altering nutrient dynamics (nitrogen fixation) and biodiversity patterns (Beyschlag et al., 2009; Falinski, 1998; Lauterbach and Nehring, 2013). Locally extreme invasions of *L. polyphyllus* occur and the reasons are not fully understood (Dengler and Tischew, 2018; Klinger et al., 2019). In Central Europe, the invasion of *L. polyphyllus* jeopardizes extensively managed semi-natural grasslands of high conservation value (Otte and Maul, 2005; Ramula and Pihlaja, 2012; Thiele et al., 2010). Thus, there is still a crucial gap of knowledge on the invasion potential of *L. polyphyllus* in Europe (Dengler and Tischew, 2018).

Most projections of future distribution patterns of plant invaders assume niche conservatism (the environmental conditions under which the species is able to grow and survive in the invasive range are similar to those of the native range), which has been shown to be the case for several invader species

(Petitpierre et al., 2012). However, niche shifts (a change in the centroid and/or limits of the niche envelope in the environmental space of the invaded range as compared to the native range) have been observed in other species as well (Alexander and Edwards, 2010; Broennimann et al., 2007; Tingley et al., 2014). Species distribution models (SDMs) correlate environmental conditions with the occurrence of species to assess the occupied environmental space. They are commonly applied to estimate the drivers of species' distributions as well as to project range changes of (invasive) species especially in times of global climate change. One major focus of SDMs lies on the projection of a potential spread of invasive species to assess management implications. The potential to correctly project the future ranges of invasive species using classical distribution models depends on 1) whether or not the species was tested for a niche shift, 2) the spatial resolution, and 3) if non-climatic factors were additionally included into the model (Bellard et al., 2018; Guisan et al., 2014; Hulme, 2017).

Here, we tested for a shift in the realized niche of *L. polyphyllus* at a relatively fine spatial resolution (2.5 minutes) and also included non-climatic factors to get a more detailed understanding of the niche dynamics in the invaded range (Callen and Miller, 2015; Guisan et al., 2014). With a subsequently applied SDM, which we fitted based on the results of the niche shift analysis, we projected the amount of suitable habitat on the European continent in the near future as well as performed large-scale analyses of the geographic responses of the invader to different climate change scenarios in both native and invaded range.

We focused on two main objectives: 1) we calculated niche indices to verify whether or not *L. polyphyllus'* niche has shifted towards a broader range of suitable environmental conditions in its invasive range of the European continent compared to its native range in North America, and 2) we estimated the potential distribution of *L. polyphyllus* to identify the propagation limits of the invader on the European continent under current and future environmental conditions.

STUDY SPECIES

Lupinus polyphyllus (Fabaceae) is native to the United States (lower 48 states, without Alaska and Hawaii) and Canada (Beuthin, 2012), but invasive globally, including many European countries, Chile, southern Australia and New Zealand (Fremstad, 2010; Jauni and Ramula, 2016; Ramula and Sorvari, 2017). The species was originally introduced to Europe in the 1900s as a cover crop for soil amelioration, fodder, and as an ornamental plant (Fremstad, 2010), but currently represents a threat for native plant communities and is rapidly spreading across Europe (Dengler and Tischew, 2018; Fremstad, 2010; Thiele et al., 2010). *Lupinus polyphyllus* has recently started to spread into new habitats without major human interference and now threatens large areas of species-rich mountain meadows (Dengler and Tischew, 2018; Hejda et al., 2009; Otte and Maul, 2005; Thiele et al., 2010). In its native range, North America, *L. polyphyllus* prefers rather moist habitats, seasonally wet soils but is also found in seasonally dry habitats (Beuthin, 2012). *Lupinus polyphyllus* is found at the Pacific coast with an oceanic, humid and warm to temperate climate, as well as in the eastern parts of North America with a more continental climate (Beuthin, 2012; Fremstad, 2010; Volz, 2003). According to the Federal Agency for Nature Conservation Germany, *L. polyphyllus* prefers acid to moderately acid soils and silicate bedrock in its invasive range Europe, but is seldom found in organic rich soils and regions with low summer precipitation (Fremstad and Elven, 2008; Starfinger and Kowarik, 2011).

MATERIAL AND METHODS

All analyses as well as the preparation of spatial data were performed using the open source software R version 3.4.2 (R Core Team, 2017) and QGIS 2.16.3.

Data preparation

We pre-selected climate and soil data, which are associated with the range limits of *L. polyphyllus* according to literature, by expert knowledge (Table 1). We downloaded eleven bioclimatic layers (WorldClim 2.0, Fick and Hijmans, 2017) as well as two soil variables, pH and plant available water content, each at seven standard depths summing up to 14 soil layers (SoilGrids, Hengl et al., 2014). Climate and soil data for current conditions were obtained at a spatial resolution of 2.5 minutes ($\approx$ 25 km^2) and a projection of WGS84. All environmental layers (raster) were cropped to the study extent of North America and Europe including whole of Russia, Turkey and Kazakhstan.

The species occurrence data of *L. polyphyllus* was obtained from the Global Biodiversity Information Facility (Gbif.org, 2019). To ensure a consistent quality of data, the 103752 available species records were checked and sorted out as follows: we excluded all species occurrence records without latitude and longitude coordinates, all countries not relevant for our study extent (New Zealand, Chile, Mexico) or without any country information, and all occurrence records with basis of record “fossil specimen”, “literature”, ”material sample”, “preserved specimen”, and “unknown”. We only kept occurrence records with basis of record “(human) observation”, and “living specimen”. We excluded all occurrence records without a given collection code and institution code. Additionally, we only kept occurrences with a scientific institution or collection code, or which were recorded by citizen science. Finally, we made sure that the remaining subspecies and varieties are all synonyms for *L. polyphyllus* (Beuthin, 2012). From the remaining 44293 occurrences we removed 25611 duplicate entries and 1057 occurrences laying slightly outside of the two continents, Europe and North America. Finally, we thinned out clusters of heaped occurrences in the realized niches of *L. polyphyllus* separately for the remaining 211 native and 17414 invasive occurrence points. Therefore, we run two principal component analyses (PCA), one for each range, taking into account the spatial heterogeneity of the respective environment. Based on these PCAs we spatially rarefied our occurrence points range-wise using the spThin package (version 0.1.0; Aiello-Lammens et al. 2014). For the native range a minimum distance of 10 km (thin.par = 10) between two occurrence records was determined, while in the invasive range a minimum distance of 14 km (thin.par = 14) gave the best results for the thinning process. The spatial rarefication resulted in 190 native and 1531 invasive occurrence points, which characterized the respective realized niches of *L. polyphyllus* in each range.

We selected the final variables for the niche shift calculations and the SDM via hierarchical partitioning (package hier.part version 1.0-4, Walsh and Mac Nally 2013; Table 1) based on the 25 pre-selected environmental variables for current climate conditions and the processed occurrence points of *L. polyphyllus*. We selected all soil variables with a total explained variance > 16%, while the threshold of the climate variables was set to > 10% total explained variance (Table S1).

Table 1: Environmental predictor variables pre-selected by expert knowledge. Variables in bold were chosen by hierarchical partitioning. The latter were used for the niche shift calculations and to calibrate the species distribution model of *L. polyphyllus* under current climate conditions. For projections under future climate conditions, only climate variables were used.

Category	**Variables**	**Source**	**Reference**
Climate data	max. temperature of warmest month, **min. temperature of coldest month**, **temperature annual range**, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, precipitation of wettest month, **precipitation of driest month**, precipitation of wettest quarter, **precipitation of driest quarter**, precipitation of warmest quarter	Bioclimatic variables WorldClim 2.0 – Global Climate Data of the current (1970-2000) climate conditions. (Fick and Hijmans, 2017) Bioclimatic variables for future climate scenarios (CMIP5; reference period 2041-2060) MPI_ESM-LR (RCP 4.5, RCP 8.5) HadGEM2-ES (RCP 4.5, RCP 8.5) (Hijmans et al., 2005)	Own consideration in accordance with (Becker et al., 2005; Beuthin, 2012; Fremstad, 2010; Vetter et al., 2019)
Soil	pH (in KCL solution) 0 cm, 5 cm, **15 cm**, **30 cm**, 60 cm, 100 cm, **200 cm** available water content 0 cm, 5 cm, 15 cm, 30 cm, **60 cm**, **100 cm**, **200 cm**	(Hengl et al., 2014)	(Fremstad and Elven, 2008; Starfinger and Kowarik, 2011; Thiele et al., 2010)

Niche calculations

Following the COUE-approach proposed by Guisan et al. (2014) to quantify and decompose niche changes between native and invasive ranges, we tested for a centroid shift (C), niche overlap (O, also known as niche stability), niche unfilling (U) and niche expansion (E) of *L. polyphyllus*.

We subjected the variables selected by hierarchical partitioning as well as the occurrence records of both ranges to a principal component analysis to characterize the environmental niche space of *L. polyphyllus* (Broennimann et al., 2012). All niche analyses were based on the first two axes of the PCA, which spanned a two-dimensional gridded environmental space (100 x 100 grid).

We used Euclidean distances to calculate the potential shifts in the centroid of 1) the niche space as well as 2) the occurrences within the overall niche envelope (Broennimann et al. 2012; Guisan et al. 2014). Niche overlap was tested using Schoener's D (Schoener, 1970; Warren et al., 2008). Schoener's D varies between 0 and 1, indicating either no overlap between the two niches or a complete overlap respectively (Schoener, 1970). Based on the metric Schoener's D we tested for niche equivalency and niche similarity (Warren, Glor, and Turelli 2008; Broennimann et al. 2012; Tingley et al. 2014) implemented in the R package ecospat (version 3.0; Di Cola et al. 2017; Broennimann, Di Cola, and Guisan 2018). We assessed the statistical significance (α = 0.05) of both tests by running 1000 randomizations (Broennimann, Di Cola, and Guisan 2018).

Niche expansion and unfilling were calculated (R package ecospat; Di Cola et al. 2017; Broennimann, Di Cola, and Guisan 2018) using all available environments of each range, thus also including marginal environments, which we believe are likely to depict the invasion front of *L. polyphyllus* (Tingley et al. 2014; Broennimann et al. 2012). Niche unfilling represents the part of the native niche that is not overlapping with the invasive niche, whereas niche expansion reflects the part of the invasive niche that is not overlapping with the native niche (Tingley et al., 2014).

Species distribution model

We developed four species distribution models (SDM) to project the potential distribution of *L. polyphyllus* across the European continent as well as in its native range North America under current and future climate conditions. We had two basic SDM types: 1) the SDM was fitted and trained under current conditions in both ranges, native and invasive, using all of the rarefied species occurrence records; 2) the SDM was fitted and trained under current conditions in the invasive range, using only the spatially rarefied occurrence records on the European continent. Each of these two basic SDMs was fitted twice: 1) with all variables chosen by hierarchical partitioning and 2) using only the climate variables. SDMs fitted with all environmental predictor variables were used only to project the potential distribution of *L. polyphyllus* under current climate conditions, while SDMs that were fitted with the climate variables only were used to project the potential distribution of *L. polyphyllus* under future climate conditions.

We did not include the soil data selected by hierarchical partitioning into the future projections of our SDMs, as there are no future scenarios of soil pH and soil moisture available. Climate change will very likely have an impact upon soils in general, and on soil moisture and soil pH in particular (Collins et al., 2009; Rengel, 2011; Stastny, 2008). Soil moisture is highly dependent upon the prevailing precipitation regime and thus, the current soil moisture layers cannot be used to project *L. polyphyllus'* distribution under a changing future climate. Accordingly, soil pH is also likely to change along with climate due to higher carbon depositions and increased leaching of basic cations due to heavy rainfalls (Rengel, 2011).

Analogous to the current climate variables (bioclimatic layers, WorldClim 2.0) we used downscaled and calibrated climate data from the global climate models (GCM) HadGEM2-ES and MPI_ESM-LR for the years 2041-2060 (Hijmans et al. 2005, WorldClim 1.4, Tab. 1) as climate variables for future projections. We calculated projections for both, the medium stabilization (RCP 4.5) (Thomson et al., 2011) and very high baseline emission (RCP 8.5) (Riahi et al., 2011) representative concentration pathways of the IPCC's fifth assessment report (IPCC, 2013). Future climate projections were obtained at a spatial resolution of 2.5 minutes ($\approx$ 25 km^2) and were cropped to the study extent of North America and Europe including whole of Russia, Turkey and Kazakhstan.

For both SDMs, we used the ensemble modeling approach implemented in the biomod2 package version 3.3-7 (Thuiller et al. 2016) using four different modelling algorithms: generalized linear models (GLM), generalized boosted models (GBM), random forests (RF), and Maxent. The benefit of ensemble predictions across several model algorithms is that it reduces the uncertainties which arise with single model predictions. We used the "probability mean" provided by biomod2 to calculate the ensemble, as it has been reported to be the most robust consensus method (Jaeschke et al., 2012; Marmion et al., 2009). Individual model runs were validated using one-time data splitting by randomly partitioning the data set in 70% training and 30% test data (Jaeschke et al., 2012). To assess the accuracy of the SDMs we used the area under the receiver operating characteristic curve (AUC) and true skill statistics (TSS). We used the AUC cutoff of the ensemble model as a threshold for identifying suitable habitat for *L. polyphyllus*.

In the main manuscript we only show results for the SDMs fitted and trained in both ranges. Results of the SDMs fitted and trained in the invasive range only, can be found in the appendix (Figure S1 and Figure S2).

RESULTS

Niche calculations

The first two axes of the principal component analysis (PCA), based on the variables chosen by the hierarchical partitioning (Table 1), accounted for 76.73%, while the first three axes accounted for 92.88% of the variation in the data. The first PCA axis was positively related to the minimum temperature of the coldest month, and the precipitation of the driest month and quarter, but negatively associated with the temperature annual range, whereas the second axis was positively associated with soil pH but negatively with soil moisture (Figure 1c).

The native and invasive range of *L. polyphyllus* were equivalent to each other as the observed overlap was not higher than between two random niches (Schoener's D = 0.158, niche equivalency test: p = 0.960). Both, the native and the invasive niche, were more similar to each other than would be expected by chance (niche similarity test: $p_{\text{niche conservatism}} = 0.002$; $p_{\text{niche divergence}} = 0.998$ for niches randomly shifted in both ranges). However, we observed a shift in the niche centroid (Euclidean distance = 3.452), as well as in the occurrences within the overall niche envelope (Euclidean distance = 3.661, Figure 1a-b). Including all marginal climates in both the native and invasive range, niche stability of *L. polyphyllus* was 79.61%, while 20.39% of the invasive niche were non-overlapping with the native niche (expansion), and 1.24% of the native niche were non-overlapping with the invasive niche (unfilling). Thus, our results suggest very low variance in the native realized niche of *L. polyphyllus* compared to its invasive European niche, but increased variance in the invasive realized niche.

The main difference in the two realized niches of *L. polyphyllus* in the respective ranges are based on different characteristics in the preferences of climate and soil moisture variables (Figure 2). For the climate variables, the main difference lies in the density of the occurrences of the respective parameter characteristic (Figure 2a-d). Although the species tolerates similar temperature ranges, its prevalence/main occurrence in the native range lies in significantly colder areas (-10°C to -20°C) than in the invasive range (-5°C; Figure 2a). In the annual temperature range as well, the main density of occurrence lies in more continental areas in its native range compared to the invasive range of Europe (Figure 2b). Precipitation-wise, the native realized niche of *L. polyphyllus* is characterized by two major peaks, likely representing the major differences in precipitation of the two main distribution areas of the invader. One main area of occurrence is at < 2.5 mm/< 10 mm precipitation of the driest month/quarter, and the other peaks at 7.5 mm/25 mm respectively, while the majority of the invasive occurrences is located exactly between these two extremes (5 mm/15 mm precipitation of the driest month/quarter).

Across all three soil depths tested, *L. polyphyllus* prefers rather wet soil conditions in its invasive range, while coping with drier soils in its native range (Figure 2e,f,g). The width of the soil moisture niche is significantly wider in the invasive range compared to the native niche.

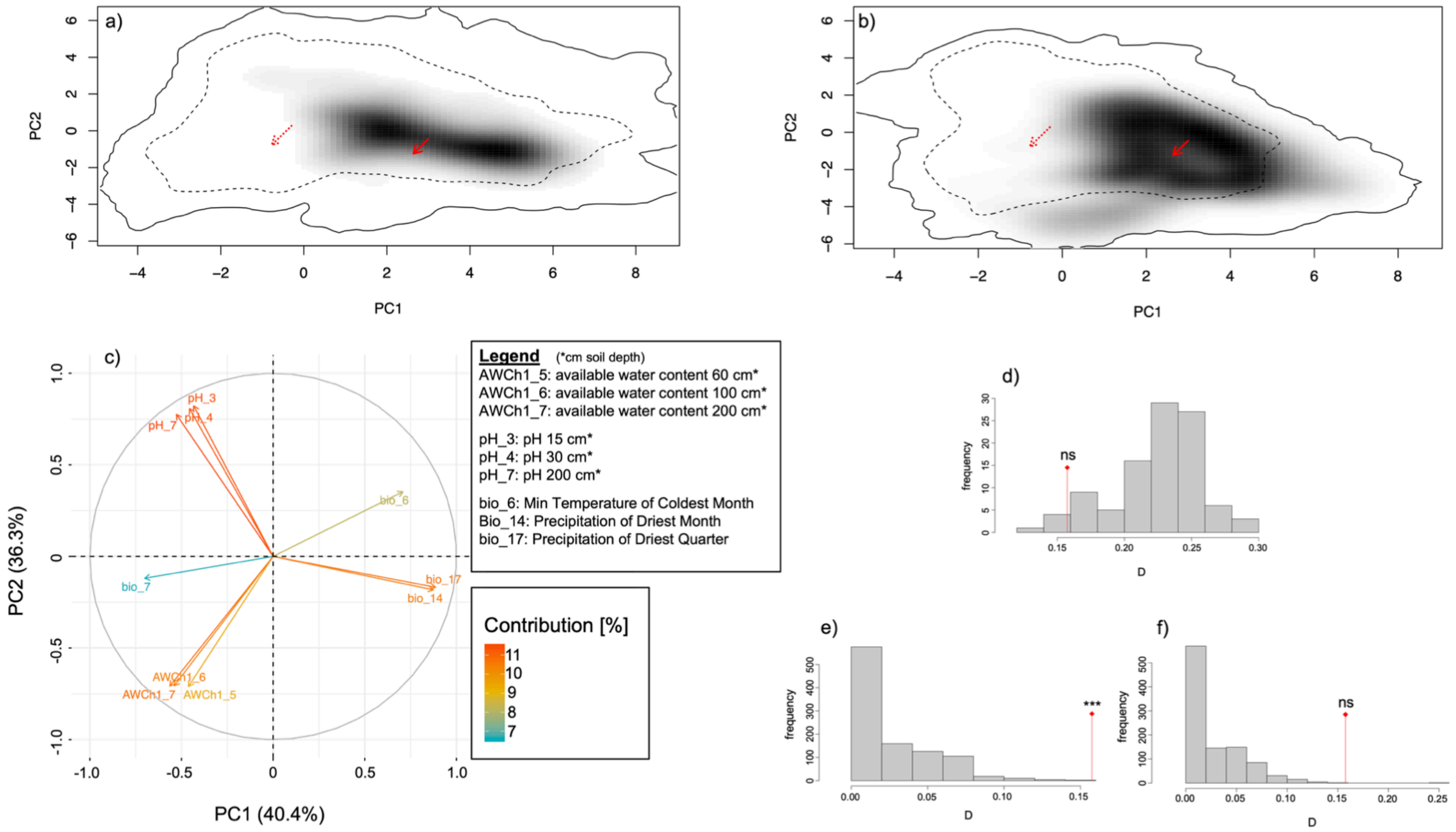


Figure 1: Niche of *L. polyphyllus* in environmental space, shown along the first two axes of the PCA **a)** in its native range North America (NA) and **b)** in its invasive range Europe (EU). Density of the occurrences of *L. polyphyllus* is depicted in grey shading: the darker the more occurrences there are in this area of the environmental space. Solid contour line: 100% of the available background environment, dashed contour line: 50 % of the available background environment. Arrows indicate the shift of the centroid of the niche between NA and EU. **c)** The contribution of the environmental variables on the two axes of the PCA (PC1, PC2) and the percentage of variability explained by PC1 and PC2. **d) – f)** Observed niche overlap based on Schoener's D between the two ranges (red bars with a diamond) and the simulated niche overlaps (grey bars) shown as histograms. **d)** Niche equivalency, **e)** niche conservatism and **f)** niche divergence between the native and invasive range. Both niches are randomly shifted in both areas and significance tests are calculated from 1000 iterations (ns = not significant; *** = P < 0.001) (Broennimann et al., 2012). Figures 1 a, b and d to f were built using the R package ecospat version 3.0 (Broennimann et al., 2018), while figure 1 c was built using the R package factoextra version 1.0.5. (Kassambara and Mundt, 2017).

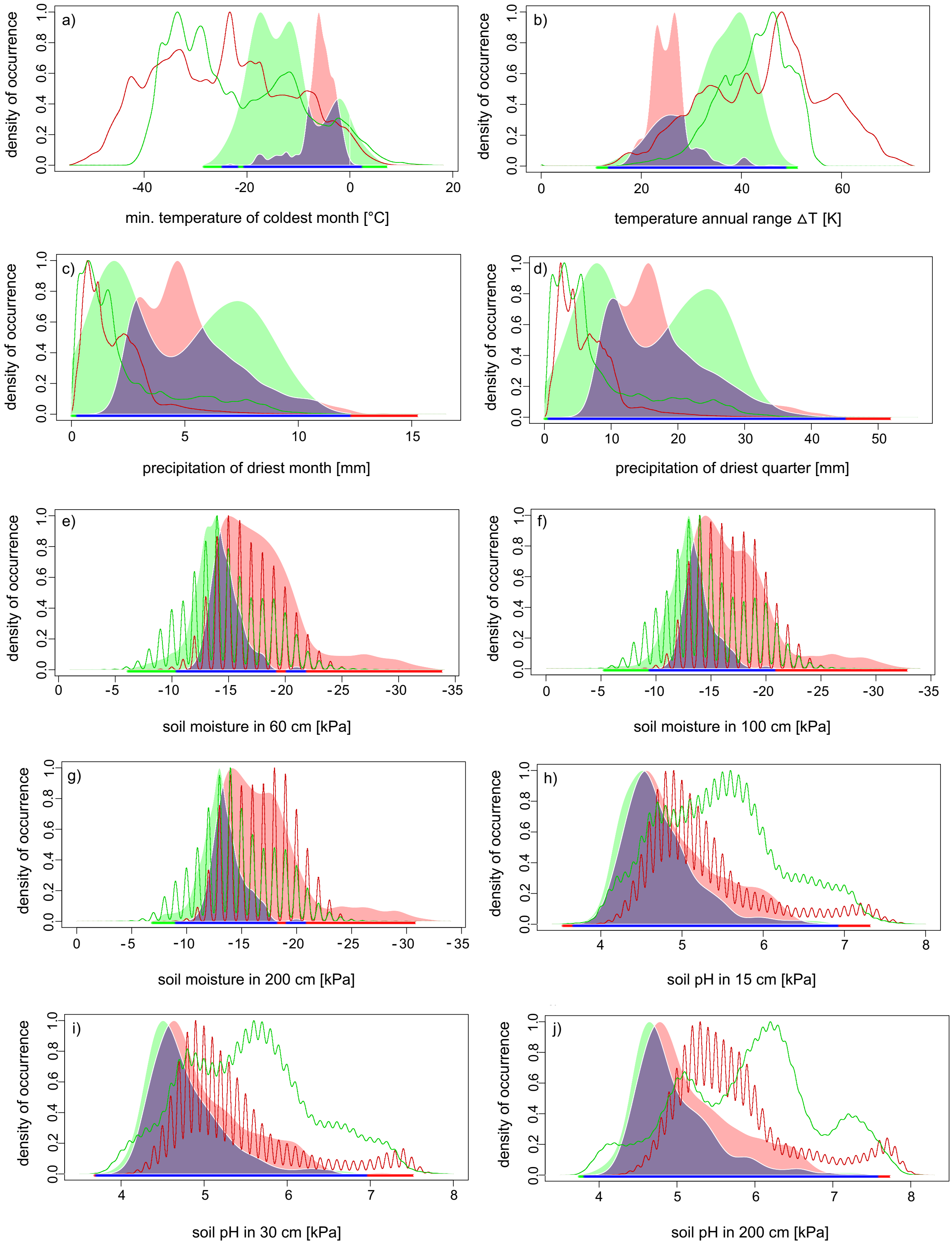


Figure 2: Niche dynamics of *L. polyphyllus* shown along the gradient of predictor variables used in the PCA. Densities of occurrences in the native (NA) and invasive range (EU) of *L. polyphyllus* show areas of niche unfilling in green and areas of niche expansion in red. Niche overlap is depicted in purple. Green and red lines delimit the native and the invasive extent of the predictor variables, respectively.

Species distribution model

Both SDMs showed a good predictive ability as measured by the area under the curve ($\text{AUC}_{\text{SDM all variables}}$ = 0.982; $\text{AUC}_{\text{SDM climate only}}$ = 0.980) and the true skill statistics ($\text{TSS}_{\text{SDM all variables}}$ = 0.871; $\text{TSS}_{\text{SDM climate only}}$ = 0.857). All values above the AUC cutoff point ≥ 360 (all variables) and ≥ 334 (climate only) respectively were interpreted as suitable lupine habitat.

Under current climate conditions, Central Europe as well as the European mountain ranges and coast lines seem to be most exposed to lupine invasion. Main occurrences of *L. polyphyllus* are to be expected in Central Europe and Great Britain, spreading up to Iceland and the coast lines of Norway and Sweden, and down in a southerly direction to Greece and the coast of northern Turkey (Pontic Mountains). Another area of main occurrences are the European mountains, especially the Carpathian Mountains, the Alps, the Apennines, the Pyrenees and the Cantabrian Mountains, as well as parts of the Caucasus Mountains (Figure 3a-b).

Under future climate conditions, *L. polyphyllus* showed an increase of its range while the models projected a decrease of habitat suitability with proceeding climate change especially in large areas of those regions of Central Europe which are projected to be highly suitable under current climate conditions (Figure 3c-f). Climate change seems not to particularly promote the spread of *L. polyphyllus* in its invasive range (Figure 3c-f). Depending on the GCM and the respective concentration pathway scenario it seems likely that *L. polyphyllus* will be forced to move to higher latitudes and/or altitudes of Europe under future climate conditions. However, due to climate change, *L. polyphyllus* might be able to significantly expand its invasive range into large parts of Russia, although the general habitat suitability of these regions will not be very well suited for the invader.

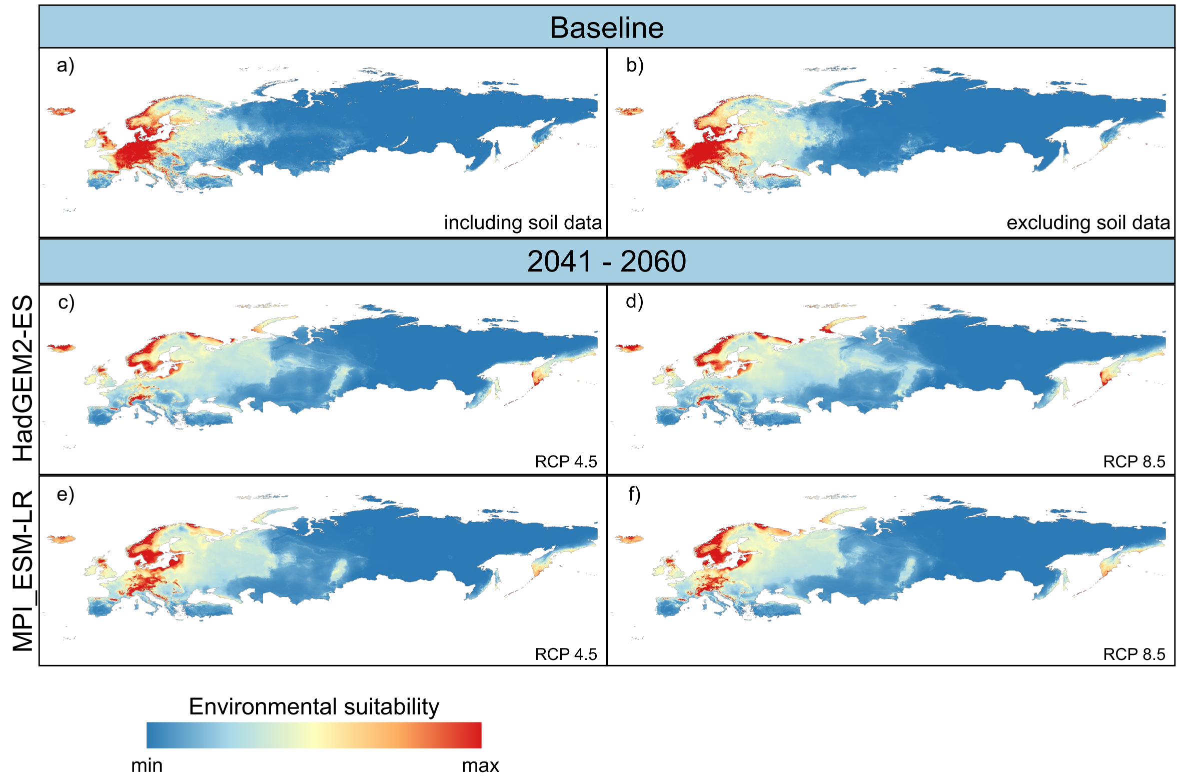


Figure 3: Projected potential distribution of *L. polyphyllus* across its invasive range in Europe under current (baseline) and future climate conditions (2041-2060). SDMs were fitted using all occurrence records of the native and invasive range, as well as using **a)** all 10 predictor variables, including soil and climate data and **b)** only the climate variables selected by hierarchical partitioning. The climate-based SDM (b) was used to project the potential distribution of *L. polyphyllus* under future climate conditions (panel c-f). Future climate conditions were modeled with the global climate models HadGEM2-ES and MPI_ESM-LR each in the medium stabilization (RCP 4.5) and very high baseline emission scenario (RCP 8.5). Environmental suitability ranges from: minimum = 0 to maximum = 1. AUC cutoff points of the probability mean of the ensemble predictions: a) 360, scaled to 0.360 and b) 334, scaled to 0.334 (depicted in yellow) respectively. Yellow and reds indicate occurrences, while shades of blue indicate absences. Yellow indicates the respective cutoff point of the SDM.

In its native range under current climate conditions, *L. polyphyllus'* main distribution is projected to be along the West Coast of the United States and Canada up to Alaska (Figure 4a-b). In its native range, the invader also seems to prefer coastal areas and mountainous regions comparable to the trend observed for its invasive range in Europe. At the East Coast of the United States and Canada, large areas are also well suited for *L. polyphyllus*, however, these regions do not achieve as high of a habitat suitability as the West Coast.

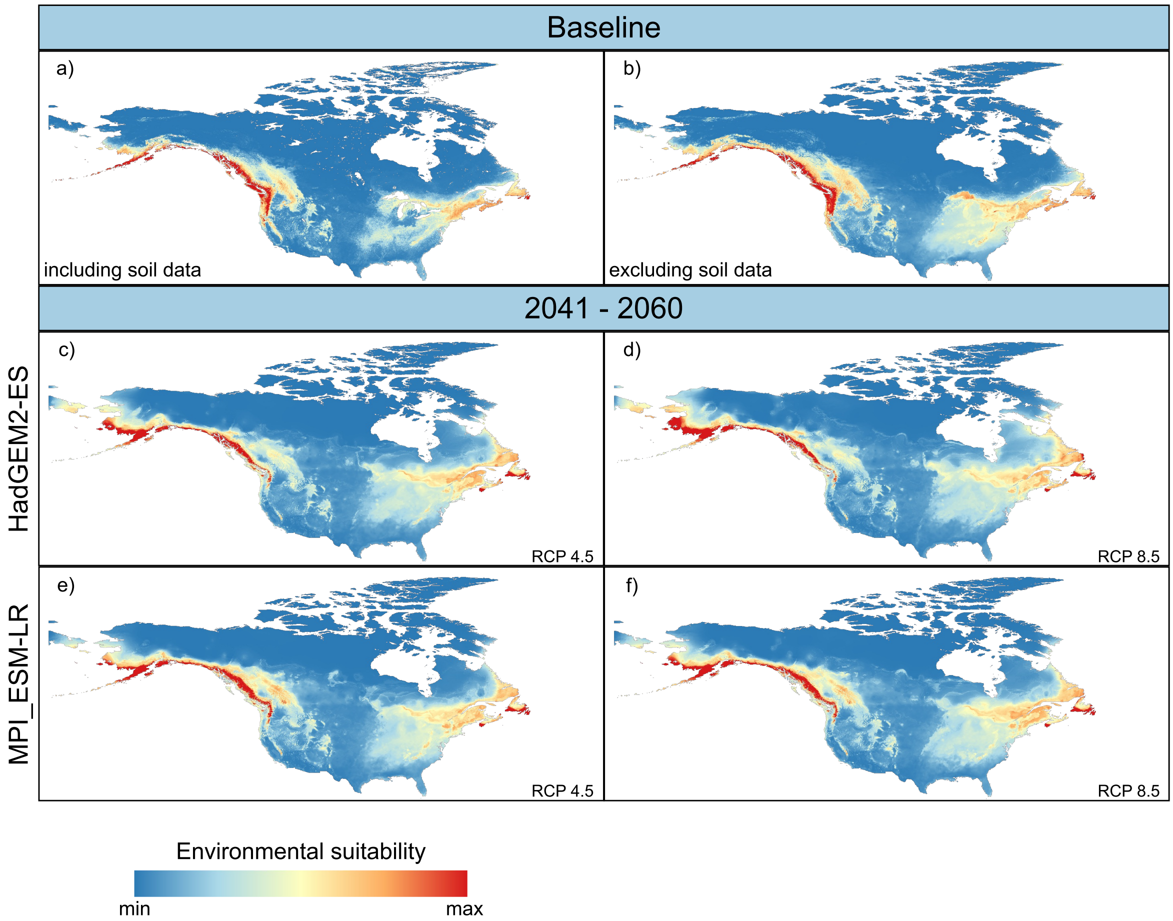


Figure 4: Projected potential distribution of *L. polyphyllus* across its native range in North America under current (baseline) and future climate conditions (2041-2060). SDMs were fitted using all occurrence records of the native and invasive range, as well as using a) all 10 predictor variables, including soil and climate data and b) only the climate variables selected by hierarchical partitioning. The climate-based SDM (b) was used to project the potential distribution of *L. polyphyllus* under future climate conditions (panel c-f). Future climate conditions were modeled with the global climate models HadGEM2-ES and MPI_ESM-LR each in the medium stabilization (RCP 4.5) and very high baseline emission scenario (RCP 8.5). Environmental suitability ranges from: minimum = 0 to maximum = 1. AUC cutoff points of the probability mean of the ensemble predictions: a) 360, scaled to 0.360 and b) 334, scaled to 0.334 (depicted in yellow) respectively. Yellow and reds indicate occurrences, while shades of blue indicate absences. Yellow indicates the respective cutoff point of the SDM.

Projections with soil variables are more conservative than projections with climate variables only. However, the projections do not differ in their general trend: the overall trend of which areas are suitable for *L. polyphyllus* can be seen in both projections and the SDMs mainly differ in the extent of habitat suitability. According to our projections, climate change will lead to an expansion of the amount of suitable habitat for *L. polyphyllus* in its native range (Figure 4c-f). Both GCMs project a habitat expansion to a northerly direction in its native range, however, the range expansion to the

North is much more pronounced in the HadGEM2-ES (Figure 4c-d) compared to the more conservative projections of the MPI_ESM-LR (Figure 4e-f).

DISCUSSION

Lupinus polyphyllus' **niche shifted to a broader range of environmental conditions**

Our results of the niche calculations confirm a high niche stability between the native and the invasive range of *L. polyphyllus*. The niches of *L. polyphyllus* were equivalent between the native range North America and the invasive range Europe. However, *L. polyphyllus* experiences an increased proportion of variance in the invasive range, thus the invaders niche seems to have shifted towards a broader range of suitable environmental conditions (Guisan et al., 2014; Tingley et al., 2014) on the European continent compared to its native range in North America. Consequently, it is highly likely that *L. polyphyllus* experiences niche shift (niche stability < 100%, niche expansion > 0%), in terms of a niche expansion in its invasive range (Cunze et al., 2018). The observed shift in the niche centroid might be perceived as an additional indication for the ongoing process of niche differentiation between the two ranges, as well as the shift in the density of occurrences within the overall niche envelope (Guisan et al., 2014; Tingley et al., 2014).

It is, however, unlikely that this niche expansion took place in the fundamental niche but in the realized niche. The environmental conditions which are new to the niche of *L. polyphyllus*, leading to the higher variation in the invasive range, might not be available to *L. polyphyllus* in its native range, either due to 1) biotic interactions and/or 2) dispersal limitations or because 3) environmental conditions do simply not exist in this combination in North America (non-analogous environmental conditions) (Guisan et al., 2014; Hutchinson, 1957; Tingley et al., 2014). The niche overlap test revealed that 64.78% of habitats are shared between the two niches of the invader. But, after we corrected for the availability of the environmental conditions in each range, only 15.75% of all the environments tested were shared. Thus, according to our results, the environmental conditions, in which *L. polyphyllus* experiences niche expansion, are likely already part of its fundamental niche but do not occur in the realized niche of the native range.

Those vacant parts in the niche of *L. polyphyllus'* native range are probably occupied by a variety of other lupine species in North America. While 200-300 *Lupinus* species co-occur with *L. polyphyllus* in a great variety of habitats in Northern and Southern America, only 12 *Lupinus* species are present in Europe and Africa (Panter et al., 2017; Wink, 1995). For example, *Lupinus nootkatensis* might restrict *L. polyphyllus'* expansion into more northern, cold-temperate to subarctic areas with shallow, nutrient poor and basic/alkaline soils in its native (Wink, 1995) as well as in its invasive range (Vetter et al., 2018; Wasowicz, 2016). Although our models projected suitable environmental conditions and *L. polyphyllus* is already present in Iceland (Fremstad, 2010), the majority of the suitable environmental niches might already be covered by *L. nootkatensis* under current, and most likely also under future climate conditions (Vetter et al., 2018; Wasowicz, 2016; Wasowicz et al., 2013).

In Central Europe, *L. polyphyllus* is primarily recorded from (slightly) acid soils and silicate bedrock (Starfinger and Kowarik, 2011), but is seldom found in organic rich soils and regions with low summer precipitation. However, in one of its invasive areas, Rhineland-Palatinate, *L. polyphyllus* is able to grow on soils with pH-values ranging from 3 to > 7 (unpublished data Vetter et al.). According to our niche calculations, *L. polyphyllus* seems to have expanded its realized niche towards more neutral to alkaline soil pH values in its invasive range while simultaneously covering the whole range of soil pH values of its native realized niche. Across all three soil depths tested, *L. polyphyllus* prefers rather wet soil conditions in its invasive range, while coping with drier soils in its native range. *Lupinus polyphyllus* might be restricted to dry, alkaline soil conditions in its native range due to competition effects/biotic interactions. Consequently, niche expansion might be due to a lack of competitors in its invasive range, thus, the invader can expand into areas already present in its fundamental niche. This is also evidenced by the very low proportion of niche unfilling, which indicates that the species occupies nearly all suitable habitats, which it can occupy based on the niche preferences of its home range. A high proportion of niche unfilling might be interpreted as an incomplete invasion process (Cunze et al., 2018). Conversely, a very low proportion of niche unfilling, as observed in *L. polyphyllus*, might thus indicate a far advanced, perhaps even completed, invasion process as the invader seems to be in an equilibrium between the potentially suitable niche space and the already occupied niche space. But, due to the ongoing niche expansion, a saturation of the invasion process of *L. polyphyllus* in Europe is unlikely.

Potential distribution and propagation limits of *L. polyphyllus*

Despite the fact that climate change is expected to lead to a decrease of invasive plant species range sizes (Bellard et al., 2018), the amount of suitable habitat of *L. polyphyllus* is projected to increase under future climate conditions (measured in total area suitable). Vetter et al. (2019) showed that *L. polyphyllus* – although displaying reduced performance under increased abiotic stress – still had a superior performance after an extreme drought event relative to native plant species. Consequently, *L. polyphyllus* might enforce its impact on native species under climate change, especially since the total amount of suitable habitat increases.

However, the overall habitat suitability for *L. polyphyllus* is projected to decrease in both ranges along with climate change, which can be attributed to the invader's cool area of origin (Beuthin, 2012). Large areas which are very well suited under current climate conditions are projected to be at the edge of suitability under future climate conditions. Therefore, it is highly likely that *L. polyphyllus* will not significantly profit from climate change in the amount of suitable habitat, but at the same time climate change might also not considerably limit its further spread across Europe. Because of its performance reduction under extreme drought events (Vetter et al., 2019) and the declining overall habitat suitability projected by our models, climate change might also support the management and targeted containment of *L. polyphyllus*. In those areas where *L. polyphyllus* tends to form mono-dominant stands, e.g. in species rich mountain hay meadows (Dengler and Tischew, 2018; Hejda et al., 2009; Otte and Maul, 2005; Thiele et al., 2010), the targeted containment of the species could be facilitated by a combination of management measures and extreme weather events (Guo et al., 2018). It is important to inform managers of areas with a high degree of risk of invasion by *L. polyphyllus* at an early stage, so that mass proliferation could be contained or prevented in areas of high conservational or agricultural value. Consequently, climate change might lead to different reactions in the two ranges, for example an opportunity for restoration and invasive species management in *L. polyphyllus'* invasive range, but a potential cause for conservation actions in its native range. However, a recent study indicates that a slight performance advantage of *L. polyphyllus* under combined extreme drought and competition effects might be enough for the legume invader to outcompete native species during phases of increased abiotic stress and thus, to use the arising "invasion window" (Vetter et al., 2019).

It seems as if *L. polyphyllus* will be forced to move upwards or northwards along with the native cold-adapted plant species which will possibly be expelled and forced to migrate with their shifting climatic niche (Parmesan, 2006; Phoenix and Lee, 2004; Vetter et al., 2018). Due to rising temperatures, (sub-)artic regions e.g. Iceland and the mountainous regions of Europe, will likely become a refuge for cold-adapted native plant species, but at the same time become more and more accessible to *L. polyphyllus* and possibly other alien plant species (Crumpacker et al., 2001; Kreyling, 2010; Vetter et al., 2018). The habitat expansion of the nitrogen fixing invader *L. polyphyllus* into cold biomes of Europe might lead to a replacement of the native species, which are adapted to nutrient-poor soils and might therefore possess poorer competitive performance compared to non-native species when faced with increased nutrient availability (Hiltbrunner et al., 2014; Liška and Soldán, 2004; Wasowicz, 2016). As a result, the impact of *L. polyphyllus* on native plants (and animals) which are already visible today (Hejda et al., 2009; Ramula and Pihlaja, 2012; Ramula and Sorvari, 2017; Thiele et al., 2010) might become more pronounced due to climate change. Further, due to the increasing accessibility of these habitats – warmer climate and increasingly favorable soil conditions as *L. polyphyllus* enriches it with nitrogen (Fremstad, 2010; Thiele et al., 2010) – presence of lupine might facilitate the establishment of invasive species (Simberloff and Von Holle, 1999). This phenomenon is already visible today, not only in *L. polyphyllus* (Otte and Maul, 2005; Thiele et al., 2010), but also in other legume invaders like *L. nootkatensis* (Magnusson, 2010; Magnusson et al., 2008).

Furthermore, and in addition to the negative effects on native ecosystems, the potential expansion of *L. polyphyllus* habitat also has economic consequences. Hay meadows invaded by *L. polyphyllus* lose their economic value as high quality fodder, e.g. for horses, due to the piperidine alkaloid content of the legume invader and its indigestibility for livestock (Beuthin, 2012; Hensgen and Wachendorf, 2016; Panter et al., 2017).

Challenges and the way forward

So far, there are no soil pH and soil moisture scenarios available for future climate conditions. Both soil parameters, pH and moisture, will likely change along with the prevailing climate (Collins et al., 2009; Rengel, 2011; Stastny, 2008). Therefore, future soil scenarios are very much needed to correctly project the future habitat suitability of species. Due to the lack of future scenarios for most environmental predictor variables besides climate, species distribution modelling is highly dependent on climate variables only, although recent publications showed that inclusion of non-climatic factors significantly improves both, niche shift calculations as well as the projections of SDMs (Bellard et al., 2018; Guisan et al., 2014; Hulme, 2017).

High-quality, structured species occurrence data sets are often rarely available for species distribution modeling (Dennis et al., 2017; Kamp et al., 2016; Sumner et al., 2019), neither for the native nor for the invasive range of a species. However, citizen scientists can generate valid and useful data (Pocock et al., 2015; Sumner et al., 2019), especially when the species of interest is easy to distinguish like *L. polyphyllus*. We did not exclude citizen science data in our model. However, since citizen science data has a high potential to be spatially biased, we corrected for a potential spatial bias in both ranges by spatially rarefying our occurrence points based on their distribution in the environmental space.

We modelled the probability of arrival of *L. polyphyllus* across the European continent (Ibáñez et al., 2009), but actual arrivals are a rare stochastic event (Pocock et al., 2017). The opportunistic reporting of observations by the general public (citizen science) might be a potential cost-effective method for early detection of *L. polyphyllus’* arrival across large spatio-temporal scales (Pocock et al., 2017; Roy et al., 2015), especially when focusing on the areas around existing occurrences as well as areas at high risk of invasion by *L. polyphyllus* under current and future climate conditions.

CONCLUSION

Lupinus polyphyllus is a recent global invader of high conservational interest in Europe. Our study contributes to the urgently needed precautionary risk assessment and management of *L. polyphyllus* on a continental scale by providing conservation managers with information on the niche dynamics and therewith associated amount of suitable habitat under current and future climate conditions. In sum, our results show that the lupine has not yet reached its niche saturation. On the contrary, its niche in Europe seems to be expanding as the amount of suitable habitat is projected to increase due to climate change. And although the general habitat suitability is expected to decrease, it is highly probable that the invasion process of *L. polyphyllus* in Europe will continue to progress. Consequently, also invasive species originating from northern regions might benefit from climate change.

Based on our projections, we suggest a strict monitoring of the areas at risk of invasion by *L. polyphyllus* possibly with the help of citizen scientists. A targeted application of the ecosystem engineer – e.g. for soil amelioration or as an ornamental plant – should be prohibited, at least in areas with highly suitable habitat conditions, as the main propagation pathways of *L. polyphyllus* are deliberate seeding in gardens or in forestry management due to its ability to improve and stabilize soil conditions. We emphasize the importance of future scenarios of non-climatic predictor variables to be able to project the behavior of (non-native) species under future climate change conditions as accurately as possible.

ACKNOWLEDGEMENTS

The authors want to thank Samuel Hoffmann for his valuable suggestions to our species distribution models and Prof. Dr. Hermann Jungkunst for his valuable suggestions to an early version of this manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Concepts and ideas of the study: VV, AJa, AJe, CB. VV and AJa designed the methodology. Statistical analyses: VV lead the analyses and AJa contributed substantially. Writing: VV lead the writing, all other co-authors contributed substantially in revising the manuscript. All authors gave final approval for publication.

REFERENCES

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., and Anderson, R. P. (2014). spThin: Functions for Spatial Thinning of Species Occurrence Records for Use in Ecological Models. R package version 0.1.0. Available at: https://CRAN.R-project.org/package=spThin.

Alexander, J. M., and Edwards, P. J. (2010). Limits to the niche and range margins of alien species. *Oikos* 119, 1377–1386. doi:10.1111/j.1600-0706.2009.17977.x.

Ayanu, Y., Jentsch, A., Müller-Mahn, D., Rettberg, S., Romankiewicz, C., and Koellner, T. (2015). Ecosystem engineer unleashed: Prosopis juliflora threatening ecosystem services? *Reg. Environ. Change* 15, 155–167. doi:10.1007/s10113-014-0616-x.

Becker, T., Dietz, H., Billeter, R., Buschmann, H., and Edwards, P. J. (2005). Altitudinal distribution of alien plant species in the Swiss Alps. *Perspect. Plant Ecol. Evol. Syst.* 7, 173–183. doi:10.1016/j.ppees.2005.09.006.

Bellard, C., Cassey, P., and Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biol. Lett.* 12, 20150623. doi:10.1098/rsbl.2015.0623.

Bellard, C., Jeschke, J. M., Leroy, B., and Mace, G. M. (2018). Insights from modeling studies on how climate change affects invasive alien species geography. *Ecol. Evol.* 8, 5688–5700. doi:10.1002/ece3.4098.

Beuthin, M. (2012). Plant guide for bigleaf lupine (Lupinus polyphyllus). *USDA-Nat. Resour. Conserv. Serv. Plant Mater. Cent. Corvallis OR*. Available at: https://nitcnrcsbase-www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/orpmcpg11723.pdf [Accessed July 14, 2016].

Beyschlag, W., Hanisch, S., Friedrich, S., Jentsch, A., and Werner, C. (2009). ^{15} N natural abundance during early and late succession in a middle-European dry acidic grassland. *Plant Biol.* 11, 713–724. doi:10.1111/j.1438-8677.2008.00173.x.

Boltovskoy, D., Sylvester, F., and Paolucci, E. M. (2018). Invasive species denialism: Sorting out facts, beliefs, and definitions. *Ecol. Evol.* 8, 11190–11198. doi:10.1002/ece3.4588.

Broennimann, O., Di Cola, V., and Guisan, A. (2018). ecospat: Spatial Ecology Miscellaneous Methods. R package version 3.0. Available at: https://CRAN.R-project.org/package=ecospat.

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., et al. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data: Measuring niche overlap. *Glob. Ecol. Biogeogr.* 21, 481–497. doi:10.1111/j.1466-8238.2011.00698.x.

Broennimann, O., Treier, U. A., Müller-Schärer, H., Thuiller, W., Peterson, A. T., and Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* 10, 701–709. doi:10.1111/j.1461-0248.2007.01060.x.

Buhk, C., and Jungkunst, H. (2019). "Effects of Plant Invasions on the Soil Carbon Storage in the Light of Climate Change," in *Soil and climate* Advances in soil science., eds. R. Lal and B. A. Stewart (Boca Raton London New York: CRC Press, Taylor & Francis Group).

Callen, S. T., and Miller, A. J. (2015). Signatures of niche conservatism and niche shift in the North American kudzu (*Pueraria montana*) invasion. *Divers. Distrib.* 21, 853–863. doi:10.1111/ddi.12341.

Catford, J. A., Vesk, P. A., Richardson, D. M., and Pyšek, P. (2012). Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Glob. Change Biol.* 18, 44–62. doi:10.1111/j.1365-2486.2011.02549.x.

Collins, R., Kristensen, P., and Thyssen, N. (2009). *Water resources across Europe: confronting water scarcity and drought.* Luxembourg: Office for Official Publ. of the Europ. Communities.

Crumpacker, D. W., Box, E. O., and Hardin, E. D. (2001). Implications of Climatic Warming for Conservation of Native Trees and Shrubs in Florida. *Conserv. Biol.* 15, 1008–1020.

Cunze, S., Kochmann, J., Koch, L. K., and Klimpel, S. (2018). Niche conservatism of Aedes albopictus and Aedes aegypti - two mosquito species with different invasion histories. *Sci. Rep.* 8, 7733. doi:10.1038/s41598-018-26092-2.

Dengler, J., and Tischew, S. (2018). "Grasslands of Western and Northern Europe—Between intensification and abandonment.," in *Grasslands of the world: diversity, management and conservation.* (Boca Raton, US: CRC Press), 27–63.

Dennis, E. B., Morgan, B. J. T., Brereton, T. M., Roy, D. B., and Fox, R. (2017). Using citizen science butterfly counts to predict species population trends: Citizen Science Butterfly Trends. *Conserv. Biol.* 31, 1350–1361. doi:10.1111/cobi.12956.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., et al. (2017). ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40, 774–787. doi:10.1111/ecog.02671.

Ehrenfeld, J. G. (2003). Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems* 6, 503–523. doi:10.1007/s10021-002-0151-3.

Ehrenfeld, J. G. (2010). Ecosystem Consequences of Biological Invasions. *Annu. Rev. Ecol. Evol. Syst.* 41, 59–80. doi:10.1146/annurev-ecolsys-102209-144650.

Falinski, J. B. (1998). "Invasive alien plants and vegetation dynamics," in *Plant invasions, ecological mechanisms and human responses* (Backhuys, Leiden), 3–21.

Fei, S., Phillips, J., and Shouse, M. (2014). Biogeomorphic Impacts of Invasive Species. *Annu. Rev. Ecol. Evol. Syst.* 45, 69–87. doi:10.1146/annurev-ecolsys-120213-091928.

Fick, S. E., and Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas: NEW CLIMATE SURFACES FOR GLOBAL LAND AREAS. *Int. J. Climatol.* 37, 4302–4315. doi:10.1002/joc.5086.

Fremstad, E. (2010). NOBANIS - Invasive Alien Species Fact Sheet - Lupinus polyphyllus. Available at: www.nobanis.org [Accessed May 24, 2012].

Fremstad, E., and Elven, R. (2008). "Perennial Lupins in Fennoscandia," in *Lupins for health and wealth: 12th International Lupin Conference , Fremantle, Western Australia, 14-18 September 2008*, eds. J. A. Palta and J. D. Berger (Canterbury, New Zealand: International Lupin Association).

Gbif.org (2019). GBIF Occurrence Download. Available at: https://doi.org/10.15468/dl.tf2mfl.

Goodenough, A. (2010). Are the ecological impacts of alien species misrepresented? A review of the "native good, alien bad" philosophy. *Community Ecol.* 11, 13–21. doi:10.1556/ComEc.11.2010.1.3.

Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., and Kueffer, C. (2014). Unifying niche shift studies: insights from biological invasions. *Trends Ecol. Evol.* 29, 260–269. doi:10.1016/j.tree.2014.02.009.

Guo, Q., Brockway, D. G., Larson, D. L., Wang, D., and Ren, H. (2018). Improving Ecological Restoration to Curb Biotic Invasion—A Practical Guide. *Invasive Plant Sci. Manag.* 11, 163–174. doi:10.1017/inp.2018.29.

Hejda, M., Pyšek, P., and Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393–403. doi:10.1111/j.1365-2745.2009.01480.x.

Hengl, T., de Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B. M., Ribeiro, E., et al. (2014). SoilGrids1km — Global Soil Information Based on Automated Mapping. *PLoS ONE* 9, e105992. doi:10.1371/journal.pone.0105992.

Hensgen, F., and Wachendorf, M. (2016). The Effect of the Invasive Plant Species Lupinus polyphyllus Lindl. on Energy Recovery Parameters of Semi-Natural Grassland Biomass. *Sustainability* 8, 998. doi:10.3390/su8100998.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. doi:10.1002/joc.1276.

Hiltbrunner, E., Aerts, R., Bühlmann, T., Huss-Danell, K., Magnusson, B., Myrold, D. D., et al. (2014). Ecological consequences of the expansion of N2-fixing plants in cold biomes. *Oecologia* 176, 11–24. doi:10.1007/s00442-014-2991-x.

Hulme, P. E. (2017). Climate change and biological invasions: evidence, expectations, and response options: Alien species and climate change in Great Britain. *Biol. Rev.* 92, 1297–1313. doi:10.1111/brv.12282.

Hutchinson, G. E. (1957). Cold sring harbor symposium on quantitative biology. Concluding remarks. 22, 415–427.

Ibáñez, I., Silander Jr, John. A., Allen, J. M., Treanor, S. A., and Wilson, A. (2009). Identifying hotspots for plant invasions and forecasting focal points of further spread: Hot spots for plant invasions. *J. Appl. Ecol.* 46, 1219–1228. doi:10.1111/j.1365-2664.2009.01736.x.

IPCC (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC (2014). Climate change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N.

Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. *Camb. Univ. Press Camb. U. K. N. Y. NY USA*, 688.

Jaeschke, A., Bittner, T., Jentsch, A., Reineking, B., Schlumprecht, H., and Beierkuhnlein, C. (2012). Biotic Interactions in the Face of Climate Change: A Comparison of Three Modelling Approaches. *PLoS ONE* 7, e51472. doi:10.1371/journal.pone.0051472.

Jauni, M., and Ramula, S. (2016). Demographic mechanisms of disturbance and plant diversity promoting the establishment of invasive *Lupinus polyphyllus*. *J. Plant Ecol.*, rtw049. doi:10.1093/jpe/rtw049.

Jones, C. G., Lawton, J. H., and Shachak, M. (1994). Organisms as Ecosystem Engineers. *Oikos* 69, 373. doi:10.2307/3545850.

Kamp, J., Oppel, S., Heldbjerg, H., Nyegaard, T., and Donald, P. F. (2016). Unstructured citizen science data fail to detect long-term population declines of common birds in Denmark. *Divers. Distrib.* 22, 1024–1035. doi:10.1111/ddi.12463.

Kassambara, A., and Mundt, F. (2017). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.5. Available at: https://CRAN.R-project.org/package=factoextra.

Klinger, Y. P., Harvolk-Schöning, S., Eckstein, R. L., Hansen, W., Otte, A., and Ludewig, K. (2019). Applying landscape structure analysis to assess the spatio-temporal distribution of an invasive legume in the Rhön UNESCO Biosphere Reserve. *Biol. Invasions*. doi:10.1007/s10530-019-02012-x.

Kreyling, J. (2010). Winter climate change: a critical factor for temperate vegetation performance. *Ecology* 91, 1939–1948.

Lauterbach, D., and Nehring, S. (2013). Naturschutzfachliche Invasivitätsbewertung Lupinus polyphyllus - Vielblättrige Lupine. *Bundesamt Für Naturschutz Bonn 2S* Bundesamt für Naturschutz, Konstantinstrasse 110, 53179 Bonn; Phone: +492288491-0; www.bfn.de; neobiota@bfn.de.

Liška, J., and Soldán, Z. (2004). Alien vascular plants recorded from the Barentsburg and Pyramiden settlements, Svalbard. *Preslia* 76, 279–290.

Liu, Y., Oduor, A. M. O., Zhang, Z., Manea, A., Tooth, I. M., Leishman, M. R., et al. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Glob. Change Biol.* 23, 3363–3370. doi:10.1111/gcb.13579.

Magnusson, B. (2010). NOBANIS - Invasive Alien Species Fact Sheet - Lupinus nootkatensis.

Magnusson B., Magnusson S.H., and Sigurdsson B.D. (2008). "Plant succession in areas colonized by the introduced Nootka Lupin in Iceland," in *Lupins for health and wealth*, eds. J. A. Palta and J. D. Berger (Canterbury, New Zealand: International Lupin Association).

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., and Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Divers. Distrib.* 15, 59–69. doi:10.1111/j.1472-4642.2008.00491.x.

Otte, A., and Maul, P. (2005). Verbreitungsschwerpunkt und strukturelle Einnischung der Stauden-Lupine (Lupinus polyphyllus Lindl.) in Bergwiesen der Rhön. *Tuexenia* 25, 151–182.

Panter, K. E., Taylor, J. B., Lee, S. T., Strong, N. K., Wierenga, T., Cook, D., et al. (2017). Lupine Poisoning in Sheep on the USDA-ARS US Sheep Experiment Station (USSES), Dubois, Idaho. *Int. J. Poisonous Plant Res.*, 79.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.

Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., and Guisan, A. (2012). Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science* 335, 1344–1348. doi:10.1126/science.1215933.

Phoenix, G. K., and Lee, J. A. (2004). Predicting impacts of Arctic climate change: past lessons and future challenges. *Ecol. Res.* 19, 65–74.

Pocock, M. J. O., Roy, H. E., Fox, R., Ellis, W. N., and Botham, M. (2017). Citizen science and invasive alien species: Predicting the detection of the oak processionary moth Thaumetopoea processionea by moth recorders. *Biol. Conserv.* 208, 146–154. doi:10.1016/j.biocon.2016.04.010.

Pocock, M. J. O., Roy, H. E., Preston, C. D., and Roy, D. B. (2015). The Biological Records Centre: a pioneer of citizen science. *Biol. J. Linn. Soc.* 115, 475–493. doi:10.1111/bij.12548.

R Core Team (2017). R: A language and environment for statistical computing. *R Found. Stat. Comput. Vienna Austria*. Available at: https://www.R-project.org/.

Ramula, S., and Pihlaja, K. (2012). Plant communities and the reproductive success of native plants after the invasion of an ornamental herb. *Biol. Invasions* 14, 2079–2090. doi:10.1007/s10530-012-0215-z.

Ramula, S., and Sorvari, J. (2017). The invasive herb Lupinus polyphyllus attracts bumblebees but reduces total arthropod abundance. *Arthropod-Plant Interact.* 11, 911–918. doi:10.1007/s11829-017-9547-z.

Rengel, Z. (2011). “Soil pH, Soil Health and Climate Change,” in *Soil Health and Climate Change*, eds. B. P. Singh, A. L. Cowie, and K. Y. Chan (Berlin, Heidelberg: Springer Berlin Heidelberg), 69–85. doi:10.1007/978-3-642-20256-8_4.

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., et al. (2011). RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Clim. Change* 109, 33–57. doi:10.1007/s10584-011-0149-y.

Richardson, D. M., Pyšek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D., and West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6, 93–107.

Roy, H. E., Rorke, S. L., Beckmann, B., Booy, O., Botham, M. S., Brown, P. M. J., et al. (2015). The contribution of volunteer recorders to our understanding of biological invasions: Biological Records and Invasions. *Biol. J. Linn. Soc.* 115, 678–689. doi:10.1111/bij.12518.

Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51, 408–418.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., et al. (2013). Impacts of biological invasions: what’s what and the way forward. *Trends Ecol. Evol.* 28, 58–66. doi:10.1016/j.tree.2012.07.013.

Simberloff, D., and Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1, 21–32.

Starfinger, U., and Kowarik, I. (2011). Lupinus polyphyllus Lindl. (Fabaceae), Vielblättrige Lupine. *Neobiotade Geb. Invasive Arten Dtschl.* Available at: https://neobiota.bfn.de/handbuch/gefaesspflanzen/lupinus-polyphyllus.html [Accessed March 6, 2019].

Stastny, P. (2008). Impacts of Europe’s changing climate — 2008 indicator-based assessment. 38.

Sumner, S., Bevan, P., Hart, A. G., and Isaac, N. J. B. (2019). Mapping species distributions in 2 weeks using citizen science. *Insect Conserv. Divers.* doi:10.1111/icad.12345.

Thiele, J., Isermann, M., Otte, A., and Kollmann, J. (2010). Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *J. Veg. Sci.* 21, 213–220. doi:10.1111/j.1654-1103.2009.01139.x.

Thomson, A. M., Calvin, K. V., Smith, S. J., Kyle, G. P., Volke, A., Patel, P., et al. (2011). RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Clim. Change* 109, 77–94. doi:10.1007/s10584-011-0151-4.

Thuiller, W., Georges, D., Engler, R., and Breiner, F. (2016). biomod2: Ensemble Platform for Species Distribution Modeling. R package version 3.3-7. Available at: https://CRAN.R-project.org/package=biomod2.

Tingley, R., Vallinoto, M., Sequeira, F., and Kearney, M. R. (2014). Realized niche shift during a global biological invasion. *Proc. Natl. Acad. Sci.* 111, 10233–10238. doi:10.1073/pnas.1405766111.

Vetter, V. M. S., Tjaden, N. B., Jaeschke, A., Buhk, C., Wahl, V., Wasowicz, P., et al. (2018). Invasion of a Legume Ecosystem Engineer in a Cold Biome Alters Plant Biodiversity. *Front. Plant Sci.* 9. doi:10.3389/fpls.2018.00715.

Vetter, V., Walter, J., Wilfahrt, P. A., Buhk, C., Braun, M., Clemens, S., et al. (2019). Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters. *Plant Biol.* doi:https://doi.org/10.1111/plb.12987.

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D., and Matson, P. A. (1987). Biological Invasion by Myrica faya Alters Ecosystem Development in Hawaii. *Sci. New Ser.* 238, 802–804.

Volz, H. (2003). Ursachen und Auswirkungen der Ausbreitung von Lupinus polyphyllus Lindl. im Bergwiesenökosystem der Rhön und Maßnahmen zu seiner Regulierung.

Walsh, C., and Mac Nally, R. (2013). hier.part: Hierarchical Partitioning. R package version 1.0-4. Available at: https://CRAN.R-project.org/package=hier.part.

Warren, D. L., Glor, R. E., and Turelli, M. (2008). ENVIRONMENTAL NICHE EQUIVALENCY VERSUS CONSERVATISM: QUANTITATIVE APPROACHES TO NICHE EVOLUTION. *Evolution* 62, 2868–2883. doi:10.1111/j.1558-5646.2008.00482.x.

Wasowicz, P. (2016). Non-native species in the vascular flora of highlands and mountains of Iceland. *PeerJ* 4, e1559. doi:10.7717/peerj.1559.

Wasowicz, P., Przedpelska-Wasowicz, E. M., and Kristinsson, H. (2013). Alien vascular plants in Iceland: Diversity, spatial patterns, temporal trends, and the impact of climate change. *Flora - Morphol. Distrib. Funct. Ecol. Plants* 208, 648–673. doi:10.1016/j.flora.2013.09.009.

Wink, M. (1995). “The cell culture medium—a functional extracellular compartment of suspension-cultured cells,” in *Primary and Secondary Metabolism of Plants and Cell Cultures III* (Springer), 307–319. Available at: http://link.springer.com/chapter/10.1007/978-94-011-0237-7_27 [Accessed November 12, 2014].

10.3.1 Supporting information Manuscript 3

Niche conservatism or niche shift? Implications for the management of a legume invader

Vanessa M.S. Vetter, Anja Jaeschke, Constanze Buhk, Anke Jentsch

Corresponding author: Vanessa Vetter, vanessa.vetter@uni-bayreuth.de, phone: 0049 (0) 921-552305

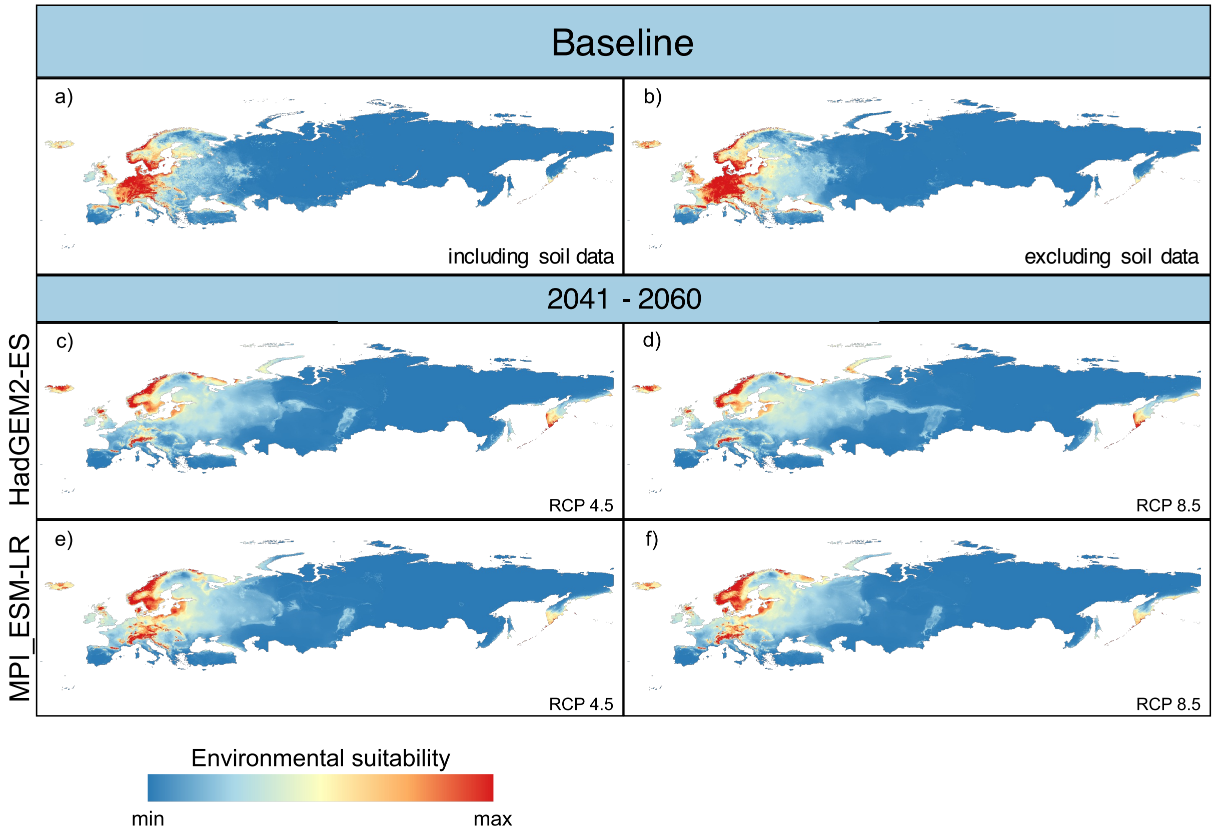


Figure S1: Projected potential distribution of *L. polyphyllus* across its invasive range Europe under current climate conditions (baseline) and future climate conditions (2041-2060). SDMs were fitted using all occurrence records of the invasive range, as well as using a) all 10 predictor variables, including soil data and b) only the climate variables selected by hierarchical partitioning. The latter SDM (b) was used to project the potential distribution of *L. polyphyllus* under future climate conditions (panel c-f). Future climate conditions were modeled with the global climate models HadGEM2-ES and MPI_ESM-LR each in the medium stabilization (RCP 4.5) and very high baseline emission scenario (RCP 8.5). Environmental suitability ranges from: minimum = 0 to maximum = 1, with AUC cutoff points a) 391 and b) 372 (depicted in yellow) respectively. Yellow and reds indicate occurrences, while shades of blue indicate absences. Yellow indicates the respective cutoff point of the SDM.

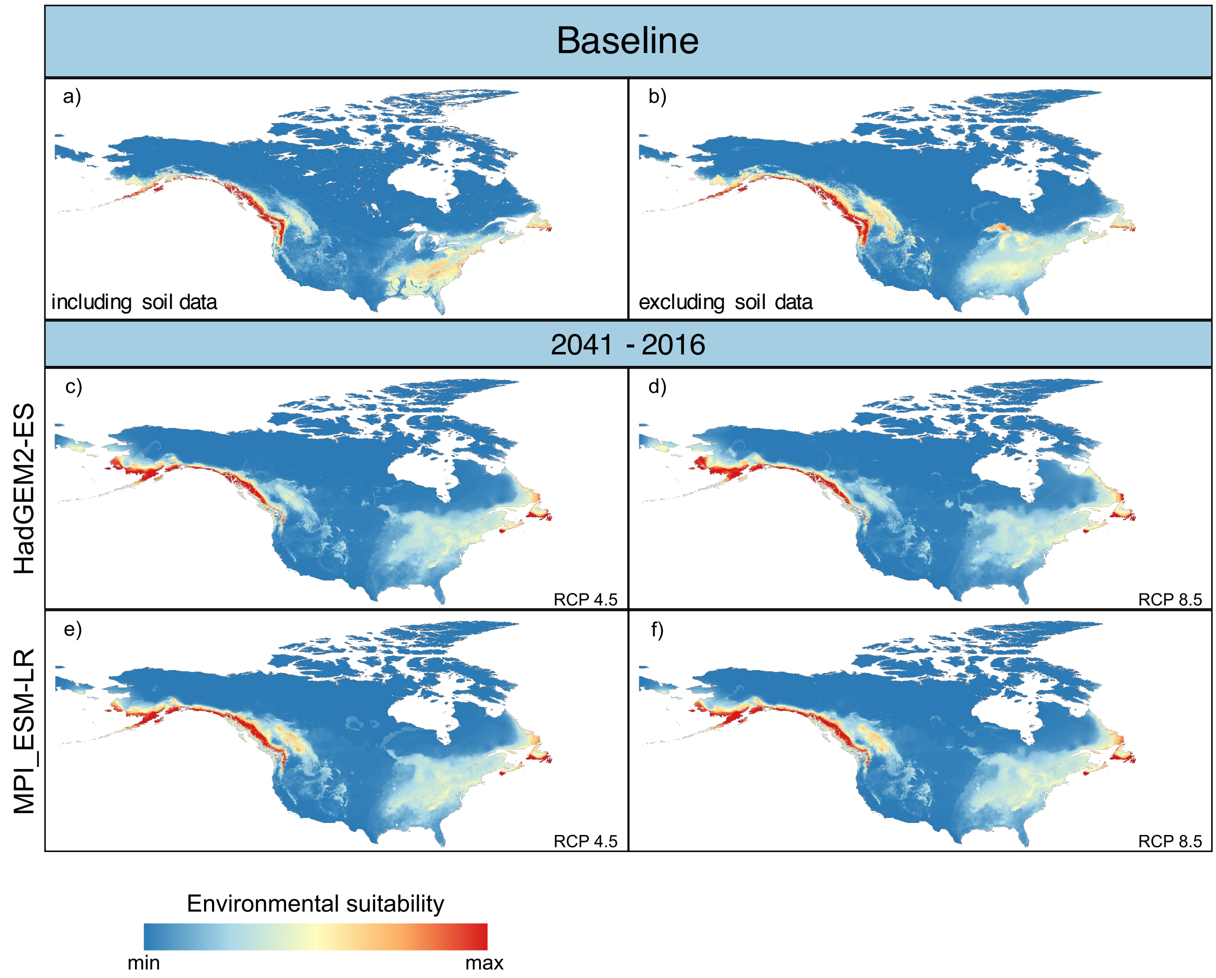


Figure S2: Projected potential distribution of *L. polyphyllus* across its native range North America under current climate conditions (baseline) and future climate conditions (2041-2060). SDMs were fitted using all occurrence records of the native range, as well as using a) all 10 predictor variables, including soil data and b) only the climate variables selected by hierarchical partitioning. The latter SDM (b) was used to project the potential distribution of *L. polyphyllus* under future climate conditions (panel c-f). Future climate conditions were modeled with the global climate models HadGEM2-ES and MPI_ESM-LR each in the medium stabilization (RCP 4.5) and very high baseline emission scenario (RCP 8.5). Environmental suitability ranges from: minimum = 0 to maximum = 1, with AUC cutoff points a) 391 and b) 372 (depicted in yellow) respectively. Yellow and reds indicate occurrences, while shades of blue indicate absences. Yellow indicates the respective cutoff point of the SDM.

10.4 Manuscript 4

Received: 2 April 2019 | Revised: 3 December 2019 | Accepted: 14 January 2020
DOI: 10.1111/gcb.15025

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought

Vanessa M. S. Vetter[1,2] | **Juergen Kreyling**[3] | **Jürgen Dengler**[4,5,6] | **Iva Apostolova**[7] | **Mohammed A. S. Arfin-Khan**[1,8] | **Bernd J. Berauer**[1] | **Sigi Berwaers**[9] | **Hans J. De Boeck**[9] | **Ivan Nijs**[9] | **Max A. Schuchardt**[1] | **Desislava Sopotlieva**[7] | **Philipp von Gillhausen**[1] | **Peter A. Wilfahrt**[1] | **Maja Zimmermann**[1] | **Anke Jentsch**[1]

[1]Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Bayreuth, Germany
[2]Geoecology/Physical Geography, Institute for Environmental Sciences (iES), University of Koblenz-Landau, Landau, Germany
[3]Experimental Plant Ecology, Greifswald University, Greifswald, Germany
[4]Plant Ecology, Bayreuth Center of Ecology and Environmental Research BayCEER, University of Bayreuth, Bayreuth, Germany
[5]Vegetation Ecology Group, Institute of Natural Resource Management (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland
[6]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[7]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria
[8]Department of Forestry and Environmental Science, Shahjalal University of Science and Technology, Sylhet, Bangladesh
[9]Plants and Ecosystems (PLECO), Department of Biology, University of Antwerp, Antwerp, Belgium

Correspondence and present address
Vanessa M. S. Vetter, Geoecology/Physical Geography, Institute for Environmental Sciences (iES), University of Koblenz-Landau, Campus Landau, Landau, Germany.
Email: vanessa.vetter@uni-bayreuth.de; vetter@uni-landau.de

Funding information
ERA-Net BiodivERsA, Grant/Award Number: 01LC1201; German Federal Ministry of Education and Research (BMBF); BonaRes, Grant/Award Number: 031B0027C; Belgian Federal Science Policy Office (BELSPO); Bulgarian Science Found

Abstract

Higher biodiversity can stabilize the productivity and functioning of grassland communities when subjected to extreme climatic events. The positive biodiversity–stability relationship emerges via increased resistance and/or recovery to these events. However, invader presence might disrupt this diversity–stability relationship by altering biotic interactions. Investigating such disruptions is important given that invasion by non-native species and extreme climatic events are expected to increase in the future due to anthropogenic pressure. Here we present one of the first multisite invader × biodiversity × drought manipulation experiment to examine combined effects of biodiversity and invasion on drought resistance and recovery at three semi-natural grassland sites across Europe. The stability of biomass production to an extreme drought manipulation (100% rainfall reduction; BE: 88 days, BG: 85 days, DE: 76 days) was quantified in field mesocosms with a richness gradient of 1, 3, and 6 species and three invasion treatments (no invader, *Lupinus polyphyllus*, *Senecio inaequidens*). Our results suggest that biodiversity stabilized community productivity by increasing the ability of native species to recover from extreme drought events. However, invader presence turned the positive and stabilizing effects of diversity on native species recovery into a neutral relationship. This effect was independent of the two invader's own capacity to recover from an extreme drought event. In summary, we found that invader presence may disrupt how native community interactions lead to stability of ecosystems in response to extreme climatic events. Consequently, the interaction of three global change drivers, climate extremes, diversity decline, and invasive species, may exacerbate their effects on ecosystem functioning.

KEYWORDS
alien invasive species, biological invasion, climate extreme, disturbance, ecosystem functioning, grassland ecosystem, plant–environment interaction, recovery, resilience, resistance

1 | INTRODUCTION

Loss of biodiversity tends to affect ecosystem functioning and stability of grasslands negatively and is likely to affect human society (Cardinale et al., 2012; Hautier et al., 2015, 2018; Tilman, Isbell, & Cowles, 2014). A more diverse plant community leads to an overall more stable community functioning under a wider range of conditions when species react in asynchrony due to compensatory responses (sensu insurance hypothesis: de Mazancourt et al., 2013; Loreau & de Mazancourt, 2013; Tilman et al., 2014; Yachi & Loreau, 1999). Increased stability maintains community productivity while the availability of free resource declines (Gross et al., 2014; Tilman, Reich, & Isbell, 2012). Global change drivers lead to exogenous changes in resource availability and the introduction of non-native species, leading to uncertainty as to whether the diversity–stability relationship persists in the face of extreme climatic events (De Boeck et al., 2018) and invasion (Pinto & Ortega, 2016).

The frequency and magnitude of extreme climatic events, such as drought (Dai, 2013), are predicted to increase in Europe as a result of climate change (Hewitson et al., 2014). Altered drought regimes in semi-natural grasslands might lead to plant mortality, species composition shifts, degradation and desertification, and erosion (Craine et al., 2012; Reichstein et al., 2013; Wang et al., 2011). Strong droughts can cause lasting effects on community composition by selecting for drought tolerant species (e.g. Mediterranean species), resulting in dominance shifts and/or local extinction of drought intolerant species (Alba, NeSmith, Fahey, Angelini, & Flory, 2017; Reichstein et al., 2013; Török, Janišová, Kuzemko, Rusina, & Stevanovic, 2018). Such drought-induced changes in the plant community structure of grasslands might subsequently affect plant productivity as well as ecosystem functioning and the delivery of ecosystem services (Caldeira et al., 2015; Cantarel, Bloor, & Soussana, 2013; Reichstein et al., 2013).

In Europe, species invasions show a stable rate of increase (Butchart et al., 2010; Caldeira et al., 2015; Seebens et al., 2017) which might lead to large scale homogenization and reduced ecosystem (multi-) functioning (Dornelas et al., 2014; Hautier et al., 2018; Vellend et al., 2013). A globally unique feature of Europe is the extensive semi-natural grasslands, whose species-rich communities originate from millennia of low-intensive agricultural use (pastures, hay-meadows) on sites that would naturally support forests (Török & Dengler, 2018). These semi-natural grasslands are of high importance for dairy and meat production as well as for biodiversity conservation, among other things (Dengler & Tischew, 2018; Török et al., 2018). Generally, European grasslands seem to be rather resistant against plant invasions, being one of the least invaded habitat types in Europe (Chytrý et al., 2008, 2009; Pyšek, Chytrý, & Jarošík, 2010). The exception is invasions by tall forbs, with the reasons not being fully understood (Dengler & Tischew, 2018). Invasives like *Lupinus polyphyllus* and *Senecio inaequidens* increasingly colonize semi-natural grasslands while the former tends to form dominance stands, changing the vegetation structure and species diversity drastically (Hejda, Pyšek, & Jarošík, 2009; Lachmuth, Durka, & Schurr, 2010; Scherber, Crawley, & Porembski, 2003; Thiele, Isermann, Otte, & Kollmann, 2010; Volz & Otte, 2001). Those changes will likely also affect biotic interactions, abiotic processes and consequently ecosystem stability of the invaded habitats (Sousa, Morais, Dias, & Antunes, 2011; Strayer, 2012).

There is a decades-long scientific discussion about the role of biodiversity, in terms of species richness, for ecosystem stability with a large scientific consensus that biodiversity, in terms of (plant) species richness, infers greater temporal stability to ecosystems in case of disturbance or extreme events (e.g. Isbell et al., 2015; Kreyling et al., 2017; Tilman, Reich, & Knops, 2006). However, counterexamples exist (e.g. Hillebrand et al., 2018; Pfisterer & Schmid, 2002) and the question of whether the diversity–stability relationship is linear, hump-, or U-shape is not definite yet (Pennekamp et al., 2018). Ecosystem stability against extreme events—which is often measured as the reciprocal of temporal variability in community biomass (Cardinale et al., 2012)—can be separated into resistance (Pimm, 1984) and recovery (Hodgson, McDonald, & Hosken, 2015). Here we consider resistance as the degree of change of an ecosystem property in response to an extreme climatic event; no change would indicate complete resistance. Recovery is defined as the degree to which an ecosystem property returns to control or predrought levels after the cessation of the extreme event (Bahn & Ingrisch, 2018; Hodgson et al., 2015; Kreyling et al., 2017). Resistance and recovery can be affected differently by biodiversity (De Boeck et al., 2018; Kreyling et al., 2017; Van Ruijven & Berendse, 2010), with the nature and duration of the extreme event potentially playing an important role. Resistance may be more important during ‘press’ events (long-lasting extremes with brief periods of recovery, e.g. the Californian 2012–2016 drought), as acclimation responses (Zhou, Medlyn, & Prentice, 2016) and species reordering (Evans, Byrne, Lauenroth, & Burke, 2011) have more time to develop. These efficient longer term defences are less likely to manifest during short but intense pulse events (such as in the current study). On the other hand, alleviation of stress following a pulse event is usually more pronounced, promoting fast recovery. In the case of pulse droughts, nutrient flushes upon rewetting can further stimulate recovery (Dreesen, Boeck, Janssens, & Nijs, 2014). Several recent studies on pulse events have indeed found that plant species richness increased the recovery but not the resistance of grasslands (e.g. Kreyling et al., 2017; Van Ruijven & Berendse, 2010). However, counter examples highlighting the importance of biodiversity for the resistance of grasslands against extreme pulse drought events also exist (e.g. Tilman & Downing, 1994).

It is unclear if the diversity–stability-relationship is maintained in the presence of an invader (Pinto & Ortega, 2016). Climate extremes might impact all of the mechanisms conferring ecosystem stability (Cardinale et al., 2012; De Boeck et al., 2018), thus, enabling the establishment of non-native species in the first place (Hautier et al., 2018; Török et al., 2018; Wardle, Bardgett, Callaway, & Putten, 2011). Invasive species might be able to affect the diversity–stability relationship by altering the ability of communities to resist to and/or recover from an extreme event (Wilsey, Daneshgar, Hofmockel, & Polley, 2014). A highly competitive invader or an invader that tolerates abiotic stress more effectively than the native species might be able to outcompete natives before or during an extreme event respectively (Diez et al., 2012). Even with increased resistance of the invader, such indirect competitive effects could diminish the overall resistance of an ecosystem (e.g. to biomass fluctuations) if competitive pressure leads to native species loss (Bernard-Verdier & Hulme, 2019). The same accounts for recovery: if the invader recovers more quickly from harsh climatic conditions then it might impede the partitioning of resources after stress release as the invader instead captures the majority of available resources (De Boeck et al., 2018; Diez et al., 2012).

Here we quantified the effects on community productivity of two invasive species in Europe, the legume *L. polyphyllus* Lindl. and the non-legume forb *S. inaequidens* DC. We further studied their impacts on community resistance and recovery of biomass production to an extreme climatic event (ambient conditions, extreme drought manipulation) in field mesocosms differing in diversity (1, 3, 6 species) at three sites across Europe (Germany, Belgium, Bulgaria). We hypothesized (a) a positive diversity–recovery relationship in native communities exposed to drought, (b) that the presence of invasive species disrupts this relationship, and (c) that extreme drought events facilitate the studied invader species in these semi-natural grasslands.

The work presented here contributes to the global framework of the diversity–stability debate led by long-term, globally distributed grassland experiments such as Drought-Net and Nutrient Network. These investigate the diversity–stability effect across large spatial and temporal scales, taking into account different disturbances yet generally not including issues related to invasive species (Anderson et al., 2018; but see Flores-Moreno et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Experimental design

We tested the effects of invaders on the diversity–stability relationship of grassland communities in a coordinated-distributed mesocosm experiment in the field at three climatically (Table S1) and ecologically different sites across Europe: Belgium (BE), Bulgaria (BG), Germany (DE). Richness levels and species composition, including invader presence, were experimentally established in mesocosms. Then, we exposed them to an artificial severe drought event to study the joint effects of drought, invasion, and species richness on biomass production. The experiment was carried out with three fully crossed factors: (a) invader presence (three factor levels: native species only [no invader]; native species and the invader *L. polyphyllus*; native species and the invader *S. inaequidens*); (b) climatic extremes (two factor levels: severe drought, ambient control); (c) community richness (three factor levels: 1, 3 and 6 species).

The coordinated experiment was implemented using buried field mesocosms. At each site, 132 mesocosms were set up: 72 mesocosm with native communities and 60 mesocosms with invader presence (Figure S1). Each mesocosm had 18 individuals planted, split evenly among the number of species assigned to it. For mesocosms with only native species, 12 locally frequent, native species that naturally occur together on the local soil were selected for each site (Figure S1). From these, 12 different compositions were created which were considered as replicates for the species richness levels (3 sites × 3 species richness levels × 12 species compositions × 2 climate treatments = 216 native species mesocosms in total). Invader monocultures were replicated three times for each invader, while the other two richness levels each had six unique assemblages using the site-specific native species and one invader, yielding a total of 30 compositions × 2 climate treatments × 3 sites = 180 mesocosms with invader presence or monocultures of invaders (Figure S1). Each unique species composition was exposed to both a drought treatment and ambient weather conditions (control) at each of three sites. Native study species included three functional groups (forbs, graminoids, legumes) with four species representing each functional group per site (Table S2).

All plants were grown from seed under standardized conditions at each site and planted into field mesocosms in early spring 2014 (more than 3 months before the start of the drought manipulation). Seeds were collected from autochthonous populations close to the study sites (relying on expert knowledge; Table S2). Each mesocosm consisted of a PVC tube of 30 cm diameter and 50 cm height. The base of mesocosms was closed with root matting, permeable for water but impermeable for roots. Consequently, rooting depth was limited to 50 cm in order to standardize the climate treatment effects. This may have interfered with deep-rooting strategies (e.g. Nippert & Knapp, 2007) in turn limiting niche differentiation and the potential diversity effects (Dimitrakopoulos & Schmid, 2004). Mesocosms were buried in the soil to ensure realistic temperature and drainage patterns, and filled with local soil substrate (homogenized, sieved to 2 cm). Mesocosms were planted with 18 pregrown plant individuals in a systematic arrangement, avoiding conspecific neighbours, and ensuring that edge/centre ratios were similar for each species. Each species had the same number of individuals per mesocosm within each species richness level. Thus, invader mesocosms of species richness level 1 had an invader fraction of 100%; mesocosms of species richness level 3 had an invader fraction of 33.3% (6 out of 18 individuals), and mesocosms with a species richness level of 6 had an invader fraction of 16.7% (3 out of 18 individuals). Upon planting, plants were cut to a height of 6 cm above ground level to standardize the initial conditions. No fertilization was applied. Mortality was checked regularly, and dead individuals were replaced during the first month after planting. Non-target species were weeded out at a monthly interval.

2.2 | Invader species

Two non-native species invasive to Europe, the legume forb *L. polyphyllus* Lindl. and the non-legume forb *S. inaequidens* DC., were selected for this study. Both species exhibit rapid population growth, an ability to alter their local environment, and are habitat generalists, making them interesting study subjects for invasion processes in European semi-natural grasslands (additional information can be found in the supporting information, p. 3; EPPO, 2006; Fremstad, 2010; Global Invasive Species Database [GISD], 2015; Lauterbach & Nehring, 2013; Scherber et al., 2003). *L. polyphyllus* (Fabaceae), the garden lupine, is native to the western parts of North America and Canada (Beuthin, 2012) and was introduced in Europe in the early 1900s (Fremstad, 2010). *S. inaequidens* (Asteraceae), the South African ragwort, is native to South Africa and Lesotho and was introduced in Europe during the late 19th century (Ernst, 1998; Lachmuth et al., 2010). To date, the occurrence and the impact of both invasive species in Europe is more localized (Dengler & Tischew, 2018; Lachmuth et al., 2010), but both invaders are expected to profit from climate change in terms of increasingly favourable conditions and a possible expansion in range (GISD, 2015; Heger & Böhmer, 2006; Lauterbach & Nehring, 2013).

We expect the Mediterranean type invader *S. inaequidens* to cope well with drought (GISD, 2015). Additionally, *S. inaequidens* is highly efficient in capturing free resources (Dassonville et al., 2008; GISD, 2015) and thus, might be able to compromise the resistance as well as the recovery of our native communities. *L. polyphyllus* is a deep-rooting legume which is able to store nutrients in its rhizomes in the event of disturbance and to resprout when conditions are more favourable (Fremstad, 2010; Volz & Otte, 2001). We expect *L. polyphyllus* to recover more quickly from the extreme event, and thus to disrupt the partitioning of resources after stress release. Consequently, we expect *L. polyphyllus* to hamper the recovery of our native species. However, due to its profound root system *L. polyphyllus* might also be able to outcompete native species during the extreme event.

2.3 | Climate treatment

We simulated a pulsed drought event using rainout shelters with 100% rainfall reduction for specific periods during the local growing season. The rainout shelters covered the buried mesocosms and additionally >1.5 m as lateral buffer zones. A randomized block design was applied at each site with either two or three blocks (with each block containing both a rainout shelter and a control). Mesocosms were completely randomized within each drought treatment-block combination. Drought length was standardized across sites with the aim to be extreme compared to past conditions (De Boeck et al., 2019; Schär et al., 2004) and on the basis that such events might become common in the future (Dai, 2013; Seneviratne et al., 2012; Hewitson et al., 2014). Drought length was calculated for each site as 1.5 times the number of consecutive days with <2.5 mm precipitation estimated from the statistical 1,000 year recurrence of such events based on historical data of local precipitation (series length: BE = 111 years, DE = 63 years, BG = 30 years), and constrained within the local growing season (months with mean temperature >5°C and precipitation sum [mm] >2 × mean temperature [°C]; Kreyling et al., 2017). Thus, the extremity of the manipulation is relative to each site, thereby increasing comparability. Ecologically, this is a more meaningful standardization of drought length than simply applying the same drought length to systems under different climatic conditions and, consequentially, different evolutionary adaptation of species and plant traits. The drought treatment started 2/5 of the way into the site-specific growing season (see Table S1 for starting dates). The durations of drought were 76 days in Germany, 85 days in Bulgaria, and 88 days in Belgium. In case of natural drought during the manipulation period, mesocosms growing under ambient weather conditions were irrigated (DE: 4 × 10 mm; BE and BG: never necessary). The drought manipulations were ended by irrigating the droughted mesocosms with 20 mm and the ambient mesocosms with 5 mm, to ensure a temporal synchrony between the postmanipulation rainfall events.

2.4 | Biomass production

Above-ground biomass (B) was harvested at three dates during the experiment: (B0) 2 weeks before the start of the drought treatment ('before drought'), to allow for a standardized quantification of biomass production during the drought period; (B1) directly at the end of drought ('end of drought'); and (B2) at peak biomass the following growing season ('peak following year', used for assessing recovery after drought). Biomass was always harvested at 3 cm above ground, and included all plant material rooted inside the mesocosms. We discarded all biomass of species rooted outside, but growing into, the mesocosm communities (Cancellieri, Mancini, Sperandii, & Filibeck, 2017). We did not sample root biomass. Species-specific biomass harvests were conducted directly after the drought (harvest B1) and at the peak of the following year (harvest B2; BG and DE only). Community biomass harvests were conducted at harvest B0. We sampled the same mesocosms repeatedly because regular cutting 2–5 times per year is the management regime applied in these semi-natural grasslands across Europe (Blüthgen et al., 2012; Dengler & Tischew, 2018; Ellenberg, 1996).

2.5 | Response parameters

We used relative measures of resistance and recovery to examine different facets of ecological stability (Donohue et al., 2016; Kreyling et al., 2017; Pimm, 1984). Both metrics are dimensionless, and thus directly comparable between sites and communities with different levels of productivity. We calculated resistance to and recovery from drought for each unique species composition by comparing biomass production between drought treatment and ambient control as:

$$\text{Resistance} = \frac{(B1)_{\text{drought}}}{(B1)_{\text{control}}},$$

$$\text{Recovery} = \frac{(B2)_{\text{drought}}}{(B2)_{\text{control}}},$$

where B1 is the biomass of each community at the end of the drought period and B2 is the biomass of each community at the peak of biomass production in the following year. The resistance index equals 1 for complete resistance and 0 for no resistance (no biomass production during drought). The recovery index equals 1 for complete recovery and is <1 for incomplete recovery. Values >1 indicate overcompensation. Community compositions with <1.5 g dry weight per mesocosm under control conditions (1.5% of all cases) were disregarded because of their high relative uncertainty (e.g. incremental differences in cutting height can have strong relative effects) and their potential to disproportionately inflate errors (grand mean over all measurements is 31.4 ± 1.8 [*SE*] g per mesocosm).

Survival of invader species as well as native species growing within invader mesocosms were recorded at the end of the drought treatment (B1 harvest). To further quantify the effect of invader presence on native species, we additionally analysed the biomass production of native species growing with and without invader presence. Methods and results of the parameter survival, and the impact of invader presence/absence on native species' biomass production can be found in the supplemental material (Tables S3 and S4).

2.6 | Statistical analysis

All analyses were conducted using the statistical software R 3.4.2 (R Core Team, 2017). We used linear mixed-effects models to test the productivity–richness relationship for native and invader mesocosms under ambient conditions (only for harvest B1). Here we tested the impact of the explanatory variables *species richness* and *invader presence*, as well as their interactions, on above-ground biomass production (dependent variable). With a second linear mixed-effects model we tested if resistance and recovery to climate treatment depended on the explanatory variables *species richness* and *invader presence* as well as their interactions. A third linear mixed-effects model was used to evaluate the difference in the individual biomass of the two invader species (dependent variable). Here we used the fixed-effects *climate treatment*, *species richness*, and *species* (explanatory variables) as well as their interactions. Model 3 was run four times, once each for the B1 and B2 harvests. Results for the B2 harvest can be found in Figure S2. We additionally used model 3 to test the difference in the invader biomass per community biomass (relative invader biomass) of the two invader species (Figures S3 and S4) using the same fixed-effects as in the analyses of the individual invader biomass.

In case of significant interactions between the fixed-effects *invader presence* (models 1 and 2) or *species* (model 3) with the other explanatory variables (*climate treatment*, *species richness*), we ran additional linear mixed-effects models separately for each level of the categorical variables such as *invader presence* or *species* to determine if there were significant differences in the mean values within this group caused by climate treatment/species richness with Bonferroni correction for multiple testing.

We accounted for possible random effects due to the blocked structure and the multisite character of the experiment by nesting *blocks* within *sites* in all linear mixed-effects models. As we tested for general trends across three countries, we have considered country effects as random factors in our models, not as fixed factors. We only allowed the intercept to vary as a function of the block design, but did not include any other main factors into the random term. *Species richness* was introduced into the models as a linear numeric variable, but note that log-linear and factorial response produced qualitatively the same results.

Models were fit with the lmer function in the lme4 package (version 1.1-12; Bates et al., 2014) and results were extracted with the ANOVA function in the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2016) in R. ANOVA tables for the respective models can be found in the supporting information document (part 2, pp. 13–22). We visually checked if the model assumptions of homoscedasticity and normal distribution of residuals were violated. Linear models are robust even towards rather severe violations of the model assumptions (Lo & Andrews, 2015; Wilson, 2007). Consequently, we only transformed our response variables in case of severe violations of the model assumptions. Transformation of the response variables produced qualitatively the same results as non-transformed responses. The response variables *resistance* and *individual biomass* were $\log(x + 1.1)$-transformed while the response variable *productivity* was $(1 + x)^{0.4}$-transformed (note that $\log(x + 1.1)$-transformation produced qualitatively the same results) to meet the model assumptions of homoscedasticity and normal distribution of residuals.

Additionally, we checked for effects of different sample sizes by permutated subsampling of the mesocosms containing only natives and did not see qualitatively different effects.

3 | RESULTS

3.1 | Richness–productivity relationship

Under ambient weather conditions, native species productivity increased with species richness (ANOVA subset natives: p_{richness} = .003; $\text{biomass}_{\text{natives richness level 1}} = 288\ \text{g/m}^2$, $\text{biomass}_{\text{natives richness level 3}} = 395\ \text{g/m}^2$, $\text{biomass}_{\text{natives richness level 6}} = 417\ \text{g/m}^2$; Figure 1, ANOVA-Table S1). But invader presence weakened this diversity effect (ANOVA $p_{\text{richness×invader presence}} < .001$; ANOVA-Table S1). Overall, invader communities were more productive than native communities (ANOVA-Table S1). In invaded communities, we observed a trend of increasing productivity at lower richness levels, and thus a higher invader fraction biomass (Figure 1; ANOVA-Table S1).

Native species growing with the invader *S. inaequidens* were 31.3% smaller than natives growing without invader presence (ANOVA $p_{\text{invader presence}} < .001$; ANOVA-Table S2; Table S4). Mean individual biomass of native species growing with *L. polyphyllus* was 7.1% higher compared to native species growing alone (Table S4, ANOVA-Table S2).

3.2 | Native community resistance and recovery from drought

Species richness did not have a significant effect on drought resistance of biomass production (ANOVA p_{richness} = .411; Figure 2a; ANOVA-Table S3), while the ability of native plant communities to recover from a severe drought event did increase with species richness level (ANOVA subset natives: p_{richness} = .001; $\text{recovery}_{\text{natives richness level 1}} = 0.78 \pm 0.10$, $\text{recovery}_{\text{natives richness level 3}} = 0.86 \pm 0.07$, $\text{recovery}_{\text{natives richness level 6}} = 1.29 \pm 0.15$; Figure 2d, ANOVA-Table S4; Table S5; significant higher level interaction of model 2 across all invader presence levels: see below).

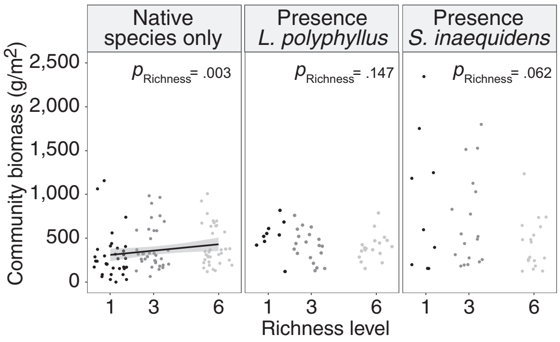


FIGURE 1 Community biomass of the mesocosms growing under ambient weather conditions at the B1 harvest (after drought) shown as a function of richness (black = richness 1, grey = richness 3, light grey = richness 6) considered across all countries, separately for each invasion status. Shown is the community biomass of each mesocosm per invasion status ($n_{\text{natives}} = 213$; $n_{\textit{Lupinus polyphyllus}} = 90$; $n_{\textit{Senecio inaequidens}} = 90$). Data points were jittered along the *x*-axis at each richness level to improve visibility of the data distribution. Black solid lines display mixed-effects model fits of the three submodels for every invader presence level (Bonferroni-corrected significance level: $p < .017$; ANOVA-Table S1), and grey shades indicate their respective 95% confidence intervals

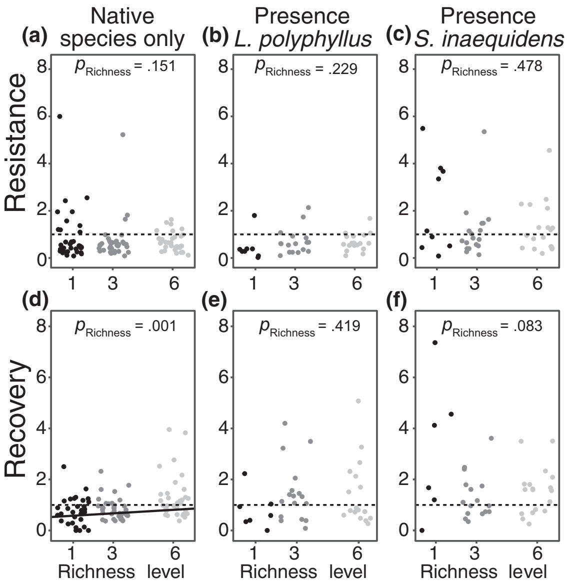


FIGURE 2 Resistance (B1 ANPP harvest; a–c) and recovery (B2 ANPP harvest; d–f) to a severe drought event, shown as a function of richness (black = richness 1, grey = richness 3, light grey = richness 6), separately for each invasion status (resistance: $n_{\text{natives}} = 107$; $n_{\textit{Lupinus polyphyllus}} = 45$; $n_{\textit{Senecio inaequidens}} = 45$; recovery: $n_{\text{natives}} = 106$; $n_{\textit{Lupinus polyphyllus}} = 45$; $n_{\textit{Senecio inaequidens}} = 45$). All mesocosms with a ratio above 1 (the dashed line) showed higher biomass production in drought compared to ambient conditions, while all mesocosms with ratios below 1 showed lower biomass production in drought than under ambient conditions. Bonferroni-corrected significance level $p < .017$ for the three submodels of invader presence in recovery to drought. Data points were jittered at each richness level to improve visibility of the data distribution

3.3 | Invader impact on resistance and recovery

Invasion status did not alter the richness–resistance relation compared to the (non-significant) relation observed in the native species mesocosms (ANOVA $p_{\text{richness×invader presence}}$ = .379; Figure 2a–c; ANOVA-Table S3). However, invader presence changed the drought resistance of the affected plant communities (ANOVA $p_{\text{invader presence}}$ = .011; ANOVA-Table S3). Depending on the invader species, drought resistance—in terms of sheer biomass production—increased in *S. inaequidens* communities (+83.2%) and decreased in *L. polyphyllus* communities (−18.2%; Figure S7) compared to native species communities.

Invader presence altered the richness–recovery relationship in our experiment (ANOVA $p_{\text{richness×invader presence}}$ = .026; Figure 2d–f;

ANOVA-Table S4). The presence of both invasive species nullified the positive effect of species richness on the recovery of plant communities (ANOVA subset *L. polyphyllus* p_{richness} = .419; ANOVA subset *S. inaequidens* p_{richness} = .083; ANOVA-Table S4; Figure 2e), possibly due to their high productivity in monocultures (*S. inaequidens*) and intermediate richness levels (*L. polyphyllus*). Both invader species showed increased recovery compared to native species across all species richness levels (ANOVA-Table S4).

3.4 | Invader performance

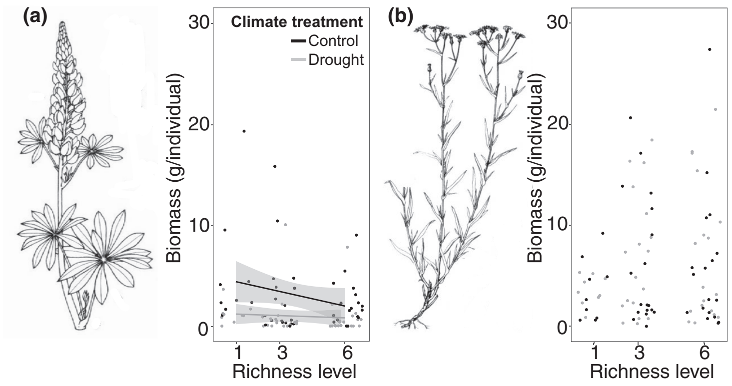
Performance per individual of the two invaders in response to the drought treatment differed marginally (ANOVA $p_{\text{species×climate treatment}}$ = .081; ANOVA-Table S5a; Figure 3). Under drought, *L. polyphyllus* on average produced less biomass than under ambient conditions (−67.9%), while the drought treatment showed no significant impact upon *S. inaequidens* (on average +12.9% more biomass compared to control mesocosms, but this effect was not significant; ANOVA-Table S5a subset *S. inaequidens*; Figure 3). During the treatment phase of the first year (B1 harvest, resistance), native species showed marginally different effects on the invaders (ANOVA $p_{\text{species×richness}}$ = .058; ANOVA-Table S5a; Figure 3): under ambient conditions, *L. polyphyllus'* biomass production showed a tendency to be negatively affected by interspecific competition, although this effect was superimposed by the strong negative effect of drought upon the individual biomass of *L. polyphyllus* (ANOVA subset *L. polyphyllus*: p_{richness} = .056; $p_{\text{climate treatment}}$ = .007; ANOVA-Table S5a; Figure 3). We did not observe a significant effect of species richness on the drought resistance of *S. inaequidens*.

One year after the extreme event (harvest B2, recovery), performance of the invader species was affected by both, climate treatment and species richness (ANOVA $p_{\text{species×climate treatment×richness}}$ = .027; ANOVA-Table S5b). Formerly drought-treated *S. inaequidens* individuals growing in interspecific competition with native species were able to regrow significantly more biomass than individuals growing in intraspecific competition (monocultures) or under ambient weather conditions (ANOVA subset *S. inaequidens* $p_{\text{climate treatment×richness}}$ = .0098; Figure S2; ANOVA-Table S5b). While drought recovery of *L. polyphyllus* seemed not to be dependent on climate treatment or species richness (Figures S2 and S4; ANOVA-Table S5b).

Invader fraction per community biomass at the end of the drought treatment (B1 harvest), as expected, decreased with increasing species richness level in both invader species (ANOVA $p_{\text{species×richness}}$ = .055; ANOVA-Table S6a). However, the steepness of the decline varied between the two invader species. *S. inaequidens*, contributed 47.2% to the total biomass even in the six species high-diversity mesocosms (ANOVA subset *S. inaequidens* p_{richness} < .001; ANOVA-Table S6a; Figure S3), while the percentage share of *L. polyphyllus* was <20%, outside monocultures (ANOVA subset *L. polyphyllus* p_{richness} < .001; ANOVA-Table S6a; Figure S3). One year after the extreme event (B2 harvest, recovery), the relative share of invader species to the total community biomass was still determined by species richness, but had decreased in total and was more similar between the invader species (ANOVA p_{richness} < .001; ANOVA-Table S6b; Figure S4).

3.5 | Survival

Invader presence during drought (B1 harvest) changed the viability of plant communities depending on invader species and species richness level (ANOVA $p_{\text{richness×invader presence}}$ = .002; Table S3a, ANOVA-Table S7): Survival of *S. inaequidens* communities showed a tendency to decrease with species richness level (ANOVA subset *S. inaequidens* p_{richness} = .042; ANOVA-Table S7), while those of



Lupinus polyphyllus ***Senecio inaequidens***

FIGURE 3 Individual invader biomass at the end of the drought treatment (B1 harvest) presented as a function of richness separately for every climate treatment. The mean biomass of an individual calculated for every mesocosm is shown, separately for (a) *Lupinus polyphyllus* (n_{control} = 45; n_{drought} = 45) and (b) *Senecio inaequidens* (n_{control} = 45; n_{drought} = 45). Data points were jittered at each richness level to improve visibility of the data distribution. Solid lines display mixed-effects model fits of the invader specific submodels (Bonferroni-corrected significance level p < .025; ANOVA-Table S5a), and grey shades indicate their respective 95% confidence intervals

L. polyphyllus communities increased with decreasing invader fraction (ANOVA subset *L. polyphyllus* p_{richness} = .015; ANOVA-Table S7). We observed a decrease in the survival differences of native plant communities versus invader plant communities with decreasing invader fraction (ANOVA $p_{\text{richness×invader presence}}$ = .002; ANOVA-Table S7). Survival of *L. polyphyllus* individuals after drought was lower, while the survival of *S. inaequidens* individuals was higher (Table S3b) compared to native species (Table S3a). Presence of invader species decreased the viability of natives (natives within *L. polyphyllus*/*S. inaequidens*; Table S3b) compared to native plant species communities (Table S3a).

The drought treatment decreased the viability of native communities by 11.1%, of *L. polyphyllus* communities by 11.9% and those of *S. inaequidens* by 5.6% (ANOVA $p_{\text{climate treatment}}$ = .072; ANOVA-Table S7).

4 | DISCUSSION

4.1 | Presence of the two studied invader species disrupts the positive richness–recovery relationship of semi-natural grasslands in the face of drought

We found a positive diversity–stability relationship of our native species communities for recovery after drought across three European sites. Invader presence disrupted this positive relationship irrespective of the overall invader performance under drought conditions.

One year after the extreme drought event, community productivity had fully recovered and in some cases even overcompensated, particularly in the high-diversity mesocosms of native communities. Native species richness improved the drought recovery of biomass production in our multisite experiment and, thus, provided ecosystem stability in the face of extreme climatic events in uninvaded assemblages. These findings are consistent with previous studies showing positive relationships between diversity and recovery after extreme climatic events independent from the overall productivity of the communities (Allison, 2004; DeClerck, Barbour, & Sawyer, 2006; Kreyling et al., 2017; Van Ruijven & Berendse, 2010; Vogel, Scherer-Lorenzen, & Weigelt, 2012).

The presence of *L. polyphyllus* and *S. inaequidens* nullified the positive richness–recovery effect found in our native communities. The disruption of the positive richness–recovery relationship in the presence of invasive species is most likely due to their high productivity and the decreasing relative invader fraction with increasing richness. *S. inaequidens* communities showed a stronger resistance and recovery than *L. polyphyllus* communities and the native species communities. This resulted in the neutralization of the positive diversity–stability relationship of native communities wherever *S. inaequidens* contributed more to the community biomass. *S. inaequidens*' ability for enhanced nutrient uptake modifies ecosystem functions by depleting the topsoil nutrient pools and thus reduces the above-ground biomass of the invaded sites (Dassonville et al., 2008; GISD, 2015). Consequently, *S. inaequidens* might have been able to capture free resources more efficiently than natives both during and after the drought event, likely leading to competitive advantages due to greater growth and development. The highly competitive invader *S. inaequidens* might be able to dominate native communities through increased stress tolerance (Daehler, 2003; Davis, Grime, & Thompson, 2000; Diez et al., 2012), more efficient uptake of limiting resources during the extreme drought (Funk & Vitousek, 2007; Huston, 2004; Vilà & Weiner, 2004), and by more rapid uptake of available resources after stress relief compared to slower growing native species. Thus, *S. inaequidens* seems to increase the competitive pressure on the native species during the drought event and likely disturbs the partitioning of resources after stress release.

L. polyphyllus communities also showed a higher and overcompensating recovery compared to native species, despite an average drought resistance in terms of above-ground biomass production. This high ability to recover from a severe drought event in *L. polyphyllus* suggests increased resource allocation to the roots. *L. polyphyllus* is resistant to above-ground biomass removal due to its rhizomes, which enable the invader to resprout multiple times as well as to spread vegetatively by polycormons up to 0.2 m/year (Volz, 2003; Volz & Otte, 2001). Consequently, *L. polyphyllus* might be able to dominate native communities due to its ability to recover quickly after an extreme event (Daehler, 2003; Davis et al., 2000; Diez et al., 2012), and is likely to benefit from the reduced competitive strength of drought-affected native species. However, *L. polyphyllus* does not seem to disturb the partitioning of resources after stress release as natives growing with the non-native legume produced more biomass in both control and drought conditions compared to native species without invader presence.

Many invasive species show such opportunistic traits (Burns & Winn, 2006; Daehler, 2003; Funk, 2008; Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006). Consequently, the presence of competitive and stress tolerant invaders might be able to overturn the positive diversity–stability relationship of native grassland communities (Wilsey et al., 2014). While stability, in terms of biomass production, of native species communities seems to have profited from species richness, that is native species growing in a mixture of potentially asynchronous species, stability of the invader mesocosms seems to be inferred largely by highly productive invasives and their respective share in the entire community (Wilsey et al., 2014). Consequently, the overall stability of the native versus the invader communities may be inferred by two different mechanisms but might ultimately lead to stable—in terms of sheer biomass production—grassland communities (Wilsey et al., 2014). However, both invasive species tested in this study are pasture weeds and their presence might lead to a reduction in fodder value and thus, to economic losses (since the quality of hay production is reduced due to the presence of those species) especially if they occupy large parts of the affected grasslands (Bossdorf, Lipowsky, & Prati, 2008; Hensgen & Wachendorf, 2016). Additionally, invader presence in semi-natural grasslands will certainly lead to significant change with respect to species richness, habitat provision, nutrient cycling, and water regulations (Klinger et al., 2019; Ramula & Sorvari, 2017; Thiele et al., 2010).

Resistance to the applied pulsed drought event was unrelated to species richness in our study. Current state of the art knowledge reports contrasting effects of sudden pulse events (De Boeck et al., 2018; Dreesen et al., 2014; Kreyling et al., 2017; our study) versus prolonged chronic drought events in grassland communities (De Boeck et al., 2018; Zhou et al., 2016). Prolonged chronic drought events give time to trigger acclimation processes and therefore ecosystems have time to build up resistance in the case of press events (De Boeck et al., 2018; Zhou et al., 2016); while in pulse drought events stability is usually inferred via recovery due to a sudden increase of available resources at the end of the climatic event (De Boeck et al., 2018; Dreesen et al., 2014). However, interpretation of results is not always straight forward as the diversity–stability effect, in terms of insurance due to species asynchronous reactions to stress, might heavily depend upon the characteristics of the stressor (e.g. intensity), the affected community, and the response variable under consideration (Allison, 2004; Blake & Duffy, 2010).

The diversity effects observed in this experiment appear to be relatively small. This might be due to the chosen community composition used in the experiment, or due to the relatively short spatial and temporal scales tested. Previous literature has shown that different stability components do not necessarily covary positively along a diversity gradient, but are rather likely to show opposing effects (Pennekamp et al., 2018). That is, species richness may have had no effect on resistance in this study, but might have increased temporal stability in the long run. Extreme drought can induce stochastic effects in community development and therefore impair predictability even under homogeneous abiotic conditions (Kreyling, Jentsch, & Beierkuhnlein, 2011). For example, if immigration and extinction follow different temporal dynamics, a reduction in environmental quality (here, due to drought) could lead to a temporal increase of species richness (Hillebrand et al., 2018). Additionally, recent evidence suggests that non-monotonic effects, that is hump- or U-shaped effects of diversity, on overall ecosystem stability are likely (Pennekamp et al., 2018). Thus, depending on the ecosystem under consideration biodiversity may increase stability when biodiversity is low, and decrease stability in cases of high biodiversity or the other way round in cases of a U-shaped relationship (Pennekamp et al., 2018). Note that the level of abiotic stress tested in this study (drought-induced biomass reduction of 28%) is comparable to those of natural drought events such as the Central European summer heat waves in 2003 and 2018 (Ciais et al., 2005; Toreti et al., 2019) as well as preceding studies on diversity–stability relationships (Isbell et al., 2015; Kreyling et al., 2017; Pfisterer & Schmid, 2002; Van Ruijven & Berendse, 2010).

4.2 | Extreme drought events lead to a facilitation of the two studied invader species in semi-natural grasslands

Our results revealed facilitation of invasive species in semi-natural grasslands due to extreme drought events, though the pathway to this effect varied between the two invaders. *S. inaequidens* showed increased resistance of biomass production during drought as well as an increased ability to recover from such an extreme event. The increased biomass (relative to plants in ambient conditions) of *S. inaequidens* in the recovery to drought indicates a high potential of the species to acquire free resources, such as those released from soil C and N mineralization that follows re-wetting of the dry soil (sensu Birch effect; Birch, 1958; Borken & Matzner, 2009; Ingrisch et al., 2018) and the decreased survival of natives in the presence of *S. inaequidens*. Such an effect was not visible in the recovery of biomass production of *L. polyphyllus* (relative to plants in ambient conditions), nor was the survival of the non-native legume better compared to the native species in either climate treatment (even to the contrary). Windows of opportunity for establishment and spread of invasive species arise in the time lag between when invasive species are able to recover and when abiotic conditions become suitable again for native communities (Diez et al., 2012). According to our results, *L. polyphyllus* might not be able to use the 'invasion window' (Diez et al., 2012) arising during the drought event, but the slightly improved recovery of the legume invader might be sufficient enough to outcompete native species after the drought event. A recent study indicates that a slight performance advantage of *L. polyphyllus* under combined extreme drought and competition effects might be enough for the legume invader to outcompete native species during phases of increased abiotic stress and thus, to use the arising 'invasion window' (Vetter et al., 2019). But, it is likely that *S. inaequidens* will profit from a future increase of extreme climatic events (Hewitson et al., 2014) by using this key temporal aspect—the arising invasion window during drought—to expand its competitive advantage over native species and thus increasing its cover.

The invader impact upon native species performance—in terms of reduction in biomass production of the native species—was more pronounced in *S. inaequidens* relative to *L. polyphyllus*. The observed asymmetric competition is likely due to *S. inaequidens* being a better interspecific competitor and the combination of both stressors seemed to be beneficial for its biomass production. *L. polyphyllus* seemed to be a weaker interspecific competitor which suffered under the presence of the native species as well as the drought treatment, thus it struggled with both, the single effect of competition as well as the combination of competition and extreme climatic events. Native plants growing with *L. polyphyllus* in communities did not suffer from the presence of the non-native legume—in terms of reduced biomass production—as strongly as native plants growing within *S. inaequidens* communities. *S. inaequidens* seems to be better adapted to a possibly drier future climate (EPPO, 2006) than *L. polyphyllus*. *S. inaequidens* and *L. polyphyllus* have different plant–soil relationships, with the former being adept at depleting topsoil nutrient content (Dassonville et al., 2008; GISD, 2015) and the latter being a legume and potentially increasing the plant available nitrogen in the invaded habitats (Otte & Maul, 2005; Thiele et al., 2010; Volz, 2003). In other words, where *S. inaequidens* directly competes with natives, *L. polyphyllus* may facilitate native species due to (a) direct fertilization or (b) by using the rhizobia's nitrogen instead of the available soil nitrogen content, thus resulting in higher net soil N availability for the native species in both ambient and stressful environmental conditions.

In sum, we showed that the interaction of extreme climatic events and invasive species might not only disrupt the ability of native communities to recover from drought, but that extreme events might also facilitate non-native invaders, at least if they are well adapted to the future climate (Wilsey et al., 2014). Generalizing from our two target invader species, invaders of warm origin may profit from a drier future climate in Central Europe, while invaders from cold regions may struggle with the combined effects of drought and native species competition.

ACKNOWLEDGEMENTS

This work was funded by ERA-Net, BiodivERsA (SIGNAL; http://www.bayceer.uni-bayreuth.de/signal/index.php?lang=de; Funding ID 01LC1201), the German Federal Ministry of Education and Research (BMBF), BonaRes (SUSALPS; https://www.susalps.de/en/; Funding ID: 031B0027C), the Belgian Federal Science Policy Office (BELSPO), and the Bulgarian Science Found. We thank numerous students and technicians for field assistance, and two anonymous reviewers for their thoughtful recommendations, which helped to further improve our manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTION

A.J. and J.K. conceived the project and the experiment. Organization of the experimental sites and data collection was split per site: H.J.D.B., I.N., and S.B. contributed experimental data for site BE; D.S. and I.A. contributed experimental data for site BG; and A.J., B.J.B., J.D., J.K., M.A.S.A.-K., M.A.S., P.v.G., P.A.W., V.M.S.V., and M.Z. contributed experimental data for site DE. B.J.B., M.A.S. and V.M.S.V. designed the figures; and M.A.S. and B.J.B. produced the graphics. V.M.S.V. assembled and analyzed the data; and V.M.S.V. wrote the manuscript with substantial input from J.K. and P.A.W. All other co-authors contributed substantially in revising the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.11766231.v1. R scripts are available from the corresponding author upon reasonable request.

ORCID

Vanessa M. S. Vetter https://orcid.org/0000-0003-2082-9177
Juergen Kreyling https://orcid.org/0000-0001-8489-7289
Jürgen Dengler https://orcid.org/0000-0003-3221-660X
Iva Apostolova https://orcid.org/0000-0002-2701-175X
Mohammed A. S. Arfin-Khan https://orcid.org/0000-0001-6275-7023
Bernd J. Berauer https://orcid.org/0000-0002-9472-1532
Sigi Berwaers https://orcid.org/0000-0003-2637-8119
Hans J. De Boeck https://orcid.org/0000-0003-2180-8837
Ivan Nijs https://orcid.org/0000-0003-3111-680X
Max A. Schuchardt https://orcid.org/0000-0003-3103-8063
Desislava Sopotlieva https://orcid.org/0000-0002-9281-7039
Peter A. Wilfahrt https://orcid.org/0000-0003-1594-6512
Anke Jentsch https://orcid.org/0000-0002-2345-8300

REFERENCES

Alba, C., NeSmith, J. E., Fahey, C., Angelini, C., & Flory, S. L. (2017). Methods to test the interactive effects of drought and plant invasion on ecosystem structure and function using complementary common garden and field experiments. *Ecology and Evolution*, *7*(5), 1442–1452. https://doi.org/10.1002/ece3.2729

Allison, G. (2004). The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs*, *74*(1), 117–134. https://doi.org/10.1890/02-0681

Anderson, T. M., Griffith, D. M., Grace, J. B., Lind, E. M., Adler, P. B., Biederman, L. A., … Borer, E. T. (2018). Herbivory and eutrophication mediate grassland plant nutrient responses across a global climatic gradient. *Ecology*, *99*(4), 822–831. https://doi.org/10.1002/ecy.2175

Bahn, M., & Ingrisch, J. (2018). Accounting for complexity in resilience comparisons: A reply to Yeung and Richardson, and further considerations. *Trends in Ecology & Evolution*, *33*(9), 649–651. https://doi.org/10.1016/j.tree.2018.06.006

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *ArXiv:1406.5823 [Stat]*. Retrieved from http://arxiv.org/abs/1406.5823

Bernard-Verdier, M., & Hulme, P. E. (2019). Alien plants can be associated with a decrease in local and regional native richness even when at low abundance. *Journal of Ecology*, *107*(3), 1343–1354. https://doi.org/10.1111/1365-2745.13124

Beuthin, M. (2012). Plant guide for bigleaf lupine (*Lupinus polyphyllus*). *USDA-Natural Resources Conservation Service, Plant Materials Center, Corvallis, OR*. Retrieved from https://nitcnrcsbase-www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/orpmcpg11723.pdf

Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, *10*(1), 9–31. https://doi.org/10.1007/BF01343734

Blake, R. E., & Duffy, J. E. (2010). Grazer diversity affects resistance to multiple stressors in an experimental seagrass ecosystem. *Oikos*, *119*(10), 1625–1635. https://doi.org/10.1111/j.1600-0706.2010.18419.x

Blüthgen, N., Dormann, C. F., Prati, D., Klaus, V. H., Kleinebecker, T., Hölzel, N., … Weisser, W. W. (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology*, *13*(3), 207–220. https://doi.org/10.1016/j.baae.2012.04.001

Borken, W., & Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology*, *15*(4), 808–824. https://doi.org/10.1111/j.1365-2486.2008.01681.x

Bossdorf, O., Lipowsky, A., & Prati, D. (2008). Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe: Genetic differentiation in *Senecio inaequidens*. *Diversity and Distributions*, *14*(4), 676–685. https://doi.org/10.1111/j.1472-4642.2008.00471.x

Burns, J. H., & Winn, A. A. (2006). A comparison of plastic responses to competition by invasive and non-invasive congeners in the Commelinaceae. *Biological Invasions*, *8*(4), 797–807. https://doi.org/10.1007/s10530-005-3838-5

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., … Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Caldeira, M. C., Lecomte, X., David, T. S., Pinto, J. G., Bugalho, M. N., & Werner, C. (2015). Synergy of extreme drought and shrub invasion reduce ecosystem functioning and resilience in water-limited climates. *Scientific Reports*, *5*, 15110. https://doi.org/10.1038/srep15110

Cancellieri, L., Mancini, L. D., Sperandii, M. G., & Filibeck, G. (2017). In and out: Effects of shoot- vs. rooted-presence sampling methods on plant diversity measures in mountain grasslands. *Ecological Indicators*, *72*, 315–321. https://doi.org/10.1016/j.ecolind.2016.08.029

Cantarel, A. A. M., Bloor, J. M. G., & Soussana, J.-F. (2013). Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. *Journal of Vegetation Science*, *24*(1), 113–126. https://doi.org/10.1111/j.1654-1103.2012.01452.x

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Chytrý, M., Maskell, L. C., Pino, J., Pyšek, P., Vilà, M., Font, X., & Smart, S. M. (2008). Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, *45*(2), 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L. C., & Vilà, M. (2009). European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, *15*(1), 98–107. https://doi.org/10.1111/j.1472-4642.2008.00515.x

Ciais, P. H., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., … Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, *437*(7058), 529–533. https://doi.org/10.1038/nature03972

Craine, J. M., Nippert, J. B., Elmore, A. J., Skibbe, A. M., Hutchinson, S. L., & Brunsell, N. A. (2012). Timing of climate variability and grassland productivity. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(9), 3401–3405. https://doi.org/10.1073/pnas.1118438109

Daehler, C. C. (2003). Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 183–211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*(1), 52–58. https://doi.org/10.1038/nclimate1633

Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W., & Meerts, P. (2008). Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia*, *157*(1), 131–140. https://doi.org/10.1007/s00442-008-1054-6

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*(3), 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

De Boeck, H. J., Bloor, J. M. G., Aerts, R., Bahn, M., Beier, C., Emmett, B. A., … Knapp, A. K. (2019). Understanding ecosystems of the future will require more than realistic climate change experiments – A response to Korell et al. *Global Change Biology*, *26*, e6–e7. https://doi.org/10.1111/gcb.14854

De Boeck, H. J., Bloor, J. M. G., Kreyling, J., Ransijn, J. C. G., Nijs, I., Jentsch, A., & Zeiter, M. (2018). Patterns and drivers of biodiversity-stability relationships under climate extremes. *Journal of Ecology*, *106*(3), 890–902. https://doi.org/10.1111/1365-2745.12897

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J. B., … Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*, *16*(5), 617–625. https://doi.org/10.1111/ele.12088

DeClerck, F. A. J., Barbour, M. G., & Sawyer, J. O. (2006). Species richness and stand stability in conifer forests of the Sierra Nevada. *Ecology*, *87*(11), 2787–2799. https://doi.org/10.1890/0012-9658(2006)87[2787:SRASSI]2.0.CO;2

Dengler, J., & Tischew, S. (2018). Grasslands of Western and Northern Europe – Between intensification and abandonment. In V. R. Squires, J. Dengler, H. Feng, & L. Hua (Eds.), *Grasslands of the world: diversity, management and conservation* (pp. 27–63). Boca Raton, FL: CRC Press.

Diez, J. M., D'Antonio, C. M., Dukes, J. S., Grosholz, E. D., Olden, J. D., Sorte, C. J., … Miller, L. P. (2012). Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment*, *10*(5), 249–257. https://doi.org/10.1890/110137

Dimitrakopoulos, P. G., & Schmid, B. (2004). Biodiversity effects increase linearly with biotope space: Diversity effects increase with biotope space. *Ecology Letters*, *7*(7), 574–583. https://doi.org/10.1111/j.1461-0248.2004.00607.x

Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., … Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, *19*(9), 1172–1185. https://doi.org/10.1111/ele.12648

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*(6181), 296–299. https://doi.org/10.1126/science.1248484

Dreesen, F. E., De Boeck, H. J., Janssens, I. A., & Nijs, I. (2014). Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages. *Biogeosciences*, *11*(1), 109–121. https://doi.org/10.5194/bg-11-109-2014

Ellenberg, H. (1996). *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Stuttgart, Germany: Ulmer Verlag.

EPPO. (2006). Data sheet on invasive plants *Senecio inaequidens*. *European and Mediterranean Plant Protection Organization (EPPO)*. Retrieved from https://gd.eppo.int/taxon/SENIQ/documents

Ernst, W. H. O. (1998). Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in the Netherlands: From wool alien to railway and road alien. *Acta Botanica Neerlandica*, *47*(1), 131–151.

Evans, S. E., Byrne, K. M., Lauenroth, W. K., & Burke, I. C. (2011). Defining the limit to resistance in a drought-tolerant grassland: Long-term severe drought significantly reduces the dominant species and increases ruderals: Grassland response to long-term drought. *Journal of Ecology*, *99*(6), 1500–1507. https://doi.org/10.1111/j.1365-2745.2011.01864.x

Flores-Moreno, H., Reich, P. B., Lind, E. M., Sullivan, L. L., Seabloom, E. W., Yahdjian, L., … Borer, E. T. (2016). Climate modifies response of non-native and native species richness to nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1694), 20150273. https://doi.org/10.1098/rstb.2015.0273

Fremstad, E. (2010). *NOBANIS – Invasive alien species fact sheet* – Lupinus polyphyllus. Retrieved from www.nobanis.org

Funk, J. L. (2008). Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology*, *96*(6), 1162–1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, *446*(7139), 1079–1081. https://doi.org/10.1038/nature05719

Global Invasive Species Database (GISD). (2015). *Species profile* Senecio inaequidens. Retrieved from http://www.iucngisd.org/gisd/species.php?sc=1458

Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Wayne Polley, H., … van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *The American Naturalist*, *183*(1), 1–12. https://doi.org/10.1086/673915

Hautier, Y., Isbell, F., Borer, E. T., Seabloom, E. W., Harpole, W. S., Lind, E. M., … Hector, A. (2018). Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nature*

Ecology & Evolution, *2*(1), 50–56. https://doi.org/10.1038/s41559-017-0395-0

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, *348*(6232), 336–340. https://doi.org/10.1126/science.aaa1788

Heger, T., & Böhmer, H. J. (2006). NOBANIS – Invasive alien species fact sheet – *Senecio inaequidens. Online Database of the European Network on Invasive Alien Species – NOBANIS*. Retrieved from www.nobanis.org

Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, *97*(3), 393–403. https://doi.org/10.1111/j.1365-2745.2009.01480.x

Hensgen, F., & Wachendorf, M. (2016). The effect of the invasive plant species *Lupinus polyphyllus* Lindl. on energy recovery parameters of semi-natural grassland biomass. *Sustainability*, *8*(10), 998. https://doi.org/10.3390/su8100998

Hewitson, B., Janetos, A. C., Carter, T. R., Giorgi, F., Jones, R. G., Kwon, W.-T., … van Aalst, M. (2014) Regional context. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, … L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 1133–1197). Cambridge, UK and New York, NY: Cambridge University Press.

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., … Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, *55*(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology & Evolution*, *30*, 503–506.

Huston, M. A. (2004). Management strategies for plant invasions: Manipulating productivity, disturbance, and competition. *Diversity Distributions*, *10*(3), 167–178. https://doi.org/10.1111/j.1366-9516.2004.00083.x

Ingrisch, J., Karlowsky, S., Anadon-Rosell, A., Hasibeder, R., König, A., Augusti, A., … Bahn, M. (2018). Land use alters the drought responses of productivity and CO_2 fluxes in mountain grassland. *Ecosystems*, *21*(4), 689–703. https://doi.org/10.1007/s10021-017-0178-0

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., … Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*(7574), 574–577. https://doi.org/10.1038/nature15374

Klinger, Y. P., Harvolk-Schöning, S., Eckstein, R. L., Hansen, W., Otte, A., & Ludewig, K. (2019). Applying landscape structure analysis to assess the spatio-temporal distribution of an invasive legume in the Rhön UNESCO Biosphere Reserve. *Biological Invasions*, *21*(8), 2735–2749. https://doi.org/10.1007/s10530-019-02012-x

Kreyling, J., Dengler, J., Walter, J., Velev, N., Ugurlu, E., Sopotlieva, D., … Jentsch, A. (2017). Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment. *Ecology Letters*, *20*(11), 1405–1413. https://doi.org/10.1111/ele.12848

Kreyling, J., Jentsch, A., & Beierkuhnlein, C. (2011). Stochastic trajectories of succession initiated by extreme climatic events: Stochastic succession caused by drought. *Ecology Letters*, *14*(8), 758–764. https://doi.org/10.1111/j.1461-0248.2011.01637.x

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). *lmerTest: Tests in linear mixed effects models. R package version 2.0-33*. Retrieved from https://CRAN.R-project.org/package=lmerTest

Lachmuth, S., Durka, W., & Schurr, F. M. (2010). The making of a rapid plant invader: Genetic diversity and differentiation in the native and invaded range of *Senecio inaequidens*: Population genetics of a rapid plant invader. *Molecular Ecology*, *19*(18), 3952–3967. https://doi.org/10.1111/j.1365-294X.2010.04797.x

Lauterbach, D., & Nehring, S. (2013). *Naturschutzfachliche Invasivitätsbewertung* Lupinus polyphyllus *– Vielblättrige Lupine*. Bonn: Bundesamt für Naturschutz. Retrieved from www.bfn.de; neobiota@bfn.de

Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01171

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, *16*, 106–115. https://doi.org/10.1111/ele.12073

Nippert, J. B., & Knapp, A. K. (2007). Linking water uptake with rooting patterns in grassland species. *Oecologia*, *153*(2), 261–272. https://doi.org/10.1007/s00442-007-0745-8

Otte, A., & Maul, P. (2005). Verbreitungsschwerpunkt und strukturelle Einnischung der Stauden-Lupine (*Lupinus polyphyllus* Lindl.) in Bergwiesen der Rhön. *Tuexenia*, *25*, 151–182.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., … Petchey, O. L. (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, *563*(7729), 109–112. https://doi.org/10.1038/s41586-018-0627-8

Pfisterer, A. B., & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, *416*, 84–86. https://doi.org/10.1038/416084a

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, *307*, 321–326. https://doi.org/10.1038/307321a0

Pinto, S. M., & Ortega, Y. K. (2016). Native species richness buffers invader impact in undisturbed but not disturbed grassland assemblages. *Biological Invasions*, *18*(11), 3193–3204. https://doi.org/10.1007/s10530-016-1208-0

Pyšek, P., Chytrý, M., & Jarošík, V. (2010). Habitats and land use as determinants of plant invasions in the temperate zone of Europe. In C. Perrings, H. Mooney, & M. Williamson (Eds.), *Bioinvasions and globalization. Ecology, economics, management, and policy* (pp. 66–79). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199560158.001.0001

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Ramula, S., & Sorvari, J. (2017). The invasive herb *Lupinus polyphyllus* attracts bumblebees but reduces total arthropod abundance. *Arthropod-Plant Interactions*, *11*(6), 911–918. https://doi.org/10.1007/s11829-017-9547-z

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., … Wattenbach, M. (2013). Climate extremes and the carbon cycle. *Nature*, *500*(7462), 287–295. https://doi.org/10.1038/nature12350

Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J., & Pigliucci, M. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, *9*(8), 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Schär, C., Vidale, P. L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A., & Appenzeller, C. (2004). The role of increasing temperature variability in European summer heatwaves. *Nature*, *427*(6972), 332–336. https://doi.org/10.1038/nature02300

Scherber, C., Crawley, M. J., & Porembski, S. (2003). The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). *Diversity and Distributions*, *9*(6), 415–426. https://doi.org/10.1046/j.1472-4642.2003.00049.x

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., … Zhang, X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In: Field, C. B., Barros, V., Stocker, T. F., Dahe, Q., Dokken, D. J., Ebi, K. L., … Midgley, P. M. (Eds.). *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of working groups I and II of the intergovernmental panel on climate change* (pp. 109–230). Cambridge, UK, and New York, NY: Cambridge University Press.

Sousa, R., Morais, P., Dias, E., & Antunes, C. (2011). Biological invasions and ecosystem functioning: Time to merge. *Biological Invasions*, *13*(5), 1055–1058. https://doi.org/10.1007/s10530-011-9947-4

Strayer, D. L. (2012). Eight questions about invasions and ecosystem functioning. *Ecology Letters*, *15*(10), 1199–1210. https://doi.org/10.1111/j.1461-0248.2012.01817.x

Thiele, J., Isermann, M., Otte, A., & Kollmann, J. (2010). Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *Journal of Vegetation Science*, *21*(2), 213–220. https://doi.org/10.1111/j.1654-1103.2009.01139.x

Tilman, D., & Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature*, *367*, 363–365. https://doi.org/10.1038/367363a0

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tilman, D., Reich, P. B., & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(26), 10394–10397. https://doi.org/10.1073/pnas.1208240109

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632. https://doi.org/10.1038/nature04742

Toreti, A., Belward, A., Perez-Dominguez, I., Naumann, G., Luterbacher, J., Cronie, O., … Zampieri, M. (2019). The exceptional 2018 European water seesaw calls for action on adaptation. *Earth's Future*, *7*(6), 652–663. https://doi.org/10.1029/2019EF001170

Török, P., & Dengler, J. (2018). Palaearctic grasslands in transition: Overarching patterns and future prospects. In V. R. Squires, J. Dengler, H. Feng, & L. Hua (Eds.), *Grasslands of the world: Diversity, management and conservation* (pp. 15–26). Boca Raton, FL: CRC Press.

Török, P., Janišová, M., Kuzemko, A., Rusina, S., & Stevanovic, Z. D. (2018). Grasslands, their threats and management in eastern Europe. In V. R. Squires, J. Dengler, H. Feng, & L. Hua (Eds.), *Grasslands of the world: Diversity, management and conservation* (pp. 64–88). Boca Raton, FL: CRC Press.

Van Ruijven, J., & Berendse, F. (2010). Diversity enhances community recovery, but not resistance, after drought: Diversity promotes community recovery. *Journal of Ecology*, *98*(1), 81–86. https://doi.org/10.1111/j.1365-2745.2009.01603.x

Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beausejour, R., Brown, C. D., … Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(48), 19456–19459. https://doi.org/10.1073/pnas.1312779110

Vetter, V., Walter, J., Wilfahrt, P. A., Buhk, C., Braun, M., Clemens, S., … Jentsch, A. (2019). Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters. *Plant Biology*, *21*(5), 832–843. https://doi.org/10.1111/plb.12987

Vilà, M., & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? – Evidence from pair-wise experiments. *Oikos*, *105*(2), 229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x

Vogel, A., Scherer-Lorenzen, M., & Weigelt, A. (2012). Grassland resistance and resilience after drought depends on management intensity and species richness. *PLoS ONE*, *7*(5), e36992. https://doi.org/10.1371/journal.pone.0036992

Volz, H. (2003). *Ursachen und Auswirkungen der Ausbreitung von* Lupinus polyphyllus *Lindl. im Bergwiesenökosystem der Rhön und Maßnahmen zu seiner Regulierung*. Giessen, Germany: Justus-Liebig-Universität Gießen.

Volz, H., & Otte, A. (2001). Occurrence and spreading ability of *Lupinus polyphyllus* Lindl. in the Hochrhoen area (central Germany). *BfN-Skripten*, *32*, 97–98.

Wang, Y. F., Cui, X. Y., Hao, Y. B., Mei, X. R., Yu, G. R., Huang, X. Z., … Zhou, X. Q. (2011). The fluxes of CO_2 from grazed and fenced temperate steppe during two drought years on the Inner Mongolia Plateau, China. *Science of the Total Environment*, *410–411*, 182–190. https://doi.org/10.1016/j.scitotenv.2011.09.067

Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, *332*(6035), 1273–1277. https://doi.org/10.1126/science.1197479

Wilsey, B. J., Daneshgar, P. P., Hofmockel, K., & Polley, H. W. (2014). Invaded grassland communities have altered stability-maintenance mechanisms but equal stability compared to native communities. *Ecology Letters*, *17*(1), 92–100. https://doi.org/10.1111/ele.12213

Wilson, J. B. (2007). Priorities in statistics, the sensitive feet of elephants, and don't transform data. *Folia Geobotanica*, *42*(2), 161–167. https://doi.org/10.1007/BF02893882

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Zhou, S.-X., Medlyn, B. E., & Prentice, I. C. (2016). Long-term water stress leads to acclimation of drought sensitivity of photosynthetic capacity in xeric but not riparian *Eucalyptus* species. *Annals of Botany*, *117*(1), 133–144. https://doi.org/10.1093/aob/mcv161

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Vetter VMS, Kreyling J, Dengler J, et al. Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought. *Glob Change Biol*. 2020;00:1–13. https://doi.org/10.1111/gcb.15025

10.4.1 Supporting information Manuscript 4

Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought

Vanessa M.S. Vetter[1], Jürgen Kreyling, Iva Apostolova, Mohammed Arfin Khan, Bernd Berauer, Sigi Berwaers, Hans J. De Boeck, Jürgen Dengler, Ivan Nijs, Max Schuchardt, Desislava Sopotlieva, Philipp von Gillhausen, Peter A. Wilfahrt, Maja Zimmermann, Anke Jentsch

[1]Disturbance Ecology, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

MATERIAL AND METHODS

Site characteristics

Table S1: Site characteristics. Mean annual temperature (MAT) and mean annual precipitation (MAP) from www.worldclim.org (Hijmans et al., 2005).

Site	Country	Latitude (°)	Longitude (°)	Altitude (m a.s.l)	MAT (°C)	MAP (mm)	Start of drought	Duration (days)
BE	Belgium	51.24917	4.6717	13	9.9	792	19.06.2014	88
BG	Bulgaria	42.6468	23.2981	650	10.1	597	23.06.2014	85
DE	Germany	49.9219	11.5819	365	8.0	674	25.06.2014	76

Number of replicates per factor combination

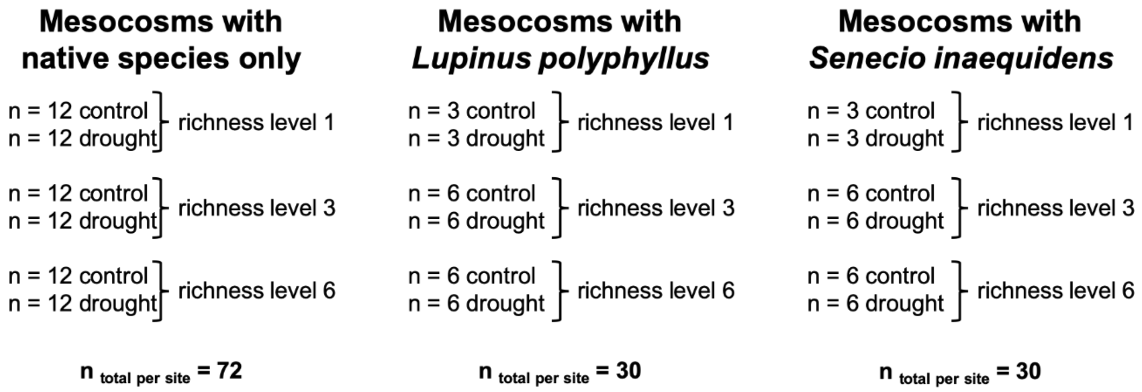


Figure S1: Number of unique assemblages per treatment combination. Treatment combination here refers to richness level x climate treatment x invader presence. Shown are the number of mesocosms (n) for the three factor levels of invader presence (no invader / *Lupinus polyphyllus* / *Senecio inaequidens*) of one site. In total, there were 396 mesocosms across all sites (132 mesocosms each in Belgium, Bulgaria and Germany).

Functional groups

Functional group richness (FGR: 1/2/3) and the presence of legumes was systematically integrated simultaneously with species richness (for additional information, see Kreyling et al., 2017).

Table S2: Target species per functional group and site. Species ID defines the occurrences of the species in the general experimental design. If available, strategy type according to Grime's CSR triangle is provided based on Klotz *et al*. (2002) as competitors (C), ruderals (R), stress –tolerators (S), and their respective combinations, retrieved from the database www.biolflor.de.

Species ID	functional group	Belgium	Bulgaria	Germany
1	graminoid	*Anthoxanthum odoratum* CSR	*Festuca pratensis* C	*Agrostis capillaris* CSR
2	graminoid	*Festuca rubra* agg. C	*Cynosurus cristatus* CSR	*Anthoxanthum odoratum* CSR
3	graminoid	*Dactylis glomerata* C	*Arrhenatherum elatius* C	*Arrhenatherum elatius* C
4	graminoid	*Holcus lanatus* C	*Holcus lanatus* C	*Festuca rubra* agg. C
5	forb	*Stellaria graminea* CS	*Lactuca saligna* CR	*Plantago lanceolata* CSR
6	forb	*Ranunculus acris* C	*Prunella vulgaris* CSR	*Hypochaeris radicata* CSR
7	forb	*Rumex acetosa* C	*Plantago lanceolata* CSR	*Knautia arvensis* C
8	forb	*Epilobium hirsutum* C	*Sanguisorba officinalis* CS	*Leontodon autumnalis* CSR
a	legume	*Trifolium pratense* C	*Lotus corniculatus* CSR	*Trifolium pratense* C
b	legume	*Vicia sativa* CR	*Vicia grandiflora* CR	*Trifolium dubium* R
c	legume	*Lotus corniculatus* CSR	*Medicago lupulina* CSR	*Lotus corniculatus* CSR
d	legume	*Trifolium dubium* R	*Trifolium pratense* C	*Vicia hirsuta* R

Invader species

Lupinus polyphyllus (Fabaceae), the garden lupine, is native to the western parts of North America (California, Oregon, Washington, Montana, Idaho, Nevada) and Canada (British Columbia, Alberta) (Beuthin 2012). Since the 1900s it has been introduced in the European countries of Austria, Denmark, England, Estonia, Finland, Germany, Italy, Latvia, Lithuania, Norway, Poland, Sweden and the central part of European Russia as an ornamental plant, for soil improvement and stabilization, and fodder (Fremstad, 2010). The leguminous species is promoted by human activities, has a high potential of reproduction and dispersal, tends to monopolize resources, and may act as an ecosystem engineer by altering nutrient dynamics (soil nitrogen enrichment), soil chemistry and biodiversity patterns (Beyschlag et al., 2009; Falinski, 1998; Lauterbach and Nehring, 2013). The invader has recently spread greatly over large areas of species-rich mountain meadows in central Europe (Hejda et al., 2009; Otte and Maul, 2005; Thiele et al., 2010; Volz, 2003). *Lupinus polyphyllus* potentially profits from climate change (Lauterbach and Nehring, 2013). In general it is expected that climate warming coupled with a prolonged growing season will lead to an increase in propagation dynamics (Kleinbauer, 2010). However, there is still a crucial gap of knowledge on how extreme weather events influence the future spread of *L. polyphyllus.*

Senecio inaequidens (Asteraceae), the South African ragwort, is native to South Africa and Lesotho and was introduced in Europe, especially in Belgium, France, Germany, Italy, Netherlands, Scotland, and Spain during the late 20th century. The species reached the Mediterranean coast, and expansion continued towards the Eastern Pyrenean region. *Senecio inaequidens* also invaded many habitats in South America (Ernst, 1998; Lachmuth et al., 2010). *Senecio inaequidens* is promoted by human activities, has an extremely high potential of reproduction and dispersal and may potentially profit from climate change (European and Mediterranean Plant Protection Organization (EPPO), 2006; Global Invasive Species Database (GISD), 2015; Heger and Böhmer, 2006). Currently, *S. inaequidens* shows a massive propagation in ruderal and semi-natural habitats throughout Europe (European and Mediterranean Plant Protection Organization (EPPO), 2006; Vacchiano et al., 2013) and regionally starts to form viable populations in grassland ecosystems (Heger and Böhmer, 2006; Scherber et al., 2003; Schmitz and Werner, 2000). Once the plant is established controlling its proliferation and spread is almost impossible (European and Mediterranean Plant Protection Organization (EPPO), 2006). *Senecio inaequidens* shows enhanced nutrient uptake and modifies ecosystem functions by changing the topsoil nutrient pools and thus affecting aboveground biomass of the invaded sites (Dassonville et al., 2008; Global Invasive Species Database (GISD), 2015). Additionally, *S. inaequidens* is threatening biodiversity as it forms dominant populations which might outcompete indigenous species especially of rocky sites (e.g. *Lactuca perennis* a plant species of importance to nature conservation) (Heger and Böhmer, 2006).

Climate treatment

The climate manipulations consisted of extreme drought and ambient conditions for control. Drought and control plots were randomly assigned to four blocks. We covered each of the two drought blocks with a rain-out shelter. The shelters were 6 m x 3 m in size and consisted of a steel frame covered with transparent polyethylene foil (thickness 0.2 mm) allowing light transmission of almost 90 % of the photosynthetically active radiation (Kreyling et al., 2012; Thiele et al., 2010). To minimize heat development by greenhouse effects, air was circulated through 80 cm gaps between the ground and rainout-shelter.

Relative neighbor effects (RNE)

We calculated the relative neighbor effects (RNE) according to Markham and Chanway (1996) to quantify the competition effect upon the performance parameter aboveground biomass (Weigelt and Jolliffe, 2003).

$$RNE = \frac{P_{control} - P_{mix}}{X}$$

with $X = P_{control}$ if $P_{control} > P_{mix}$ and $X = P_{mix}$ if $P_{mix} > P_{control}$

P is the performance per plant, while the subscripts “control” and “mix” in our case designate a plant growing in monoculture (conspecific competition) or in mixture. P_{mix} plants grew in mixture with native species (interspecific competition). Because we use the biomass of plants growing in monocultures as $P_{control}$ instead of the biomass of one single plant, our RNE values show:

-1 the plant species copes better with interspecific competition than with conspecific competition;

0 no difference between conspecific and interspecific competition;

+1 the plant species copes better with conspecific competition than with interspecific competition.

Normally, RNE values range between -1 (maximum facilitation), 0 (no interaction) and +1 (maximum competition).

Statistics

We tested survival, the relative neighbor effect (RNE) and individual biomass of native species growing with and without invader presence using a linear mixed effect model.

Concerning survival, we tested the impact of *climate treatment*, *species richness* and *invader presence*, as well as their interactions, on the percentage of individuals that survived in each mesocosm after the drought treatment (B1 harvest). The relative neighbor effect (RNE) was tested by relating *climate treatment*, *species richness* and *functional group* as well as their interactions to the quotient calculated based on the biomass of the invader communities of the B1 and B2 harvest respectively. We excluded communities that consisted of native species only as the intention here was to determine who is experiencing more competition, the invader species or the native species growing within the invader communities. We run the model three times for each harvest respectively (B1 and B2): 1) with communities of both invader species, 2) only *L. polyphyllus* communities, 3) only *S. inaequidens* communities. The individual biomass of native species growing with and without invader presence after drought (B1 harvest) was compared using the fixed factors *climate treatment*, *functional group* and *invader presence* as well as their interactions. We compared the individual biomass of plants growing in species richness 3 and 6, and actively excluded richness level 1 from the only native species communities (because this richness level is not available for native species growing within invader communities). Thus, we did not test the effect of *species richness* on the individual biomass.

We accounted for possible random effects due to the blocked structure and the multi-site character of the experiment by nesting *blocks* within *sites* in all linear mixed-effects models. As we tested for general trends across three countries, we have considered country effects as random factors in our models, not as fixed factors. We only allowed the intercept to vary as a function of the block design, but did not include any other main factors into the random term. *Species richness* was introduced into the models as a linear numeric variable, but note that log-linear and factorial response produced qualitatively the same results.

Models were fit with the lmer function in the lme4 package (version 1.1-12) (Bates et al., 2014) and results were extracted with the ANOVA function in the lmerTest package (Kuznetsova et al., 2016) in R. We visually checked if the model assumptions of homoscedasticity and normal distribution of residuals were violated. Linear models are robust even towards rather severe violations of the model assumptions (Lo and Andrews, 2015; Wilson, 2007). Consequently, we only transformed our response variables in case of severe violations of the model assumptions. The response variables survival and RNE were not transformed. While the response variable individual biomass (of native species growing with and without invader presence) was log(x + 1.1)-transformed to meet the model assumptions of homoscedasticity and normal distribution of residuals.

RESULTS

Relative neighbor effect (RNE)

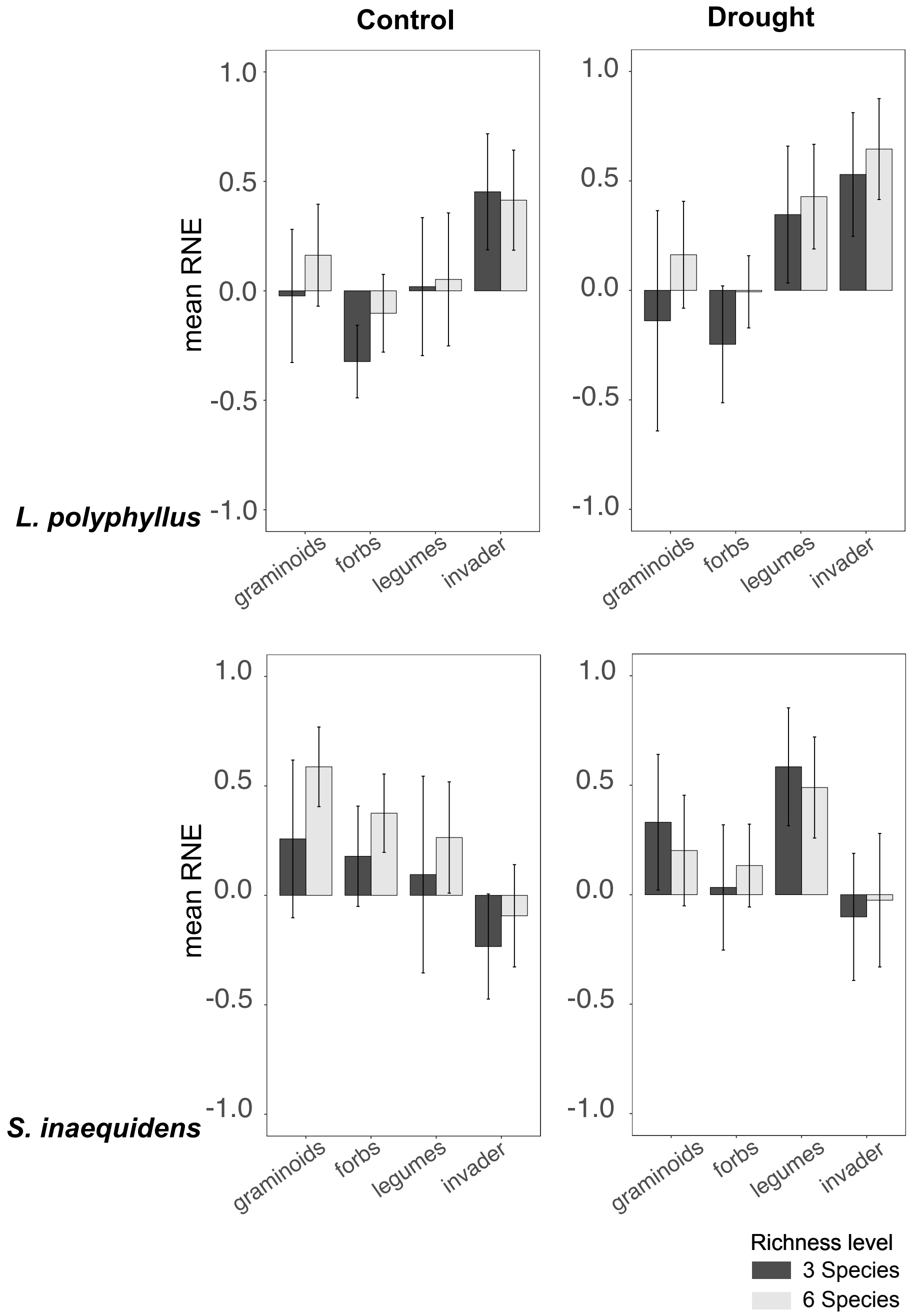


Figure S2: Relative neighbor effect at the end of the drought event (B1 harvest; resistance) of invader species a) *L. polyphyllus* and b) *S. inaequidens*, and native species growing within the respective invaded communities. *Lupinus polyphyllus* mesocosms: control plots $n_{\text{forbs richness 3/6}} = 11 / 36$; $n_{\text{graminoids richness 3/6}} = 12 / 33$; $n_{\text{legumes richness 3/6}} = 15 / 21$; $n_{\textit{L. polyphyllus}\text{ richness 3/6}} = 19 / 18$; drought plots $n_{\text{forbs richness 3/6}} = 10 / 36$; $n_{\text{graminoids richness 3/6}} = 12 / 33$; $n_{\text{legumes richness 3/6}} = 14 / 21$; $n_{\textit{L. polyphyllus}\text{ richness 3/6}} = 18 / 18$. *Senecio inaequidens* mesocosms: control plots $n_{\text{forbs richness 3/6}} = 15 / 27$; $n_{\text{graminoids richness 3/6}} = 12 / 36$; $n_{\text{legumes richness 3/6}} = 9 / 27$; $n_{\textit{S. inaequidens}\text{ richness 3/6}} = 18 / 18$; drought plots $n_{\text{forbs richness 3/6}} = 15 / 28$; $n_{\text{graminoids richness 3/6}} = 12 / 35$; $n_{\text{legumes richness 3/6}} = 9 / 27$; $n_{\textit{S. inaequidens}\text{ richness 3/6}} = 18 / 18$. Shown are the post drought mean RNE values across all countries and the standard error of the mean.

1) Both invade species: The influence of relative neighbors (RNE) on the individual performance of plants growing in invader communities at the end of the drought treatment (B1 harvest) depends on species richness (ANOVA $p_{\text{species richness}} = 0.042$) as well as marginally the functional group being considered (ANOVA $p_{\text{functional group}} = 0.056$).

2) *Lupinus polyphyllus* communities: The influence of relative neighbors (RNE) on the individual performance of plants growing in invader communities with *L. polyphyllus* at the end of the drought treatment (B1 harvest) depends on the functional group being considered (ANOVA $p_{\text{functional group}} = 0.017$) as well as on the species richness (ANOVA $p_{\text{species richness}} = 0.034$).

3) *Senecio inaequidens* communities: None of the tested fixed effects showed a significant effect on the RNE values of the plants growing in the *S. inaequidens* communities.

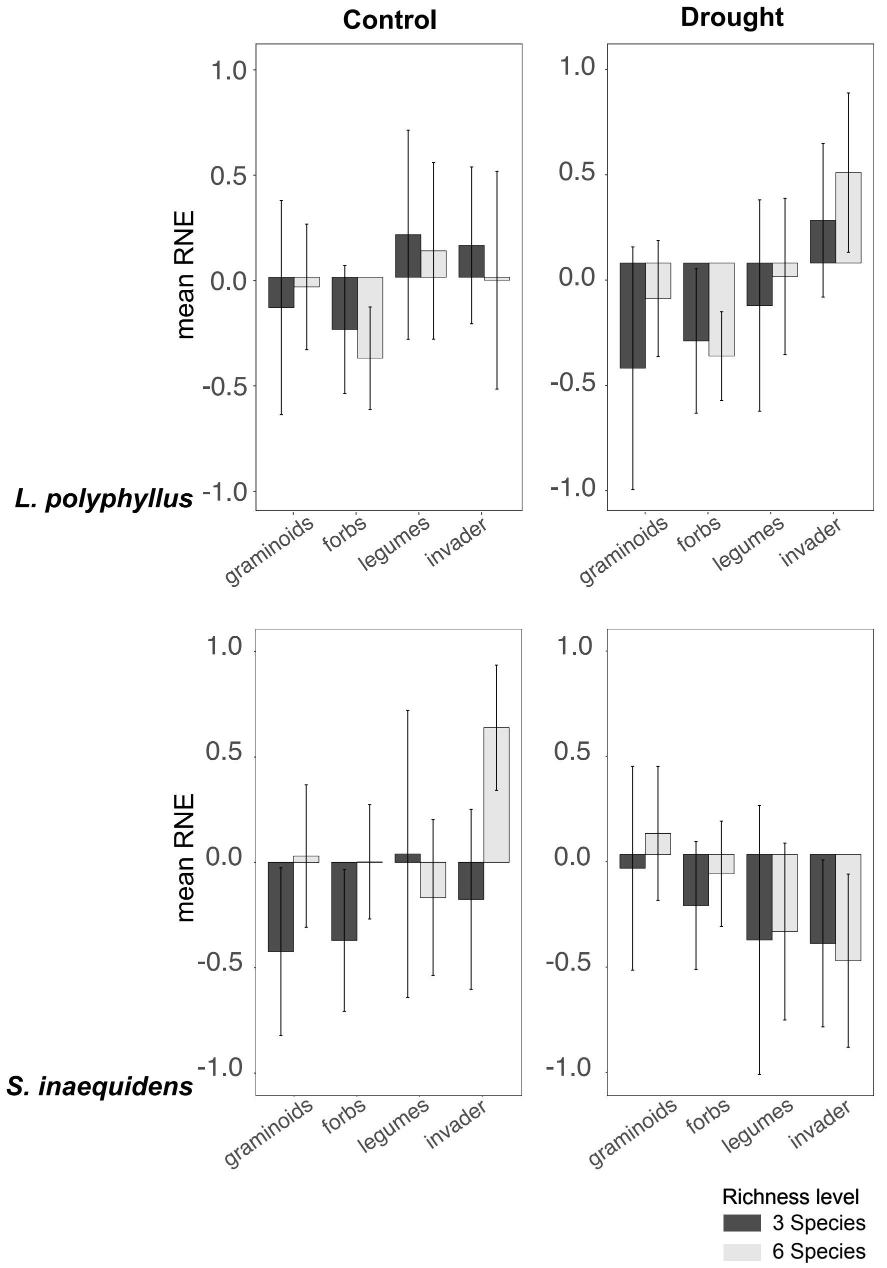


Figure S3: Relative neighbor effect at the peak growing season one year after the drought event (B2 harvest; recovery) of the invader species a) *L. polyphyllus* and b) *S. inaequidens*, and native species growing within the respective invaded communities. *Lupinus polyphyllus* mesocosms: control plots $n_{\text{forbs richness 3/6}} = 8 / 24$; $n_{\text{graminoids richness 3/6}} = 8 / 22$; $n_{\text{legumes richness 3/6}} = 10 / 14$; $n_{\textit{L. polyphyllus}\text{ richness 3/6}} = 13 / 12$; drought plots $n_{\text{forbs richness 3/6}} = 7 / 24$; $n_{\text{graminoids richness 3/6}} = 8 / 22$; $n_{\text{legumes richness 3/6}} = 9 / 14$; $n_{\textit{L. polyphyllus}\text{ richness 3/6}} = 12 / 12$.

Senecio inaequidens mesocosms: control plots $n_{\text{forbs richness 3/6}} = 10 / 18$; $n_{\text{graminoids richness 3/6}} = 8 / 24$; $n_{\text{legumes richness 3/6}} = 6 / 18$; $n_{\textit{S. inaequidens}\text{ richness 3/6}} = 12 / 12$; drought plots $n_{\text{forbs richness 3/6}} = 10 / 19$; $n_{\text{graminoids richness 3/6}} = 8 / 23$; $n_{\text{legumes richness 3/6}} = 6 / 18$; $n_{\textit{S. inaequidens}\text{ richness 3/6}} = 12 / 12$. Shown are the mean RNE values across all countries and the standard error of the mean. Please note that the RNE results of the B2 harvest (recovery) are only based on the data of Germany and Bulgaria as Belgium did not record species-specific biomass at the peak growing season one year after drought.

1) Both invade species: The influence of relative neighbors (RNE) on the individual performance of plants growing in invader communities one year after the drought treatment (B2 harvest) marginally depends on the species richness (ANOVA $p_{\text{species richness}} = 0.096$).

2) *Lupinus polyphyllus* communities: None of the tested fixed effects showed a significant effect on the RNE values of the plants growing in the *L. polyphyllus* communities.

3) *Senecio inaequidens* communities: None of the tested fixed effects showed a significant effect on the RNE values of the plants growing in the *S. inaequidens* communities.

Survival

Table S3: Mean survival in percentage (± SE) calculated for the invader communities and the native species communities at the end of the drought treatment (B1 harvest). The differences of survival between these three types of communities in dependence of climate treatment, invader presence and species richness is tested with the survival model described in the statistics part above. Please also have a look into table S11 for significant results and interactions. ($n_{\textit{L. polyphyllus}\text{ control / drought}} = 174 / 171$, $n_{\textit{S. inaequidens}\text{ control / drought}} = 171 / 171$, $n_{\text{native species control / drought}} = 356 / 359$).
In addition, the mean survival in percentage (± SE) calculated for the individual invader plants as well as for the native individuals growing within and without (native species) an invader community at the end of the drought treatment (B1 harvest) are given. ($n_{\textit{L.P}\text{ individuals control / drought}} = 45 / 45$, $n_{\textit{SI}\text{ individuals control / drought}} = 45 / 45$, $n_{\text{natives within LP control / drought}} = 128 / 126$, $n_{\text{natives within SI control / drought}} = 126 / 126$).

Community	**Survival in control [%]** ± SE	**Survival in drought [%]** ± SE
***Lupinus polyphyllus* communities**	78.7 ± 2.5	69.3 ± 2.9
***Senecio inaequidens* communities**	82.9 ± 2.7	78.3 ± 2.7
Native species	85.0 ± 1.7	75.6 ± 1.9
***L. polyphyllus* individuals**	63.3 ± 5.4	46.8 ± 5.5
***S. inaequidens* individuals**	96.5 ± 2.3	94.9 ± 2.2
Natives within *L. polyphyllus*	66.2 ± 3.5	60.6 ± 3.5
Natives within *S. inaequidens*	61.1 ± 3.7	56.6 ± 3.6

Individual biomass of native species growing with and without invader presence

The individual biomass of native species growing with the invader *S. inaequidens* were on average smaller than natives growing with *L. polyphyllus* or without invader presence (ANOVA $p_{\text{invader presence}} < 0.001$; Table S4). This effect was independent from the climate treatment and the functional group tested (graminoids, herbs, legumes).

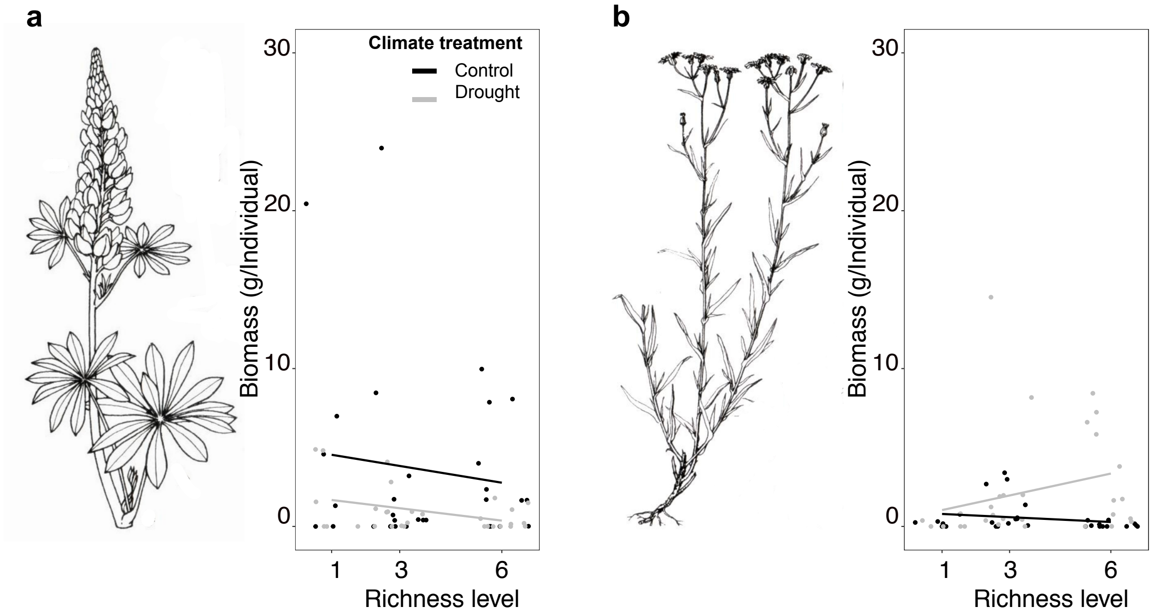
Table S4: Mean individual biomass at the end of the drought treatment (B1 harvest) of the native species growing without and with invader species, as well as of the two invader species *Lupinus polyphyllus* and *Senecio inaequidens* ($n_{\text{natives only richness control/drought}}$ = 356 / 359; $n_{\text{natives in } L. polyphyllus \text{ richness control/drought}}$ = 128 / 126; $n_{\text{natives in } S. inaequidens \text{ control/drought}}$ = 126 / 125). However, biomass of the invader species was not included in the analyzes here, as they were analyzed separately (Figure 3, Figure S2).

	Mean individual biomass [g]		
	average	**control**	**drought**
Lupinus polyphyllus	2.0	3.1	1.0
Senecio inaequidens	5.9	5.6	6.3
Natives only	1.5	1.7	1.3
Natives growing with *L. polyphyllus*	1.6	1.7	1.4
Natives growing with *S. inaequidens*	1.0	1.0	1.0

Invader performance one year after the drought event

One year after the extreme event, performance per individual of the two invaders differed (ANOVA p_{species} = 0.051) with *L. polyphyllus* producing 62.4% more biomass per individual than *S. inaequidens* (across treatments and richness level). The drought treatment, native species as well as species richness showed different effects on the invaders (ANOVA $p_{\text{species x climate treatment x richness}}$ = 0.027): Drought plants of *L. polyphyllus* still showed a lower biomass production compared to control plants (26.5%), while both climate treatments were negatively affected by interspecific competition (decreasing biomass production with increasing richness level; Figure S2). Drought plants of *S. inaequidens* produced more biomass compared to control plants (21.7%). Drought plants seemed to be limited by intraspecific competition, while control plants of *S. inaequidens* showed a tendency to be limited by interspecific competition (Figure S2).

Please note that these results of the individual invader performance are only based on the data of Germany and Bulgaria as Belgium did not record species-specific biomass at the peak growing season one year after drought (B2 harvest; recovery).



Lupinus polyphyllus ***Senecio inaequidens***

Figure S4: Individual invader biomass at the peak growing season one year after the drought event (B2 harvest) shown as a function of richness separately for every treatment. Shown is the mean biomass of an individual calculated for every mesocosm, separately for a) *S. inaequidens* ($n_{control} = 30$; $n_{drought} = 30$) and b) *L. polyphyllus* ($n_{control} = 30$; $n_{drought} = 30$). Data points were jittered at each richness level to improve visibility of the data distribution. Please note that the scaling of the y-axis differs between the invader species.

Relative invader biomass per community biomass

Resistance

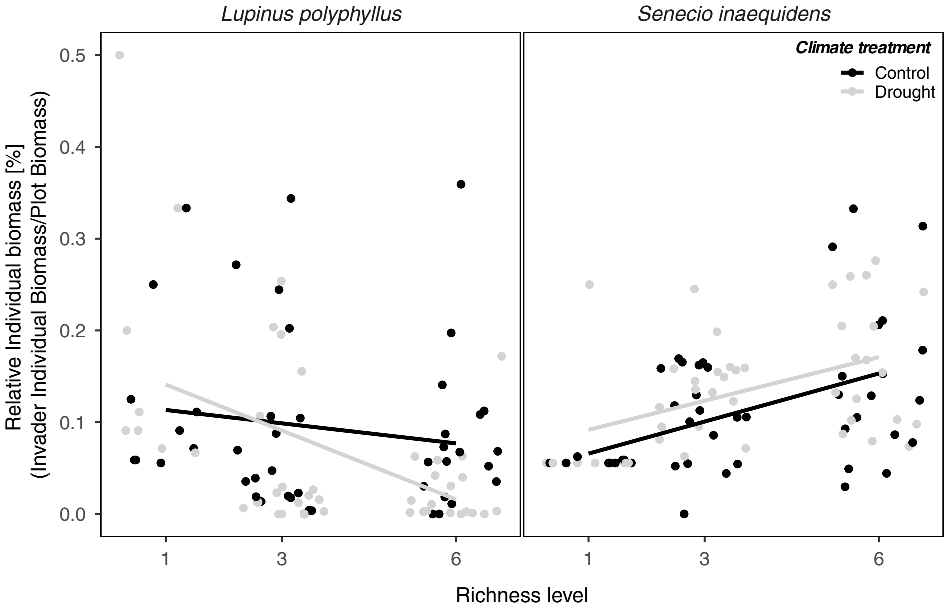


Figure S5: Relative individual invader biomass (individual biomass per community biomass) at the end of the drought treatment (B1 harvest) shown as a function of richness separately for every treatment. Shown is the mean biomass of an individual calculated for every mesocosm, separately for a) *L. polyphyllus* ($n_{control} = 45$; $n_{drought} = 45$) and b) *S. inaequidens* ($n_{control} = 45$; $n_{drought} = 45$). Data points were jittered at each richness level to improve visibility of the data distribution.

Recovery

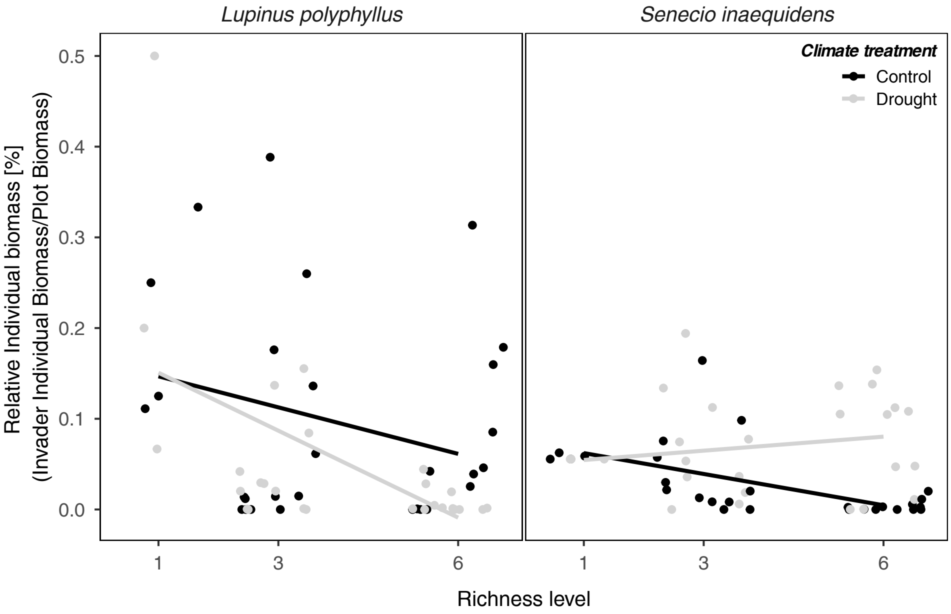


Figure S6: Relative individual invader biomass (individual biomass per community biomass) at the peak growing season one year after the drought event (B2 harvest) shown as a function of richness separately for every treatment. Shown is the mean biomass of an individual calculated for every mesocosm, separately for a) *S. inaequidens* (n $_{\text{control}}$ = 30; n $_{\text{drought}}$ = 30) and b) *L. polyphyllus* (n $_{\text{control}}$ = 30; n $_{\text{drought}}$ = 30). Data points were jittered at each richness level to improve visibility of the data distribution. Please note that these results of the individual invader performance are only based on the data of Germany and Bulgaria as Belgium did not record species-specific biomass at the peak growing season one year after drought (B2 harvest; recovery).

Resistance and recovery

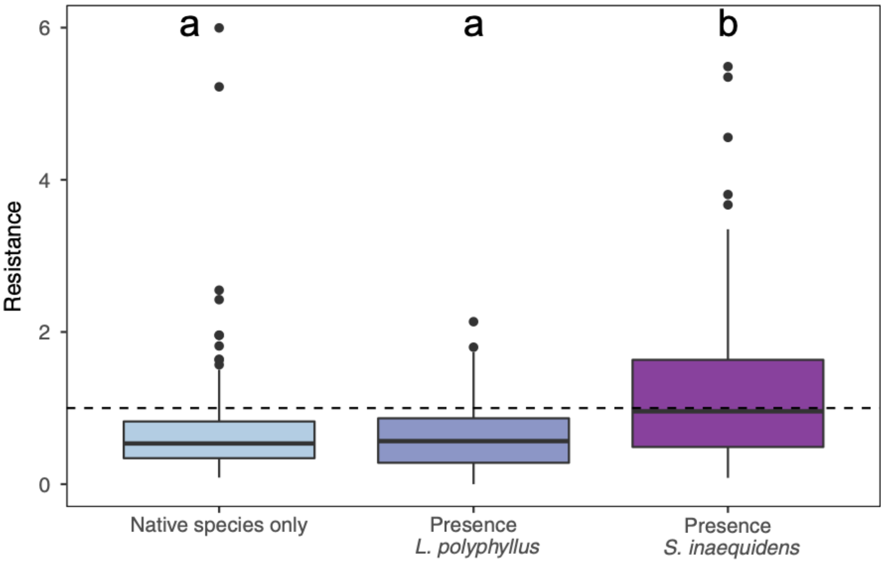


Figure S7: Resistance (B1 ANPP harvest) to a severe drought event, grouped over all richness levels but separately for each invasion status (resistance: n $_{\text{natives}}$ = 107; n $_{L. polyphyllus}$ = 45; n $_{S. inaequidens}$ = 45). All mesocosms with a ratio above 1 (the dashed line) showed higher biomass production in drought compared to ambient conditions, while all mesocosms with ratios below 1 showed lower biomass production in drought than under ambient conditions. Data points were jittered at each richness level to improve visibility of the data distribution. Small letters indicate significant differences between the invader presence levels (post-hoc test, p < 0.05).

Table S5: Mean drought resistance and recovery listed separately for every richness level within the three different plant communities (resistance: n $_{\text{natives}}$ = 107; n $_{\textit{L. polyphyllus}}$ = 45; n $_{\textit{S. inaequidens}}$ = 45; recovery: n $_{\text{natives}}$ = 106; n $_{\textit{L. polyphyllus}}$ = 45; n $_{\textit{S. inaequidens}}$ = 45). Values close to 0 equal incomplete resistance/recovery while values of 1 equal for complete resistance/recovery.

Plant community	**richness**	**Resistance** (mean ± SE)	**Recovery** (mean ± SE)
Native	1	0.93 ± 0.20	0.78 ± 0.10
	3	0.70 ± 0.15	0.86 ± 0.07
	6	0.68 ± 0.07	1.29 ± 0.15
Lupinus polyphyllus	1	0.40 ± 0.18	0.79 ± 0.27
	3	0.70 ± 0.13	1.48 ± 0.28
	6	0.68 ± 0.09	1.46 ± 0.31
Senecio inaequidens	1	2.15 ± 0.70	2.70 ± 1.04
	3	1.14 ± 0.27	1.34 ± 0.22
	6	1.31 ± 0.26	1.55 ± 0.22

References

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *ArXiv14065823 Stat*. Available at: http://arxiv.org/abs/1406.5823 [Accessed June 7, 2018].

Beyschlag, W., Hanisch, S., Friedrich, S., Jentsch, A., and Werner, C. (2009). ^{15} N natural abundance during early and late succession in a middle-European dry acidic grassland. *Plant Biol.* 11, 713–724. doi:10.1111/j.1438-8677.2008.00173.x.

Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W., and Meerts, P. (2008). Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157, 131–140. doi:10.1007/s00442-008-1054-6.

Ernst, W. H. O. (1998). Invasion, dispersal and ecology of the South African neophyte Senecio inaequidens in the Netherlands: from wool alien to railway and road alien. *Acta Bot. Neerlandica* 47, 131–151.

European and Mediterranean Plant Protection Organization (EPPO), N. (2006). Data sheet on Invasive Plants Senecio inaequidens. Available at: https://gd.eppo.int/taxon/SENIQ/documents.

Falinski, J. B. (1998). “Invasive alien plants and vegetation dynamics,” in *Plant invasions, ecological mechanisms and human responses* (Backhuys, Leiden), 3–21.

Fremstad, E. (2010). NOBANIS – invasive alien species fact sheet Lupinus polyphyllus. *Online Database Eur. Netw. Invasive Alien Species – NOBANIS*, 1–11. Available at: www.nobanis.org.

Global Invasive Species Database (GISD) (2015). Species profile Senecio inaequidens. Available at: http://www.iucngisd.org/gisd/species.php?sc=1458 [Accessed January 3, 2018].

Heger, T., and Böhmer, H. J. (2006). NOBANIS - Invasive Alien Species Fact Sheet - Senecio inaequidens. *Online Database Eur. Netw. Invasive Alien Species - NOBANIS Wwwnobanisorg*.

Hejda, M., Pyšek, P., and Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393–403. doi:10.1111/j.1365-2745.2009.01480.x.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. doi:10.1002/joc.1276.

Kleinbauer, Ingrid. (2010). *Ausbreitungspotenzial ausgewählter neophytischer Gefäßpflanzen unter Klimawandel in Deutschland und Österreich Ergebnisse aus dem F+E-Vorhaben FKZ 806 82 330*. Bonn: Bundesamt für Naturschutz.

Kreyling, J., Dengler, J., Walter, J., Velev, N., Ugurlu, E., Sopotlieva, D., et al. (2017). Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment. *Ecol. Lett.* 20, 1405–1413. doi:10.1111/ele.12848.

Kreyling, J., Thiel, D., Nagy, L., Jentsch, A., Huber, G., Konnert, M., et al. (2012). Late frost sensitivity of juvenile Fagus sylvatica L. differs between southern Germany and Bulgaria and depends on preceding air temperature. *Eur. J. For. Res.* 131, 717–725. doi:10.1007/s10342-011-0544-y.

Kuznetsova, A., Brockhoff, P. B., and Christensen, R. H. B. (2016). lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33. Available at: https://CRAN.R-project.org/package=lmerTest.

Lachmuth, S., Durka, W., and Schurr, F. M. (2010). The making of a rapid plant invader: genetic diversity and differentiation in the native and invaded range of Senecio inaequidens: POPULATION GENETICS OF A RAPID PLANT INVADER. *Mol. Ecol.* 19, 3952–3967. doi:10.1111/j.1365-294X.2010.04797.x.

Lauterbach, D., and Nehring, S. (2013). Naturschutzfachliche Invasivitätsbewertung Lupinus polyphyllus - Vielblättrige Lupine. *Bundesamt Für Naturschutz Bonn 2S* Bundesamt für Naturschutz, Konstantinstrasse 110, 53179 Bonn; Phone: +492288491-0; www.bfn.de; neobiota@bfn.de.

Lo, S., and Andrews, S. (2015). To transform or not to transform: using generalized linear mixed models to analyse reaction time data. *Front. Psychol.* 6. doi:10.3389/fpsyg.2015.01171.

Markham, J. H., and Chanway, C. P. (1996). Measuring plant neighbour effects. *Funct. Ecol.* 10, 548–549.

Otte, A., and Maul, P. (2005). Verbreitungsschwerpunkt und strukturelle Einnischung der Stauden-Lupine (Lupinus polyphyllus Lindl.) in Bergwiesen der Rhön. *Tuexenia* 25, 151–182.

Scherber, C., Crawley, M. J., and Porembski, S. (2003). The effects of herbivory and competition on the invasive alien plant Senecio inaequidens (Asteraceae). *Divers. Distrib.* 9, 415–426.

Schmitz, G., and Werner, D. J. (2000). The importance of the alien plant Senecio inaequidens DC. (Asteraceae) for phytophagous insects. *Z. Für Ökol. Naturschutz* 9, 153–160.

Thiele, J., Isermann, M., Otte, A., and Kollmann, J. (2010). Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *J. Veg. Sci.* 21, 213–220. doi:10.1111/j.1654-1103.2009.01139.x.

Vacchiano, G., Barni, E., Lonati, M., Masante, D., Curtaz, A., Tutino, S., et al. (2013). Monitoring and modeling the invasion of the fast spreading alien *Senecio inaequidens* DC. in an alpine region. *Plant Biosyst. - Int. J. Deal. Asp. Plant Biol.* 147, 1139–1147. doi:10.1080/11263504.2013.861535.

Volz, H. (2003). Ursachen und Auswirkungen der Ausbreitung von Lupinus polyphyllus Lindl. im Bergwiesenökosystem der Rhön und Maßnahmen zu seiner Regulierung.

Weigelt, A., and Jolliffe, P. (2003). Indices of plant competition. *J. Ecol.* 91, 707–720.

Wilson, J. B. (2007). Priorities in statistics, the sensitive feet of elephants, and don’t transform data. *Folia Geobot.* 42, 161–167. doi:10.1007/BF02893882.

ANOVA tables

Anova tables are based on the full model with all interaction terms, no simplifications.

Calculation of effect sizes:

$$effect\ size = \frac{treatment - control}{control}$$

“Treatment” here refers to e.g. drought treatment, invader presence etc., while “control” here refers to e.g. native species communities, control climate treatment etc. The respective meaning of "control" and "treatment" depends on the significant (interaction) term/factor and is explained in more detail in the respective table heading.

Abbreviations:

LP = *Lupinus polyphyllus*

SI = *Senecio inaequidens*

Productivity-richness relationship

Table A1: Anova table for model 1 productivity at the end of the drought treatment (B1 harvest). Only community productivity under ambient weather conditions are compared. Shown are the Anova table results for the overall model. Effect sizes here are the percentage difference in productivity of the control mesocosms of the two invader species in comparison to the native species communities growing without invader presence calculated 1) across all richness levels and 2) separately for every richness level.

Source of variation	**Sum of Squares**	**DF**	**Mean Squares**	**F statistic**	**p-value**	**slope**	**Effect size [%]**
Invader presence	240.41	2	120.21	17.97	< 0.001	Natives: 8.71 LP: 11.64 SI: 14.34	LP: + 17.62 SI: +70.26
Species richness	7.80	1	7.80	1.17	0.282		
Invader presence : richness	113.89	2	56.94	8.51	< 0.001	Natives: 0.37 LP: -0.15 SI: -0.55	$LP_{richness\ 1}$: +82.35 $LP_{richness\ 3}$: +5.19 $LP_{richness\ 6}$: -3.50 $SI_{richness\ 1}$: +209.41 $SI_{richness\ 3}$: +72.41 $SI_{richness\ 6}$: +4.58

Native species growing with and without invader presence

Table A2: Anova table for the model testing differences in the biomass production of native species growing with and without invader presence at the end of the drought treatment (B1 harvest).

Effect sizes: Invader presence effect is shown as the percentage difference of the individual biomass (indmass) of native species which grew under invader presence versus the individual biomass of native species growing in native species communities.

Source of variation	Sum of Squares	DF	Mean Squares	F statistic	p-value	slope	Effect size [%]
Climate treatment	0.53	1	0.53	2.12	0.177		
Functional group	0.99	2	0.49	1.97	0.140		
Invader presence	5.20	2	2.60	10.37	< 0.001	Natives: 0.54 LP: 0.88 SI: 0.84	Indmass $_{\text{invader presence LP}}$: +7.14 Indmass $_{\text{invader presence SI}}$: -31.32
Climate treatment : functional group	0.30	2	0.15	0.60	0.549		
Climate treatment : invader presence	0.90	2	0.45	1.79	0.167		
Functional group : invader presence	1.25	4	0.31	1.25	0.288		
Climate treatment : functional group : invader presence	1.48	4	0.37	1.47	0.208		

Resistance after drought

Table A3: Anova table for model 2 resistance at the end of the drought treatment (B1 harvest). Shown are the Anova table results for the overall model as well as the output of the three sub-models run each with one subset of the three invader presence levels. Effect sizes here are the percentage difference in resistance of the two invader species in comparison to the native species communities growing without invader presence.

Source of variation	Sum of Squares	DF	Mean Squares	F statistic	p-value	slope	Effect size [%]
Invader presence	0.91	2	0.45	4.65	0.011	Natives: 0.63 LP: 0.45 SI: 0.89	LP: -18.24 SI: +83.22
Species richness	0.07	1	0.07	0.68	0.411		
Invader presence : richness	0.19	2	0.09	0.97	0.379		
			Only native species				
Species richness	0.17	1	0.17	2.09	0.151		
			***L. polyphyllus* communities**				
Species richness	0.06	1	0.06	1.49	0.229		
			***S. inaequidens* communities**				
Species richness	0.10	1	0.10	0.51	0.478		

Recovery one year after drought

Table A4: Anova table for model 2 recovery at the peak growing season one year after drought (B2 harvest). Shown are the Anova table results for the overall model as well as the output of the three sub-models run each with one subset of the three invader presence levels. Effect sizes here are the percentage difference in recovery of the two invader species in comparison to the native species communities growing without invader presence calculated 1) across all richness levels and 2) separately for every richness level.

Source of variation	**Sum of Squares**	**DF**	**Mean Squares**	**F statistic**	**p-value**	**slope**	**Effect size [%]**
Invader presence	14.77	2	7.38	8.12	< 0.001	Natives: 0.66 LP: 1.01 SI: 2.24	LP: +28.72 SI: +107.61
Species richness	0.01	1	0.01	0.01	0.908		
Invader presence : richness	6.82	2	3.41	3.75	0.026	Natives: 0.09 LP: 0.08 SI: -0.16	$LP_{richness\ 1}$: +1.52 $LP_{richness\ 3}$: +72.05 $LP_{richness\ 6}$: +12.61 $SI_{richness\ 1}$: +247.48 $SI_{richness\ 3}$: +55.76 $SI_{richness\ 6}$: +19.59
				Only native species			
Species richness	4.52	1	4.52	11.01	0.001	0.11	See table S5
				***L. polyphyllus* communities**			
Species richness	0.72	1	0.72	0.67	0.419		
				***S. inaequidens* communities**			
Species richness	4.45	1	4.45	3.09	0.088	-0.18	See table S5

Differences between the two invaders – per individual biomass

Table A5: Anova table for model 3 individual invader performance at 1) resistance (B1 harvest) and 2) recovery (B2 harvest).

Effect sizes resistance: Percentage difference in the individual biomass of *Lupinus polyphyllus* in comparison to *Senecio inaequidens* and vice versa across all richness levels and separately for every richness level. Drought effect is shown as the percentage difference of the individual biomass of an invader species growing under drought versus control conditions.

Effect sizes recovery: Percentage difference in the individual biomass of *Lupinus polyphyllus* in comparison to *Senecio inaequidens* and vice versa across all richness levels. Drought effect separately for every richness level of every species is shown as the percentage difference of the individual biomass of an invader species growing under drought versus control conditions.

				Resistance			
Source of variation	**Sum of Squares**	**DF**	**Mean Squares**	**F statistic**	**p-value**	**slope**	**Effect size [%]**
Climate treatment	0.45	1	0.45	0.96	0.332		
Species richness	0.14	1	0.14	0.29	0.588		
Species	1.50	1	1.50	3.17	0.077	LP: 1,387 SI: 1.39	LP$_{\text{biomass versus SI}}$: -65.75 SI$_{\text{biomass versus LP}}$: +191.93
Climate treatment : species richness	0.001	1	0.001	0.002	0.962		
Climate treatment : species	1.47	1	1.47	3.09	0.081	Drought*LP: -0.63 Drought*SI: 0.17	LP$_{\text{drought effect}}$: -67.94 SI$_{\text{drought effect}}$: +12.87
Species richness : species	1.73	1	1.73	3.65	0.058	Richness*LP: -0.07 Richness*SI: 0.04	LP$_{\text{richness 1 vs. SI}}$: -9.08 LP$_{\text{richness 3 vs. SI}}$: -70.98 LP$_{\text{richness 6 vs. SI}}$: -76.01 SI$_{\text{richness 1 vs. SI}}$: +9.99 SI$_{\text{richness 3 vs. SI}}$: +244.63 SI$_{\text{richness 6 vs. SI}}$: +316.81
Climate treatment : species richness : species	0.04	1	0.04	0.08	0.783		
				Recovery			
Climate treatment	0.31	1	0.31	0.68	0.415		
Species richness	0.04	1	0.04	0.08	0.781		
Species	1.77	1	1.77	3.90	0.051	LP: 1.06 SI: 0.60	LP$_{\text{biomass versus SI}}$: +60.23 SI$_{\text{biomass versus LP}}$: -37.59

Climate treatment : species richness	0.26	1	0.26	0.58	0.448		
Climate treatment : species	0.04	1	0.04	0.09	0.769		
Species richness : species	1.18	1	1.18	2.60	0.109		
Climate treatment : species richness : species	2.27	1	2.27	4.99	0.027	Drought*richness*LP: Drought*richness*SI:	LP$_{\text{drought effect richness 1}}$: -66.24 LP$_{\text{drought effect richness 3}}$: -67.68 LP$_{\text{drought effect richness 6}}$: -85.95 SI$_{\text{drought effect richness 1}}$: -21.24 SI$_{\text{drought effect richness 3}}$: +156.62 SI$_{\text{drought effect richness 6}}$: +2961.63

RNE – Relative neighbor effect

Table A6: Anova table for the model testing differences in the RNE at 1) resistance (B1 harvest) and 2) recovery (B2 harvest).

Effect sizes: The richness effect is shown as the percentage difference of the RNE values of species growing in richness level 3 versus species growing in richness level 6. The effect of the functional group is shown as the percentage difference of the RNE values of graminoids/herbs/legumes in comparison to the RNE values of the invader.

				Resistance			
Source of variation	**Sum of Squares**	**DF**	**Mean Squares**	**F statistic**	**p-value**	**slope**	**Effect size**
Climate treatment	0.39	1	0.39	1.15	0.285		
Species richness	1.43	1	1.43	4.15	0.042	0.07	Richness $_{\text{level 3 vs. 6}}$: -44.80
Functional group	3.18	4	0.79	2.31	0.056	LP: 0.46 SI: -0.37 Grass: -0.19 Herbs: -0.06 Legumes: -0.1	LP $_{\text{RNE vs graminoids}}$: +816.91 LP $_{\text{RNE vs legumes}}$: +74.77 LP $_{\text{RNE vs herbs}}$:+120.53 SI $_{\text{RNE vs graminoids}}$: -304.02 SI $_{\text{RNE vs legumes}}$: -138.89 SI $_{\text{RNE vs herbs}}$: -149.07
Climate treatment : species richness	0.07	1	0.07	0.20	0.655		
Climate treatment : functional group	0.43	4	0.11	0.31	0.871		
Species richness : functional group	0.37	4	0.09	0.27	0.899		
Climate treatment : species richness : functional group	0.30	4	0.08	0.22	0.927		
				Recovery			
Climate treatment	0.01	1	0.01	0.03	0.863		
Species richness	1.26	1	1.26	2.80	0.096	0.09	Richness $_{\text{level 3 vs. 6}}$: + 80.95
Functional group	2.36	4	0.59	1.31	0.265		
Climate treatment : species richness	0.09	1	0.09	0.20	0.659		
Climate treatment : functional group	1.44	4	0.36	0.80	0.527		
Species richness : functional group	1.60	4	0.40	0.89	0.471		
Climate treatment : species richness : functional group	3.21	4	0.80	1.79	0.131		

Differences between the two invaders – per relative individual biomass

Table A7: Anova table for model 3 relative individual invader performance (mean relative invader biomass per community biomass) at 1) resistance (B1 harvest) and 2) recovery (B2 harvest).

Effect sizes resistance: Percentage difference in the relative individual biomass of *Lupinus polyphyllus* in comparison to *Senecio inaequidens* and vice versa across all richness levels and separately for every richness level. Effect sizes recovery: Percentage difference in the relative individual biomass of *Lupinus polyphyllus* in comparison to *Senecio inaequidens* and vice versa across all richness levels. Drought effect separately for every richness level of every species is shown as the percentage difference of the relative individual biomass of an invader species growing under drought versus control conditions.

				Resistance			
Source of variation	**Sum of Squares**	**DF**	**Mean Squares**	**F statistic**	**p-value**	**slope**	**Effect size [%]**
Climate treatment	0.01	1	0.01	1.83	0.178		
Species richness	0.000032	1	0.000032	0.008	0.929		
Species	0.04	1	0.04	8.93	0.003	LP: 0.2 SI: 0.14	$LP_{\text{biomass versus SI}}$: -35.02 $SI_{\text{biomass versus LP}}$: + 53.90
Climate treatment : species richness	0.01	1	0.01	2.43	0.121		
Climate treatment : species	0.0004	1	0.0004	0.087	0.769		
Species richness : species	0.12	1	0.12	29.06	<0.001	Richness*LP: -0.01 Richness*SI: 0.01	$LP_{\text{richness 1 vs. SI}}$: 129.60 $LP_{\text{richness 3 vs. SI}}$: -39.42 $LP_{\text{richness 6 vs. SI}}$: -65.16 $SI_{\text{richness 1 vs. SI}}$: -56.45 $SI_{\text{richness 3 vs. SI}}$: 65.07 $SI_{\text{richness 6 vs. SI}}$: 187.01
Climate treatment : species richness : species	0.01	1	0.01	1.76	0.187		
				Recovery			
Climate treatment	0.31	1	0.31	0.68	0.415		
Species richness	0.04	1	0.04	0.08	0.781		
Species	1.77	1	1.77	3.90	0.051	LP: 1.06 SI: 0.6	$LP_{\text{biomass versus SI}}$: 52.98 $SI_{\text{biomass versus LP}}$: -34.63
Climate treatment : species richness	0.26	1	0.26	0.58	0.448		
Climate treatment : species	0.04	1	0.04	0.09	0.769		

Species richness : species	1.18	1	1.18	2.60	0.109		
Climate treatment : species richness : species	2.27	1	2.27	4.99	0.027	Drought*richness*LP: Drought*richness*SI:	$LP_{\text{drought effect richness 1}}$: 24.75 $LP_{\text{drought effect richness 3}}$: -47.85 $LP_{\text{drought effect richness 6}}$: -88.55 $SI_{\text{drought effect richness 1}}$: -4.39 $SI_{\text{drought effect richness 3}}$: 55.54 $SI_{\text{drought effect richness 6}}$: 2037.37

Survival

Table A8: Anova table for the model testing differences in the survivability at the end of the drought treatment (B1 harvest). Effect sizes: Drought effect is shown as the percentage difference of the individuals which survived under drought versus control conditions. Invader presence effect is shown as the percentage difference of the individuals which survived under invader presence versus in native species communities. The interaction effect of invader presence and species richness is shown as the percentage difference of the individuals which survived under invader presence versus in native species communities separately for every richness level.

Source of variation	**Sum of Squares**	**DF**	**Mean Squares**	**F statistic**	**p-value**	**slope**	**Effect size [%]**
Climate treatment	3871.9	1	3871.9	3.31	0.072	Control: 84.88 Drought: 69.94	Natives $_{\text{drought effect}}$: -11.07 LP $_{\text{drought effect}}$: -11.91 SI $_{\text{drought effect}}$: -5.56
Species richness	398.4	1	398.4	0.34	0.559		
Invader presence	20032.1	2	10016.0	8.56	< 0.001	Natives: 84.88 LP: 63.59 SI: 97.47	LP $_{\text{survival vs natives}}$: -7.73 SI $_{\text{survival vs natives}}$: + 0.42
Climate treatment : invader presence	168.1	2	84.1	0.07	0.931		
Climate treatment : species richness	142.6	1	142.6	0.12	0.727		
Invader presence : species richness	14202.5	2	7101.2	6.07	0.002	Natives: 0.02 LP: 3.35 SI: -2.96	LP $_{\text{richness 1 vs natives}}$: -32.07 LP $_{\text{richness 3 vs natives}}$: -10.77 LP $_{\text{richness 6 vs natives}}$: -4.47 SI $_{\text{richness 1 vs natives}}$: + 21.55 SI $_{\text{richness 3 vs natives}}$: +5.70 SI $_{\text{richness 6 vs natives}}$: -4.09
Climate treatment : invader presence : species richness	302.0	2	151.0	0.13	0.879		

10.5 Manuscript 5

frontiers in Plant Science

ORIGINAL RESEARCH
published: 05 June 2018
doi: 10.3389/fpls.2018.00715

Invasion of a Legume Ecosystem Engineer in a Cold Biome Alters Plant Biodiversity

Vanessa M. S. Vetter[1,2]*, Nils B. Tjaden[2], Anja Jaeschke[2], Constanze Buhk[3], Veronika Wahl[1], Pawel Wasowicz[4] and Anke Jentsch[1]

[1] Disturbance Ecology, BayCEER, University of Bayreuth, Bayreuth, Germany, [2] Biogeography, BayCEER, University of Bayreuth, Bayreuth, Germany, [3] Geoecology, Physical Geography, University of Koblenz-Landau, Landau, Germany, [4] Icelandic Institute of Natural History, Akureyri, Iceland

Plant ecosystem engineers are widely used to combat land degradation. However, the ability of those plants to modulate limiting abiotic and biotic resources of other species can cause damage to ecosystems in which they become invasive. Here, we use *Lupinus nootkatensis* as example to estimate and project the hazardous potential of nitrogen fixing herbaceous plants in a sub-polar oceanic climate. *L. nootkatensis* was introduced to Iceland in the 1940s to address erosion problems and foster reforestation, but subsequently became a high-latitude invader. In a local field survey, we quantified the impact of *L. nootkatensis* invasion at three different cover levels (0, 10–50, and 51–100%) upon native plant diversity, richness, and community composition of heath-, wood-, and grasslands using a pairwise comparison design and comparisons of means. Afterward, we scaled impacts up to the ecosystem and landscape level by relating occurrences of *L. nootkatensis* to environmental and human-mediated variables across Iceland using a species distribution model. Plant diversity was significantly deteriorated under high lupine cover levels of the heath- and woodland, but not in the grassland. Plant species richness of the most diverse habitat, the heathland, linearly decreased with lupine cover level. The abundance of small rosettes, cushion plants, orchids, and small woody long-lived plants of the heath declined with invader presence, while the abundance of late successional species and widespread nitrophilous ruderals in wood- and grasslands increased. Distribution modeling revealed 13.3% of Iceland's land surface area to be suitable lupine habitat. Until 2061–2080, this area will more than double and expand significantly into the Central Highlands due to human mediation and increasingly favorable climatic conditions. Species-rich habitats showed a loss of plant species diversity and richness as well as a change in community composition even in low lupine cover classes. The future increase of suitable lupine habitat might lead to the displacement of cold-adapted native plant species and will certainly challenge conservation as well as restoration of ecosystems in the cold climate of Iceland, but also elsewhere. Lupine invasion speeds up succession, which may be additive with climate change effects, and accelerates ecological change in cold biomes.

Keywords: disturbance, field experiment, high latitude invader, Maxent, plant community reorganization, sub-arctic climate, transformer species, vegetation dynamics

Edited by:
José M. Grünzweig,
Hebrew University of Jerusalem, Israel

Reviewed by:
Mirko Di Febbraro,
University of Molise, Italy
Bjarni Didrik Sigurdsson,
Agricultural University of Iceland, Iceland

****Correspondence:***
Vanessa M. S. Vetter
vanessa.vetter@uni-bayreuth.de

Specialty section:
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

Received: *23 December 2017*
Accepted: *11 May 2018*
Published: *05 June 2018*

Citation:
Vetter VMS, Tjaden NB, Jaeschke A, Buhk C, Wahl V, Wasowicz P and Jentsch A (2018) Invasion of a Legume Ecosystem Engineer in a Cold Biome Alters Plant Biodiversity. Front. Plant Sci. 9:715. doi: 10.3389/fpls.2018.00715

INTRODUCTION

Invasive plants are globally threatening ecosystems and island floras leading to species endangerment and extinction (Pejchar and Mooney, 2009; Harter et al., 2015). Especially invasive ecosystem engineers can strongly influence native ecosystems by altering energy, water and/or nutrient fluxes, which consequently leads to altered ecosystem-level properties (e.g., *Myrica faya* a nitrogen fixing tree invasive in Hawaii; Vitousek et al., 1987; Vitousek and Walker, 1989). Ecosystem engineers (Jones et al., 1994) are often intentionally introduced to new environments by humans, e.g., for soil and water conservation, to restore degraded ecosystems or to solve the problems of deforestation (Lazzaro et al., 2014; Ayanu et al., 2015). They generally possess traits that can positively influence soil stability, nutrient and hydrological cycling, and light infiltration (Ayanu et al., 2015) and show protective characteristics, e.g., reduced erosion (Fei et al., 2014). But if they become invasive, those positive traits of the respective alien ecosystem engineer can have negative and long-lasting effects on native communities and ecosystem properties (Richardson et al., 2000; Catford et al., 2012; Fei et al., 2014) that often extend far beyond its life span and/or presence (Richardson et al., 2000; Ehrenfeld, 2003, 2010). Ecosystem engineers that have become invasive, are called “transformer species” (Richardson et al., 2000). Invaders that are introduced for management purposes, such as the ecosystem engineers, are usually widely and deliberately applied by humans and are thus able to spread into large areas right at the beginning of the invasion process with many starting points for the invasion.

Lupinus nootkatensis DONN ex SIMS acts as an ecosystem engineer in the sub-polar ecosystems of its invasive range Iceland. Originally from Alaska and Canada, this high-latitude invader was introduced to Iceland in 1945 for soil amelioration and reforestation. Due to repeated human introductions, *L. nootkatensis* has a high propagule pressure and is rapidly spreading across the Icelandic lowlands (Magnusson, 2010). *L. nootkatensis* stabilizes slopes and modulates limiting abiotic resources of other species by fixing atmospheric nitrogen, thus changing the nutrient cycling of invaded habitats. Cold biomes show a rapid saturation in the ecosystem’s capacity to retain N, making them prone to N_2 fixers (Hiltbrunner et al., 2014). Such changes caused by the accumulation of atmospheric nitrogen in the soil and subsequently in the plant community composition are persistent and continue even after the removal of the legume from the ecosystem or its replacement by other species (Hiltbrunner et al., 2014). The increased soil nitrogen content in old lupine stands facilitates the settlement of further invasive species, such as demonstrated for, e.g., *Anthriscus sylvestris* and *Ribes rubrum* in Iceland (Magnusson et al., 2008; Magnusson, 2010). *L. nootkatensis* modulates biotic factors such as plant–plant interactions by forming dense patches, affecting plant establishment and succession of arctic plant species via direct competition effects (Magnusson et al., 2008; Magnusson, 2010). *L. nootkatensis* is also a habitat generalist, and widely occurs across Icelandic lowland habitats (Magnusson, 2010). It transforms the native vegetation, e.g., heathlands, into *Poa pratensis* dominated grasslands (Magnusson et al., 2008), thus directly affecting plant establishment and succession. However, *L. nootkatensis’* ability to facilitate soil enrichment and succession, by building up nutrients, organic matter, and water storage capacity of soils is perceived as one solution to combat the manmade and massive problem of severe land degradation and desertification in Iceland (Arnalds and Runolfsson, 2008), which also may be exacerbated by future climate change.

The combination of species invasion and climate change might lead to negative synergistic effects, which are more powerful than the additive effects of the two single stressors. Despite the buffering effects of the surrounding oceans, climate change will lead to profound alterations of the environmental conditions on islands, which might positively affect the establishment and spread of alien species in various ways (Harter et al., 2015).

We investigate lupine invasions in different plant communities on a local scale field study and scale up to the ecosystem and landscape level using a correlation model. It is currently under debate which factors are mainly responsible for the ecosystem engineer’s ongoing spread in Iceland and how climate change will affect these factors in the future. Although, there are existing studies concerning the community impact, the invasion success and the future distribution of *L. nootkatensis* in Iceland, most of these studies only concern one or few factors of the same kind, e.g., different climate variables or biotic interactions. Here, we set out to address and quantify the relative influence of a variety of abiotic, biotic and human-mediated factors, which are probably determining the actual distribution pattern of *L. nootkatensis* across Iceland and project the likelihood of lupine-free areas to become invaded in the near future. The rapid spread, ability to alter its local environment, and its habitat generality make *L. nootkatensis* an interesting case study for invasion processes in cold biomes, e.g., the consequences of exotic invasion in niche construction (Fei et al., 2014). Combining experimental studies of local communities with predictive modeling at a landscape level, provides a more accurate overview of the potential range of the species in Iceland (Stricker et al., 2015). The spatially enclosed system of Iceland is well-suited for our approach because of its insularity, the excessive spread of *L. nootkatensis* into a great variety of plant communities of the Icelandic lowlands and the relatively precise documentation of its introduction into the sub-polar system (Magnusson et al., 2008; Magnusson, 2010).

We aim to (a) quantify the current invasion status of *L. nootkatensis* on Iceland using a distribution map of the year 2016, (b) quantify the invasion impacts of the ecosystem engineer on the native vegetation (hereafter: biotic characteristic) in Iceland, (c) understand the abiotic and biotic filters decisive for the recent invasion success, and (d) robustly project the invasion range of *L. nootkatensis* in Iceland under current (reference period: 1960–1990) and future (2061–2080) climate conditions based on the findings of a and b. We use two distinct data sets: (1) a field study to test the biotic characteristics and (2) a distribution map to model the abiotic characteristics as well as the invasion process.

MATERIALS AND METHODS

Study Species

Lupinus nootkatensis (Fabaceae) is a long-lived (up to 20 years) herbaceous plant originating from coastal regions of the Aleutian Islands and from Queen Charlotte Island, Alaska to Vancouver Island, British Columbia, Canada (Magnusson, 2010). *L. nootkatensis* prefers open habitats of frequent natural disturbance (Fremstad and Elven, 2008), e.g., early successional stages with vegetation destruction and soil erosion. In Iceland, the lupine is primarily recorded from gravel bars along the coast and rivers, roadsides, dry slopes and sandy beaches. But it is also found in disturbed landscapes, as well as in dwarf shrub-heathlands (Magnusson, 2010).

Biotic Filter Experiment and Propagule Pressure

Study Area

The study area of the local field survey, Morsádalur, is located in the Vatnajökull National Park in South-East Iceland (**Figure 1**). The Vatnajökull area is greatly influenced by glacial and volcanic processes (Steinthorsson et al., 2000; Björnsson, 2003; Björnsson and Pálsson, 2008). Within the sub-polar oceanic climate of Iceland, the valley Morsádalur is characterized by a mild climate with warm temperatures (Björnsson et al., 2007) and high annual precipitation (Crochet et al., 2007; Björnsson and Pálsson, 2008). We chose three different habitat types, which are characteristic for the native vegetation of Iceland and most dominant, and are currently invaded by *L. nootkatensis*: a heathland on the mountain slope Réttargíl, a grassland with occasional trees in the valley Morsádalur and the old birch forest (*Betula pubescens*) Bæjarstadarskógur on the adjacent western slope of Morsádalur.

Sampling Design and Methods

To test the effect of lupine invasion on plant community composition among three different habitats a pairwise comparison design, between the cover levels within and among each habitat type, was employed.

First, we defined three different levels of lupine cover density: “none,” which had no lupines in the vegetation cover, “low” which had 10–50% lupine cover, and “high” which had 51–100% lupine cover (Magnusson et al., 2008). Areas with 1–9% of lupine cover were excluded from the analysis because these areas are mainly occupied by immature lupine plants. This gradient in lupine invasion succession was observed along transects from the center to the edge of a lupine patch. While the center represents late invasion stages with high lupine cover, the edges of a lupine patch represent early invasion stages with relatively low lupine cover (Magnusson et al., 2008).

Three plots of 2 m × 2 m size for each of the three lupine cover density levels were randomly assigned to the lupine patches of each habitat (in total = 27 which consist of 3 × 3 = 9 plots per habitat). The plot size of 2 m × 2 m was determined by a minimum area analysis to cope with the heterogeneity of the habitats and represents the largest minimum area found in the heathland. Plots of the same density level were not placed within the same lupine patch, although where possible, different density levels did occur within the same patch.

Soil seed bank of *L. nootkatensis* was estimated by taking one soil core of 5 cm diameter and depth per plot. Thus, soil samples were replicated three times per cover level of each habitat ($n = 27$). All soil samples were taken at the end of the field season in August within one single day. For levels “low” (10–50%) and “high density” (51–100%) the core was randomly taken at 40 cm distance to the lupine chosen as reference for the nearest neighbor analysis. Samples were air-dried and sieved through three sieves with mesh sizes of 16, 8, and 4 mm. We sorted and counted the lupine seeds by hand.

We additionally analyzed plant community composition and nearest neighbor growth patterns of the three habitats to pinpoint potential differences between lupine cover levels (see Appendix Figures A1–A3).

Statistical Analyses

As a measure of alpha diversity within habitats and plots the Simpson (diversity) index, also called Simpson concentration, was calculated separately for each of the three plots per lupine cover level and habitat (Simpson, 1949; Lande, 1996):

$$\lambda = \sum_{i=1}^{R} \mathrm{p}_\mathrm{i}^2$$

R is the richness of each habitat type, p_i is the squared relative abundance of the respective species and λ is the probability of two randomly chosen specimen to belong to the same species. Thus, a Simpson index of 0 represents highest diversity, while a value of 1 represents no diversity.

Analyses were conducted using the statistical software R 3.4.2 (R Core Team, 2017). The effects of habitat and lupine cover level within habitats on the alpha diversity, plant species richness, seed abundance and soil depth were tested via ANOVA and *post hoc* Tukey-test in case of normally distributed data with variance homogeneity (Hothorn et al., 2008). The Kruskal–Wallis test for multiple comparisons (Giraudoux, 2017) was applied to data with an inhomogeneous variance or residuals that did not follow the normal distribution. We used the Bartlett-test and the Shapiro–Wilk test to check for variance homogeneity among the groups and normal distribution of the residuals respectively.

Modeling the Spatial Distribution of *L. nootkatensis* in Iceland

We used the model algorithm Maxent (Phillips et al., 2017) version 3.4.1 to relate occurrences of *L. nootkatensis* to environmental variables across whole Iceland.

Species Occurrence Data and Environmental Variables

Abiotic, biotic and human-mediated environmental variables, which are associated with the range limits of *L. nootkatensis* in Iceland according to literature, were pre-selected by expert

TABLE 1 | Environmental predictor variables pre-selected by expert knowledge.

Category	Variables	Source	Reference
Climate data	Annual mean temperature, temperature seasonality, **maximum temperature of warmest month**, minimum temperature of coldest month, minimum temperature of May, **mean temperature of wettest quarter**, mean temperature of warmest quarter, annual precipitation, precipitation of driest month, **precipitation seasonality**, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter	Bioclimatic variables WorldClim1.4 – Global Climate Data of the current (reference period 1960–1990) climate conditions. Bioclimatic variables for future climate scenarios (CMIP5): NorESM1-M (RCP 4.5, RCP 8.5) MPI_ESM-LR (RCP 4.5, RCP 8.5) (Hijmans et al., 2005)	Magnusson et al., 2008; Magnusson, 2010; Wasowicz et al., 2013
Topography	Altitude	Bioclimatic variables WorldClim1.4 – Global Climate Data (Hijmans et al., 2005).	Own consideration in accordance with Magnusson, 2010
	Aspect and slope	Manually calculated from altitude in R	
Soil	Age of substrate	Icelandic Institute of Natural History (http://en.ni.is/). Accessed October 17, 2016.	Own consideration in accordance with Sigurdardottir, 2008; Magnusson, 2010
	Soil type	Agricultural University of Iceland (provided February 27, 2018)	Personal communication Dr. Olafur Arnalds; Arnalds, 2015
Land cover	**Vegetation types:** grassland and cultivated land, birch woodland, moss heathland	Icelandic Institute of Natural History (http://en.ni.is/). Accessed October 17, 2016.	Hultén, 1968; Fremstad and Elven, 2008;
	Surface water: rivers, waterbodies, glaciers		Magnusson, 2010
	Substrate: sand, lava, gravel plains		
Human vector	**Distance to nearest road**	Calculated based on the road map obtained from the NLSI: National Land Survey of Iceland (http://www.lmi.is/en/). Accessed January 04, 2017.	Magnusson, 2010
	Human influence index (human population pressure; human land use and infrastructure; human access)	Wildlife Conservation Society – WCS, and Center for International Earth Science Information Network – CIESIN – Columbia University, 2005. Last of the Wild Project, Version 2, 2005 (LWP-2). Palisades, NY: NASA SEDAC. doi: 10.7927/H4BP00QC. Accessed January 04, 2017.	

Variables in bold were further selected by Pearson Correlation Coefficient, Jackknife and AIC and used to calibrate the species distribution model 1 (Maxent) of Lupinus nootkatensis. In model 2, we omitted the variable "distance to nearest road" but kept all other settings constant.

knowledge (**Table 1**) to determine the most influential variables.

We used climate data together with characteristics of the terrain (e.g., aspect and slope), soil type, geology, native vegetation cover, and aspects of human interference (**Table 1**) as a proxy to test how much of Iceland's land surface area is threatened by lupine invasion. Aspect and slope in combination with the climate variables control for the self-propagation of the invader species (Magnusson, 2010), while all other variables are potential factors determining the distributional range of *L. nootkatensis* (see e.g., Magnusson et al., 2008; Magnusson, 2010; Wasowicz et al., 2013).

Climate data for current and future conditions was obtained from Worldclim 1.4 (Hijmans et al., 2005) at a spatial resolution of 30 arc seconds (≈1 km). To predict the potential future distribution of the legume invader in Iceland, downscaled and calibrated climate data from the global climate models (GCM) NorESM1-M and MPI_ESM-LR for the years 2061–2080 was used. Both, the medium stabilization (RCP 4.5) (Thomson et al., 2011) and very high baseline emission (RCP 8.5) (Riahi et al., 2011) representative concentration pathways of the IPCC's fifth assessment report were used.

If necessary, other variables were projected to WGS84, rasterized and re-sampled (Hijmans, 2016) to the 1 km spatial resolution of the climate variables.

The species occurrence data was obtained from the Icelandic Institute of Natural History[1] in the form of spatial polygons representing *L. nootkatensis* patches derived from high-resolution satellite imagery. We converted the spatial polygons to a raster of the same spatial resolution and dimensions as the environmental data using the "rasterize" function in R (Hijmans, 2016). The center point of each grid cell containing *L. nootkatensis* patches were then used to derive the needed occurrence records for Maxent. A total of 5709 species occurrences were compiled across Iceland (**Figure 1**).

We used the open source software R version 3.4.2 (R Core Team, 2017) and QGIS 2.16.3 in order to prepare the species occurrence records as well as all environmental variables (background data) as spatial data layers.

---

[1] http://en.ni.is/

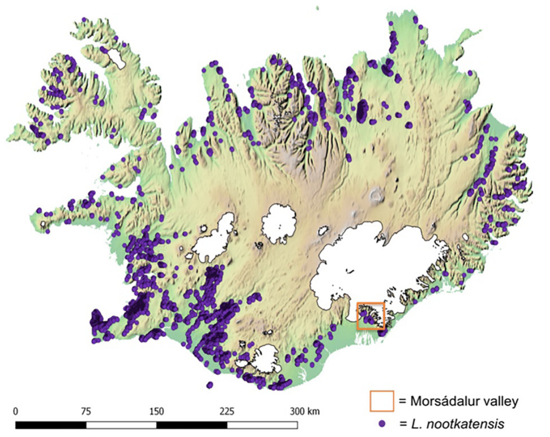


FIGURE 1 | Distribution of *Lupinus nootkatensis* across Iceland in 2016. Lupine occurrences (Icelandic Institute of Natural History http://en.ni.is/) are displayed upon an altitudinal gradient where green indicates the lower and brown the higher regions of Iceland and glaciers are displayed in white. Our study area, the Morsádalur valley in South-East Iceland, is located in the Vatnajökull National Park.

Species Distribution Model

We calculated Pearson correlation coefficients (r) in R to derive a set of fairly uncorrelated environmental variables. Because Maxent copes well with collinearity (Elith et al., 2011), cross-correlation was used as a selection criterion only to exclude the highest correlative variables ($r > 0.8$).

The remaining variables were used to calculate principal component analyses (PCAs) based on which we measured spatial heterogeneity of the environment. The derived grids of environmental heterogeneity were then used to spatially rarefy our species occurrence points ("Spatially Rarefy Occurrence Data for SDMs" tool, SDMtoolbox; Brown, 2014). Overall, 98 unbiased species occurrences were used in Maxent.

For invasive species, the absence of occurrences means not necessarily a "true absence" due to, e.g., the unsuitability of the respective habitat, but rather a reflectance of the fact that the species has not yet reached its equilibrium distribution in the new habitat. Therefore, we treated our species data as presence-only data. Maxent is a common and very effective methodology to model the ecological niche of species with presence-only data (Elith et al., 2006; VanDerWal et al., 2009; Phillips et al., 2017) but it needs to be provided with a set of background data (VanDerWal et al., 2009; Barve et al., 2011). As the dispersal potential of the invasive species might be large, e.g., due to human traffic or targeted propagation by humans, we opted for a buffer-based approach for background sampling. Following the example of VanDerWal et al. (2009), we produced a series of test models using buffer zones with radii of 1 km (size of one raster grid cell), 5, 10, 25, and 50 km. In our case, a buffer zone with a radius of 25 km gave the best result.

Jackknife testing within Maxent along with the Akaike Information Criterion (AIC) implemented in R, were used to select the final environmental variables for the species distribution model (model 1, **Table 1**). We gradually removed all variables whose regularized training gain was less than 0.1, unless the AIC and AUC of model 1 significantly deteriorated. To evaluate model performance, we ran a 10-fold cross-validation (cv) after each simplification.

The ENMeval package in R (Muscarella et al., 2014) was used to tune Maxent settings, as well as for model validation. We tested regularization multiplier (RM) values of 1, 2, 5, 10, 15, 20 (Warren and Seifert, 2011; Merow et al., 2013; Shcheglovitova and Anderson, 2013) together with different combinations of the Maxent feature classes linear (L), quadratic (Q), and hinge (H) (Merow et al., 2013; Phillips et al., 2017) with block-wise data partitioning (Roberts et al., 2017).

We fitted two final models using all of the spatially rarefied species occurrences, RM = 5, LH features, and a maximum of 1000 iterations. The cloglog output format was chosen for both models (Phillips et al., 2017). Model 1 was used to evaluate the environmental variables decisive for the actual spread pattern as well as to predict the potential distribution of *L. nootkatensis* across Iceland under current and future climate conditions. To evaluate the potential maximum area of suitable habitat available for *L. nootkatensis* under current and future climate conditions, without the restriction to roads as the vectors of propagation, we fitted a second model and calculated difference maps based on the predictions of both models (see Appendix). Model 2 was fitted with the same settings as model 1, but without the variable distance to nearest road.

The cloglog output format gives probabilities of occurrences for the respective species varying between 0 and 1. We used the maximum training sensitivity plus specificity threshold, a threshold selection method which is not affected by pseudo-absences (Liu et al., 2013), to reclassify the cloglog output in suitable (>threshold) and unsuitable habitat (<threshold).

To assess the accuracy of our species distribution model we calculated partial receiver operating characteristics (Peterson et al., 2008; Tjaden et al., 2017) with 1000 bootstrapping iterations on 50% of the test data and an expected error rate of 5%.

RESULTS

Biotic Filter Experiment and Propagule Pressure

High lupine cover levels significantly reduced the alpha diversity of the heath- and woodland (Simpson diversity index; **Figure 2A**). In the grassland, lupine cover did not have a significant effect on alpha diversity. Plant species richness of the heathland, the most diverse habitat, decreased linearly with lupine cover level (**Figure 2B**). In the woodland as well as in the grassland, species richness showed a slightly hump-shaped pattern from none to high lupine cover.

Typical heath species such as *Calluna vulgaris*, *Empetrum nigrum,* and *Arctostaphylos uva-ursi* decreased in their abundance with proceeding lupine invasion. The percentage

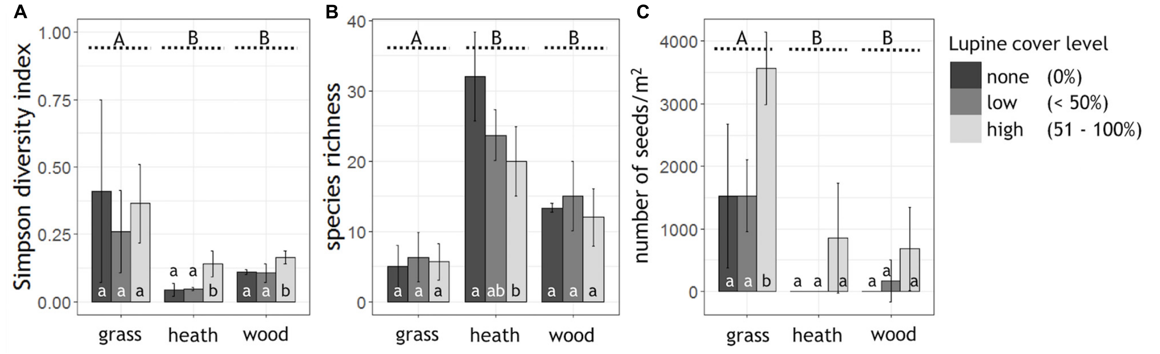


FIGURE 2 | Alpha diversity, species richness and seed abundance grouped by habitat and shown as a function of lupine cover level. Shown are the mean values of the **(A)** Simpson diversity index (0 = highest diversity, 1 = no diversity) and **(B)** plant species richness per lupine cover level and habitat (n_{grass} = 9, n_{heath} = 9, n_{wood} = 9). **(C)** Extrapolated lupine seed numbers per m^2 (n_{grass} = 3, n_{heath} = 3, n_{wood} = 3). Capital letters A, B indicate significant differences between the habitats (Kruskal–Wallis test, $p < 0.05$, black dashed lines), while small letters a, b, indicate significant differences between the lupine cover levels within one habitat (Tukey HSD or Kruskal–Wallis test, $p < 0.05$).

cover of *Calluna vulgaris* was halved in both, low and high cover classes of *L. nootkatensis* (Appendix Figure A1). Small rosettes (*Silene acaulis*), cushion plants (*Armeria maritima*), orchids (*Listera cordata*, *Dactylorhiza maculata*, *Platanthera hyperborea*) and small woody long-lived plants (e.g., *Salix herbacea*) of the heathland were absent in the presence of the invader, even in low lupine cover classes (Appendix Table A1). In the heathland as well as in the woodland, the abundance of late successional species, e.g., *Betula pubescens*, increased with lupine cover (Appendix Figure A1). In high lupine cover classes widespread nitrophilous plants – *Taraxacum* sp. in the woodland and *Geranium sylvaticum* in the grassland – appeared, while they were not present in low cover classes or without the invader (Appendix Table A1). *Poa pratensis*, the most abundant grass in the grassland decreased remarkably, while a contrasting trend was observed for *Angelica archangelica*, another late successional species (Appendix Figure A1).

Abundance of *L. nootkatensis* seeds in the soil differed significantly among habitats. The most diverse habitat, the heathland, had the lowest abundance of lupine seeds while the least diverse habitat, the grassland, showed highest seed numbers (**Figure 2C**). Propagule pressure of lupine seeds tended to be highest in patches with 51–100% lupine cover while it was indifferent in the cover classes "none" and "low," although this effect was only statistically significant in the grassland but not in the other two habitat types. Only in the woodland, the expected trend toward no seeds without lupine cover, few seeds with low lupine cover and increased seed abundance in high lupine cover stands was observed (**Figure 2C**).

Modeling the Spatial Distribution of *L. nootkatensis* in Iceland

Both Maxent models had a good predictive ability as measured by the area under the curve ($AUC_{model1} = 0.84$, $AUC_{model2} = 0.79$) and the AUC ratios of the partial receiver operating characteristics (mean $AUCratio_{model1} = 1.76$, mean $AUCratio_{model2} = 1.70$). All values ≥ 0.531 and 0.553 respectively (maximum training sensitivity plus specificity threshold) were interpreted as suitable lupine habitat. The five most important variables influencing the distribution of *L. nootkatensis* across Iceland were distance to nearest road, maximum temperature of warmest month, land cover, mean temperature of wettest quarter, and precipitation seasonality (**Table 2**).

TABLE 2 | Percent contribution and permutation importance of the environmental variables used in the final models.

Predictor variable	Contribution [%]	Permutation importance
Distance to nearest road	72.3 (–)	53.4 (–)
Maximum temperature of warmest month	12.1 (52.6)	24.3 (54.7)
Land cover	6.3 (22.8)	5.0 (7.5)
Mean temperature of wettest quarter	5.6 (13.1)	14.6 (22.0)
Precipitation seasonality	3.7 (10.0)	2.7 (15.6)
Human influence index	0 (1.3)	0 (0.2)

Results of model 2 are given in brackets. The higher the relative information of a single variable, the more decisive it is for the current pattern of propagation.

Under current climate conditions, a total of 13.3% of Iceland's land surface area was projected to be suitable lupine habitat (**Figure 3** and **Table 3**). *L. nootkatensis* was mainly found in habitats close to roads (≤0.5 km). The predicted probability of presence shows an optimum at 14.4°C for the maximum temperature of the warmest month, at 8.2°C for the mean temperature of the wettest quarter, and at 2.7 for the precipitation seasonality (Appendix Figure A4). *L. nootkatensis* was found in all land cover classes across Iceland, but the invasion risk was projected to be highest for grassland/cultivated land and lowest for moss heath and wetlands (Appendix Figure A4).

Independent from the tested emission scenarios both GCMs projected a more than double increase in the amount of suitable lupine habitat for the years 2061–2080 (**Table 3**). With proceeding climate change, the environmental suitability of Iceland was

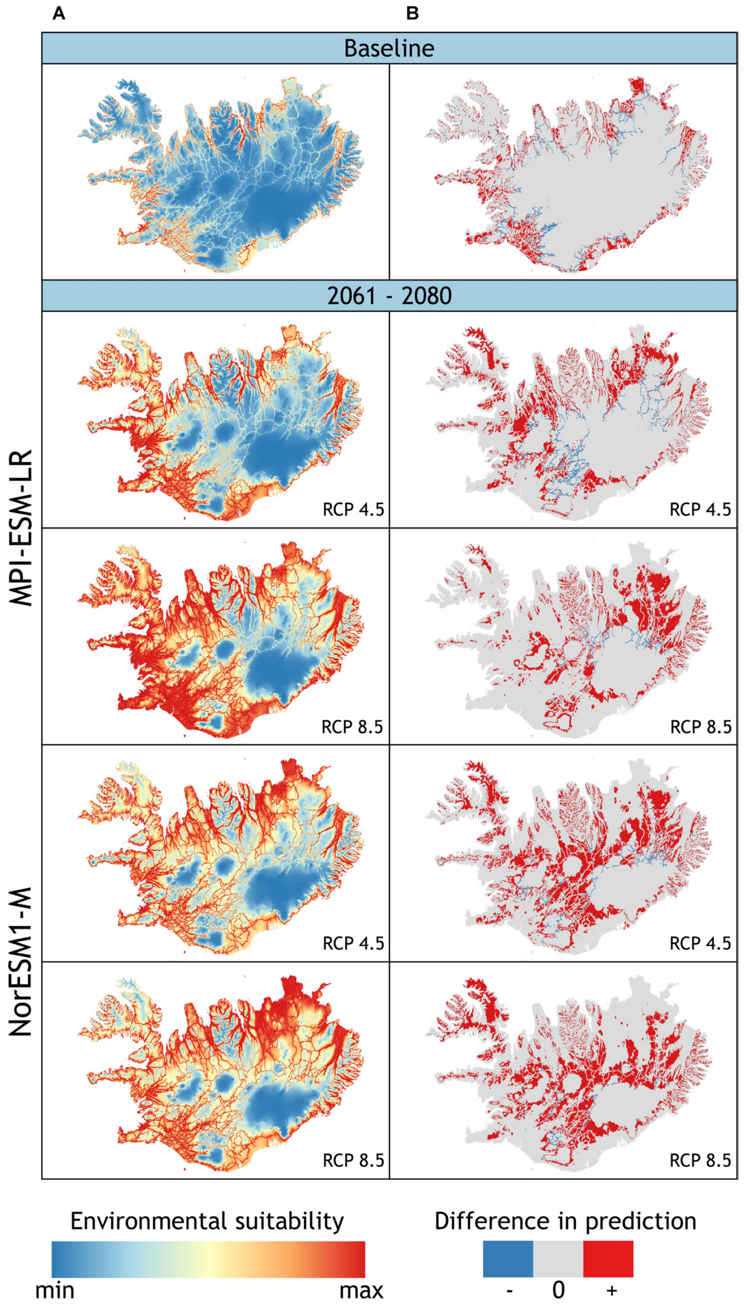


FIGURE 3 | (A) Projected potential distribution (model 1) of *L. nootkatensis* across Iceland under current climate conditions (baseline) and future climate conditions modeled with the global climate models NorESM1-M and MPI_ESM-LR each in the medium stabilization (RCP 4.5) and very high baseline emission scenario (RCP 8.5). Environmental suitability ranges from: minimum = 0 to maximum = 1 with maximum training sensitivity plus specificity threshold (MTSS) = 0.531. **(B)** Difference in prediction between the two models used to project *L. nootkaensis'* potential future distribution [difference = binary output (model 2 – model 1)] (see Appendix). The models only differ in the presence of the propagation vector "distance to nearest road": model 1 vector present, model 2 absent. Areas projected to be suitable habitat only by model 2, shown in red, are an addition to the projections of model 1 (+); areas in gray (0) are equally projected from both models, while areas in blue (–) are solely projected by model 1. Together with the projections of model 1, red areas show the maximum of suitable lupine habitat without restriction to "roads" as the vectors of propagation.

TABLE 3 | Percentage amount of land surface area of Iceland projected to be suitable habitat for *L. nootkatensis* under current and future climate conditions.

Time scale	Concentration pathway	Projected amount of suitable habitat [%] (% increase compared to current)	
		Model 1	Model 2
Current	–	13.3	20.1
MPI_ESM-LR	RCP 4.5	39.1 (+ 25.8)	53.2 (+ 33.1)
	RCP 8.5	61.7 (+ 48.4)	76.7 (+ 56.6)
NorESM1-M	RCP 4.5	50.1 (+ 36.8)	72.6 (+ 52.5)
	RCP 8.5	58.0 (+ 44.7)	81.2 (+ 61.1)

The percentage point increase in suitable habitat compared to current climate conditions is given in brackets.

projected to expand into the Central Highlands, thus the potential distribution range of *L. nootkatensis* will enlarge. For example, in 2016 *L. nootkatensis* occurred on altitudes up to 572 m but was projected to reach heights of 1087–1119 m (MPI_ESM-LR RCP 8.5, NorESM1-M RCP 8.5) in the future. *L. nootkatensis* is likely to spread from its current main distribution area – along the coasts and near the human settlements – following the main valleys and roads into the Central Highlands. While roads serve as vectors of propagation (model 1, **Figure 3A**), *L. nootkatensis*' occurrence is not dependent upon the presence of roads under future climate conditions (**Figure 3B**). The future spatial focus was projected to lie in the northern to northeastern and southwestern parts of the island.

DISCUSSION

The restrictive factor(s) controlling lupine colonization is depending on the respective area. Low propagule pressure, is impeding lupine spread in areas without major human interference, e.g., the highlands. *L. nootkatensis* is a very effective disperser, in terms of durability and amount of produced seeds, and in addition its spread is accelerated by human interference (Magnusson, 2010; Wasowicz, 2016). We detected a large quantity of seeds even in areas where currently no or only a few lupines are growing. The large amount of seeds in the rather low lupine cover classes of the grasslands are either deposited by the river Morsá which floods the valley of Morsádalur at irregular intervals – an important avenue for propagule dispersal facilitated by frequent disturbance dynamics (Magnusson, 2010) – or are part of an old seed bank (Svavarsdóttir et al., 2008). Additionally, our results imply, that a high plant species diversity seems to go along with a lower overall seed abundance of *L. nootkatensis*, potentially reducing risk of invasion. However, in high lupine cover levels the natural diversity decreases and the invader is able to build up persistent seed banks. The missing significance of these results might be due to the extreme patchiness of seed banks. Increasing the number of soil samples per plot could overcome this obstacle. Consequently, propagule pressure, one of the key drivers and a prerequisite for successful invasion (Lockwood et al., 2005; Colautti et al., 2006; Catford et al., 2009) is not limiting but delaying *L. nootkatensis*' distribution across the highlands and mountainous areas of Iceland. Biotic competition in areas void of disturbance such as the grassland, seems to impede colonization of *L. nootkatensis*, however, as the lupine seeds are durable, it is only a matter of time until disturbance occurs and colonization is facilitated (Sigurdsson and Magnusson, 2008). Abandonment of traditional management practices, e.g., free-ranging sheep grazing, might further facilitate lupine establishment as sheep graze on small seedlings and thus prevent the lupine from establishing (Magnusson et al., 2008). Based on the SDM projections, sheep grazing could now systematically be used to restrict the predicted potential distribution of *L. nootkatensis* across Iceland, while maintaining a traditional management system.

Our results suggest that *L. nootkatensis* may benefit from anthropogenic influences, though is not necessarily dependent on human presence. Initially, areas close to human infrastructure (e.g., roads) are exposed to a higher invasion risk, but as the invasion progresses, the lupine increasingly decouples from the roads as primary vectors of propagation and begins to penetrate large areas of the Central Highlands. Since propagule pressure increases with time and due to *L. nootkatensis*' long residence time in Iceland, starting with its first introduction in 1945 (Magnusson, 2010), seed swamping around human settlements can be assumed (Colautti et al., 2006; Catford et al., 2009). Human-mediated disturbance along with sufficient propagule pressure creates invasion windows as disturbances reduce competition, increase space and subsequently resource availability (Catford et al., 2009). Based on our results we are able to verify the recently postulated relation between human disturbance and occurrence of invasive species (Wasowicz, 2016) for *L. nootkatensis*.

All current hot-spots of invasive plant species occurrences in the Central Highlands are linked to human disturbance, e.g., tourism and the related infrastructure (Wasowicz, 2016). Tourism in general but also the number of visitors of the Icelandic highlands is sharply increasing in recent years (Icelandic Tourist Board, 2017). Thus, one of the last wilderness areas of Europe (Sæþórsdóttir and Saarinen, 2015) becomes gradually more accessible for propagules and at the same time more disturbed by human visitors (Wasowicz, 2016).

Arctic and sub-arctic regions will be affected by climate change in a twofold way: (1) the cold-adapted native plants will be expelled and forced to migrate with their shifting climatic niche, e.g., upwards or northwards (Phoenix and Lee, 2004; Parmesan, 2006), (2) due to the temperature increase the (sub-) arctic regions will become more and more accessible to alien plants (Crumpacker et al., 2001; Kreyling, 2010). As projected by our model – and in accordance to recent publications (Wasowicz et al., 2013) – with proceeding climate change the potential suitable habitat of *L. nootkatensis* will expand significantly into the high elevation ecosystems of Iceland during the years 2061–2080, potentially due to warming and a prolonged growing seasons. In accordance to Wasowicz et al. (2013) we found human-mediation and temperature-related variables to be the most important factors shaping the distribution of *L. nootkatensis* across Iceland under current climate conditions. Wasowicz et al.

(2013) interpreted this pattern as a limitation of the alien plant due to the harsh climatic conditions of Iceland. Although this explanation is probably true for most alien plant species of Iceland, it might not be applicable to the "high-latitude invader" lupine as the climate envelope of the native versus invasive range is very similar: both range from a cold temperate (boreal) to sub-polar climate (Wasowicz, 2016). Single plants and small lupine stands are not detected by the remote sensing technique used to derive our species occurrence data set, but are already recorded as present and invasive in the Icelandic highlands and mountainous areas (Wasowicz, 2016). Although the majority of lupine patches occur in the lowlands, the invader might not be limited to these climatically favorable regions close to manmade infrastructure. Our model neither confirmed a dependency of *L. nootkatensis* toward areas with high precipitation as indicated by Magnusson (2010), nor did the precipitation parameters show a high relative contribution to the Maxent model. We therefore assume that *L. nootkatensis* is already adapted to the climate of Iceland, but the predicted invasive range under the current climate conditions is biased, i.e., underestimates the potential distribution, due to the manmade distribution together with a dispersal lag of the invader. To partially exclude this bias as well as to estimate the maximum area at risk to be changed by the invader, we calculated two separate models one with and one without human infrastructure as propagation vectors.

The question arises whether the Central Highlands subsequently lose their function as a refuge for cold-adapted native species due to the projected habitat expansion and induced succession of *L. nootkatensis*. The Central Highlands and mountainous regions, especially of northern Iceland, are biodiversity hot-spots (Wasowicz et al., 2014). They are habitat to many native, cold-adapted plant species (Wasowicz et al., 2014), which are adjusted to the harsh climate (Wasowicz et al., 2013; Wasowicz, 2016) and nutrient-poor soils of arctic environments (Arnalds, 2004; Liška and Soldán, 2004; Dowdall et al., 2005). Via the accumulation of litter and atmospheric nitrogen *L. nootkatensis* eventually increases soil quality and depth (Sigurdardottir, 2008; Magnusson, 2010) and finally induces succession (Magnusson et al., 2008). Thus, the invasive ecosystem engineer pursues niche construction (Fei et al., 2014) and might act as a transformer species. In our experiments, species-rich habitats like the heathland showed a decrease in plant species diversity and richness as well as a change in community composition as soon as lupine invasion occurs, while species-poor habitats, e.g., grassland and woodland, showed an increase. There are reasons to believe that Arctic plant species probably do not tolerate elevated N as caused by lupine invasion and might be poorer competitors compared to non-native nitrophilous plants (Chapin et al., 1986; Lilleskov et al., 2002; Hofland-Zijlstra and Berendse, 2009). For example, elevated nitrogen levels lead to a decrease in the mycorrhiza community and, combined with shading, to a reduced production of phenols and tannins, resulting in a diminished competitive ability of heathland plants (Lilleskov et al., 2002; Hofland-Zijlstra and Berendse, 2009). Thus, as shown for the heath communities, a loss of plant species diversity and richness must be assumed. Additionally, elevated soil nutrients may lead to a facilitated settlement of further invasive species (Simberloff and Von Holle, 1999), which has already been demonstrated for old lupine stands (Magnusson et al., 2008; Magnusson, 2010). By altering plant community organization and by inducing succession (Appendix Figures A1, A2 and Table A1) *L. nootkatensis* changes the functional integrity of the respective habitats.

Most species will not be able to keep pace with the rapidly changing climate as their migration rates are considerably lower than the expected range shifts (Cunze et al., 2013). This is especially relevant for ecosystems in cold biomes such as Iceland, where suitable climate space is limited. On the other hand, invasive species may benefit from climate warming allowing accelerated spread. Both lead to significant changes in the native vegetation and therewith to the loss of unique ecosystems. The changes in soil properties and succession induced by lupine invasion will further speed up vegetation changes induced by climate change. It is unlikely that the native vegetation is able to adapt fast enough to those ecosystem changes.

In current as well as in future climate conditions, the amount of projected suitable habitat for *L. nootkatensis* will mainly cover areas without native vegetation (Appendix Table A2). Thus, the ecosystem engineer *L. nootkatensis* could induce the urgently needed succession to higher plant communities, which are able to stabilize the barren and sometimes degraded soils and subsequently reduce desertification and dust storms on Iceland (Arnalds and Runolfsson, 2008; Magnusson et al., 2008; Riege, 2008). However, up to 86.9% of the area currently domicile to the native vegetation of Iceland is projected to become suitable lupine habitat in future climate conditions and thus will be at risk of being permanently changed to a secondary vegetation. It is very probable that the emerging plant community differs in structure and composition from native plant communities of Iceland (Magnusson et al., 2008). The maps of the potential distribution of *L. nootkatensis* across Iceland only show the amount of projected suitable habitat, thus they give an estimate of which areas are generally endangered by lupine invasion. Those projected areas are not necessarily simultaneously covered by *L. nootkatensis* as succession might eventually lead to the displacement of the invader (Magnusson et al., 2008). However, as the emerging vegetation does not necessarily correspond to the original native vegetation of Iceland, the SDM projections predict the maximum potential area at risk to be permanently changed by *L. nootkatensis*. In addition, not only the plants, but also invertebrates and birds are affected by lupine induced homogenization (Davidsdottir et al., 2016).

CONCLUSION

Invasion of an ecosystem engineer into a sub-polar environment can induce very different effects. In heavily degraded habitats it can cause a fast increase in plant species richness and diversity, while in native, cold-adapted habitats it might lead to a reduction in plant species richness by outcompeting more sensitive species. In areas where positive aspects prevail, ecosystem engineers might carefully be used for restoration purposes, e.g., to induce succession toward a stable vegetation cover on severely degraded soils. However, the spread beyond such areas is very likely leading to altered energy and nutrient fluxes. The resulting changes in ecosystem-level properties are, due to the low conversion rates of those ecosystems, long-lasting, or permanent. A change in the limiting factors, e.g., due to climate change, might lead to a massive expansion of the potential habitat, which additionally hampers the targeted application of the ecosystem engineer and facilitates invasion.

AUTHOR CONTRIBUTIONS

VV and AJe conceived the ideas. VV and VW designed methodology. VV, NT, AJa, VW, and PW collected and analyzed the data. VV led the writing of the manuscript. NT, AJa, VW, CB, PW, and AJe helped with the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

We thank the Icelandic Institute of Natural History (http://en.ni.is/) and the National Land Survey of Iceland (NLSI, http://www.lmi.is/en/) for providing us with the species occurrence data of *Lupinus nootkatensis* and additional environmental predictor variables. We thank Prof. Þóra Ellen Þórhallsdóttir and Oliver Bechberger from the University of Iceland, Kristín Svavarsdóttir from the Soil Conservation Service of Iceland, and the team and rangers of the Vatnajökull National Park for their support and advice during field work. Many thanks to Prof. Dr. Olafur Arnalds for the kind permission to use the soil data provided by the Agricultural University of Iceland as well as for his valuable suggestions. Additionally, we would also like to thank the two reviewers for their thoughtful recommendations, which helped to further improve our manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2018.00715/full#supplementary-material

REFERENCES

Arnalds, O. (2004). Volcanic soils of Iceland. *Catena* 56, 3–20. doi: 10.1016/j.catena.2003.10.002

Arnalds, O. (2015). *The Soils of Iceland*. Dordrecht: Springer. doi: 10.1007/978-94-017-9621-7

Arnalds, A., and Runolfsson, S. (2008). "The role of Nootka lupin (*Lupinus nootkatensis*) for revegetation in Iceland," in *Lupins for Health and Wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Ayanu, Y., Jentsch, A., Müller-Mahn, D., Rettberg, S., Romankiewicz, C., and Koellner, T. (2015). Ecosystem engineer unleashed: Prosopis juliflora threatening ecosystem services? *Reg. Environ. Change* 15, 155–167. doi: 10.1007/s10113-014-0616-x

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., et al. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222, 1810–1819. doi: 10.1016/j.ecolmodel.2011.02.011

Björnsson, H. (2003). Subglacial lakes and jökulhlaups in Iceland. *Glob. Planet. Change* 35, 255–271. doi: 10.1016/S0921-8181(02)00130-3

Björnsson, H., Jonsson, T., Gylfadottir, S. S., and Olason, E. O. (2007). Mapping the annual cycle of temperature in Iceland. *Meteorol. Z.* 16, 45–56. doi: 10.1127/0941-2948/2007/0175

Björnsson, H., and Pálsson, F. (2008). Icelandic glaciers. *Jökull* 58, 365–386.

Brown, J. L. (2014). SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* 5, 694–700. doi: 10.1111/2041-210X.12200

Catford, J. A., Jansson, R., and Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* 15, 22–40. doi: 10.1111/j.1472-4642.2008.00521.x

Catford, J. A., Vesk, P. A., Richardson, D. M., and Pyšek, P. (2012). Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Glob. Change Biol.* 18, 44–62. doi: 10.1111/j.1365-2486.2011.02549.x

Chapin, F. S., Vitousek, P. M., and Van Cleve, K. (1986). The nature of nutrient limitation in plant communities. *Am. Nat.* 127, 48–58. doi: 10.1086/284466

Colautti, R. I., Grigorovich, I. A., and MacIsaac, H. J. (2006). Propagule pressure: a null model for biological invasions. *Biol. Invasions* 8, 1023–1037. doi: 10.1007/s10530-005-3735-y

Crochet, P., Jóhannesson, T., Jónsson, T., Sigurðsson, O., Björnsson, H., Pálsson, F., et al. (2007). Estimating the spatial distribution of precipitation in Iceland using a linear model of orographic precipitation. *J. Hydrometeorol.* 8, 1285–1306. doi: 10.1175/2007JHM795.1

Crumpacker, D. W., Box, E. O., and Hardin, E. D. (2001). Implications of climatic warming for conservation of native trees and shrubs in Florida. *Conserv. Biol.* 15, 1008–1020. doi: 10.1046/j.1523-1739.2001.0150041008.x

Cunze, S., Heydel, F., and Tackenberg, O. (2013). Are plant species able to keep pace with the rapidly changing climate? *PLoS One* 8:e67909. doi: 10.1371/journal.pone.0067909

Davidsdottir, B., Gunnarsson, T. G., Halldorsson, G., and Sigurdsson, B. D. (2016). Avian abundance and communities in areas revegetated with exotic versus native plant species. *Icel. Agric. Sci.* 29, 21–37. doi: 10.16886/IAS.2016.03

Dowdall, M., Gwynn, J. P., Moran, C., Davids, C., O'dea, J., and Lind, B. (2005). Organic soil as a radionuclide sink in a High Arctic environment. *J. Radioanal. Nucl. Chem.* 266, 217–223. doi: 10.1007/s10967-005-0895-2

Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6, 503–523. doi: 10.1007/s10021-002-0151-3

Ehrenfeld, J. G. (2010). Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 41, 59–80. doi: 10.1146/annurev-ecolsys-102209-144650

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151. doi: 10.1111/j.2006.0906-7590.04596.x

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., and Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists: statistical explanation of MaxEnt. *Divers. Distrib.* 17, 43–57. doi: 10.1111/j.1472-4642.2010.00725.x

Fei, S., Phillips, J., and Shouse, M. (2014). Biogeomorphic impacts of invasive species. *Annu. Rev. Ecol. Evol. Syst.* 45, 69–87. doi: 10.1146/annurev-ecolsys-120213-091928

Fremstad, E., and Elven, R. (2008). "Perennial Lupins in Fennoscandia," in *Lupins for Health and Wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Giraudoux, P. (2017). *Pgirmess: Data Analysis in Ecology*. Available at: https://cran.r-project.org/package=pgirmess

Harter, D. E. V., Irl, S. D. H., Seo, B., Steinbauer, M. J., Gillespie, R., Triantis, K. A., et al. (2015). Impacts of global climate change on the floras of oceanic islands – projections, implications and current knowledge. *Perspect. Plant Ecol. Evol. Syst.* 17, 160–183. doi: 10.1016/j.ppees.2015.01.003

Hijmans, R. J. (2016). *raster: Geographic Data Analysis and Modeling*. Available at: http://cran.r-project.org/package=raster

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. doi: 10.1002/joc.1276

Hiltbrunner, E., Aerts, R., Bühlmann, T., Huss-Danell, K., Magnusson, B., Myrold, D. D., et al. (2014). Ecological consequences of the expansion of N2-fixing plants in cold biomes. *Oecologia* 176, 11–24. doi: 10.1007/s00442-014-2991-x

Hofland-Zijlstra, J. D., and Berendse, F. (2009). The effect of nutrient supply and light intensity on tannins and mycorrhizal colonisation in Dutch heathland ecosystems. *Plant Ecol.* 201, 661–675. doi: 10.1007/s11258-008-9554-3

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363. doi: 10.1002/bimj.200810425

Hultén, E. (1968). *Flora of Alaska and Neighbouring Territories*. Palo Alto, CA: Stanford University Press.

Icelandic Tourist Board (2017). *Tourism in Iceland in Figures 2017*. Available at: https://www.ferdamalastofa.is/en/recearch-and-statistics/tourism-in-iceland-in-figures

Jones, C. G., Lawton, J. H., and Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* 69, 373–386. doi: 10.2307/3545850

Kreyling, J. (2010). Winter climate change: a critical factor for temperate vegetation performance. *Ecology* 91, 1939–1948. doi: 10.1890/09-1160.1

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76, 5–13. doi: 10.2307/3545743

Lazzaro, L., Giuliani, C., Fabiani, A., Agnelli, A. E., Pastorelli, R., Lagomarsino, A., et al. (2014). Soil and plant changing after invasion: the case of Acacia dealbata in a Mediterranean ecosystem. *Sci. Total Environ.* 49, 491–498. doi: 10.1016/j.scitotenv.2014.08.014

Lilleskov, E. A., Fahey, T. J., Horton, T. R., and Lovett, G. M. (2002). Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology* 83, 104–115. doi: 10.2307/2680124

Liška, J., and Soldán, Z. (2004). Alien vascular plants recorded from the Barentsburg and Pyramiden settlements, Svalbard. *Preslia* 76, 279–290.

Liu, C., White, M., and Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789. doi: 10.1111/jbi.12058

Lockwood, J. L., Cassey, P., and Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20, 223–228. doi: 10.1016/j.tree.2005.02.004

Magnusson, B. (2010). *NOBANIS - Invasive Alien Species Fact Sheet - Lupinus nootkatensis*. Reykjavik: Icelandic Institute of Natural History.

Magnusson, B., Magnusson, S. H., and Sigurdsson, B. D. (2008). "Plant succession in areas colonized by the introduced Nootka lupin in Iceland," in *Lupins for Health and Wealth 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Merow, C., Smith, M. J., and Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058–1069. doi: 10.1111/j.1600-0587.2013.07872.x

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., et al. (2014). ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol. Evol.* 5, 1198–1205. doi: 10.1111/2041-210X.12261

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100

Pejchar, L., and Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends Ecol. Evol.* 24, 497–504. doi: 10.1016/j.tree.2009.03.016

Peterson, A. T., Papeş, M., and Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* 213, 63–72. doi: 10.1016/j.ecolmodel.2007.11.008

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., and Blair, M. E. (2017). Opening the black box: an open-source release of Maxent. *Ecography* 40, 887–893. doi: 10.1111/ecog.03049

Phoenix, G. K., and Lee, J. A. (2004). Predicting impacts of Arctic climate change: past lessons and future challenges. *Ecol. Res.* 19, 65–74. doi: 10.1111/j.1440-1703.2003.00609.x

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.r-project.org/

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., et al. (2011). RCP 8.5–A scenario of comparatively high greenhouse gas emissions. *Clim. Change* 109, 33–57. doi: 10.1007/s10584-011-0149-y

Richardson, D. M., Pyšek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D., and West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6, 93–107. doi: 10.1046/j.1472-4642.2000.00083.x

Riege, D. A. (2008). "The use of Lupinus nootkatensis in a revegetation and afforestation program in Southwest Iceland," in *Lupins for Health and Wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., et al. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* 40, 913–929. doi: 10.1111/ecog.02881

Shcheglovitova, M., and Anderson, R. P. (2013). Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecol. Model.* 269, 9–17. doi: 10.1016/j.ecolmodel.2013.08.011

Sigurdardottir, H. (2008). "Earthworm activity in a lupin patch in Heidmörk, Southern Iceland," in *Lupins for Health and Wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Sigurdsson, B. D., and Magnusson, B. (2008). "Seed ecology of the Nootka lupin (*Lupinus nootkatensis*) in Iceland," in *Lupins for Health and Wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Simberloff, D., and Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1, 21–32. doi: 10.1023/A:1010086329619

Simpson, E. H. (1949). Measurement of diversity. *Nature* 163, 688–688. doi: 10.1038/163688a0

Steinthorsson, S., Hardarson, B. S., Ellam, R. M., and Larsen, G. (2000). Petrochemistry of the Gjalp-1996 subglacial eruption, Vatnajökull, SE Iceland. *J. Volcanol. Geotherm. Res.* 98, 79–90. doi: 10.1016/S0377-0273(99)00186-9

Stricker, K. B., Hagan, D., and Flory, S. L. (2015). Improving methods to evaluate the impacts of plant invasions: lessons from 40 years of research. *AoB Plants* 7:plv028. doi: 10.1093/aobpla/plv028

Svavarsdóttir, K., Pétursdóttir, T., and Gisladóttir, G. (2008). "Distribution dynamics of exotic Nootka lupin (*Lupinus nootkatensis*) on a braided river plain in Skaftafell National Park, Iceland," in *Lupins for Health and Wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14–18 September 2008*, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Sæþórsdóttir, A. D., and Saarinen, J. (2015). Challenges due to changing ideas of natural resources: tourism and power plant development in the Icelandic wilderness. *Polar Rec.* 52, 82–91. doi: 10.1017/S0032247415000273

Thomson, A. M., Calvin, K. V., Smith, S. J., Kyle, G. P., Volke, A., Patel, P., et al. (2011). RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Clim. Change* 109, 77–94. doi: 10.1007/s10584-011-0151-4

Tjaden, N. B., Suk, J. E., Fischer, D., Thomas, S. M., Beierkuhnlein, C., and Semenza, J. C. (2017). Modelling the effects of global climate change on Chikungunya transmission in the 21st century. *Sci. Rep.* 7:3813. doi: 10.1038/s41598-017-03566-3

VanDerWal, J., Shoo, L. P., Graham, C., and Williams, S. E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Model.* 220, 589–594. doi: 10.1016/j.ecolmodel.2008.11.010

Vitousek, P. M., and Walker, L. R. (1989). Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.* 59, 247–265. doi: 10.2307/1942601

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D., and Matson, P. A. (1987). Biological invasion by Myrica faya alters ecosystem development in Hawaii. *Sci. New Ser.* 238, 802–804. doi: 10.1126/science.238.4828.802

Warren, D. L., and Seifert, S. N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 335–342. doi: 10.1890/10-1171.1

Wasowicz, P. (2016). Non-native species in the vascular flora of highlands and mountains of Iceland. *PeerJ* 4:e1559. doi: 10.7717/peerj.1559

Wasowicz, P., Pasierbiński, A., Przedpelska-Wasowicz, E. M., and Kristinsson, H. (2014). Distribution patterns in the native vascular flora of Iceland. *PLoS One* 9:e102916. doi: 10.1371/journal.pone.0102916

Wasowicz, P., Przedpelska-Wasowicz, E. M., and Kristinsson, H. (2013). Alien vascular plants in Iceland: diversity, spatial patterns, temporal trends, and the impact of climate change. *Flora - Morphol. Distrib. Funct. Ecol. Plants* 208, 648–673. doi: 10.1016/j.flora.2013.09.009

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

10.5.1 Supporting information Manuscript 5

Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity.

Vanessa M.S. Vetter[1,2], Nils B. Tjaden, Anja Jaeschke, Constanze Buhk, Veronika Wahl, Pawel Wasowicz, Anke Jentsch

[1]Disturbance Ecology, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

[2]Biogeography, BayCEER, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

vanessa.vetter@uni-bayreuth.de

Material and Methods

Study species

Lupinus nootkatensis (Fabaceae;) is a long-lived (up to 20 years) herbaceous plant originating from coastal regions of the Aleutian Islands and from Queen Charlotte Island, Alaska to Vancouver Island, British Columbia, Canada (Magnusson, 2010). *L. nootkatensis* was introduced to Europe in 1795 when it became a popular garden plant in England (Magnusson, 2010). From there, it reached its present distribution across Scandinavia, Iceland and Faroe islands beginning its propagation process with Sweden in the 1840s (Magnusson, 2010). In 1945, the species was introduced to Iceland from where it was spread to Greenland in 1970 and shortly after 1970 to the Faroe Islands. Nowadays *L. nootkatensis* is "not found" across large parts of Europe except for the Faroe Islands and Ireland where it is found but "not established", Finland and Sweden ("rare"), Greenland ("local"), Norway ("common") and in Iceland where it is "very common" (Magnusson, 2010). The species is mainly dispersed by human activity since it is used as an ornamental plant, to prevent soil erosion e.g. on roadsides and for land reclamation (Magnusson, 2010). The hemicryptophyte rarely produces rhizomes but is mainly spread by seeds (up to 2000 per individual with 25 flowering stems and 1800 seeds/m^2 in patches), which are generated to a large part (70 %) via self-fertilization. Lupine patches expand 1-2 meters a year as seeds are radial dispersed up to 3 meters around the mother plant by explosively opening pods (Magnusson, 2010). Sloping ground especially in combination with landslides, melting water, watercourses or strong wind falls during winter dramatically increase the species annual self-propagation (Magnusson, 2010). Additionally, seeds are spread over long distances by wildlife, e.g. birds, rivers or humans. *L. nootkatensis* produces persistent seed banks in the soil (Magnusson, 2010). *L. nootkatensis* prefers open habitats of frequent natural disturbance (Fremstad and Elven, 2008), e.g. early successional stages with vegetation destruction and soil erosion. In Iceland, the lupine is primarily recorded from gravel bars along the coast and rivers, along railways and roads, dry slopes and sandy beaches (Magnusson, 2010). But it is also found in disturbed landscapes, e.g. vegetation destruction and soil erosion, as well as in dwarf shrub-heathlands (Magnusson, 2010). According to Wasowicz et al. (2013), annual mean temperature, maximum temperature of warmest month, mean temperature of warmest quarter and mean temperature of wettest quarter might be the most important climatic factors influencing the distribution of *L. nootkatensis* in Iceland, while altitude seems not to limit the spread of the invader. While Magnusson et al. (2008) found the species to be dependent upon relatively high precipitation, this was not confirmed by the modeling approach of Wasowicz et al. (2013).

Community composition, species abundance and nearest neighbor growth patterns

Community composition was analyzed on the basis of the Londo-scale (Londo, 1976). Species abundance was measured as the relative abundance of each single species in one plot given in percentage. As, especially in the heathland, the abundance of the different species was frequently low, all individuals of these rare species were counted. Species abundance for every species in each plot was then calculated as follows:

$$species\ abundance\ = \frac{\sum individuals\ of\ one\ species}{\sum individuals}$$

The mean species abundance is the relative species abundance of each species averaged over all plots within one lupine cover level.

Additionally, overall vegetation cover, moss cover and depth, lichen cover, percentage of organic material, soil depth, percentage of bare ground and the depth of the ash layer was measured or estimated per plot. We performed nearest neighbor analysis to evaluate growth patterns in lupine plots as well as facilitation and restriction of native plants. For that, one *L. nootkatensis* specimen was chosen for every plot of the category "low" or "high density" and the distances between the sprout base of the lupine and all neighboring plants within a radius of 40 cm were measured.

Statistical Analyses

Venn diagrams were used to visualize species composition change per habitats (Ritchie et al. 2015).
We performed cluster analysis with a Euclidean distance matrix of the recorded growth patterns to evaluate interspecific interactions between the invader and the native species of the different habitats and lupine cover levels (package stats). To assess the effects of the presence of *L. nootkatensis* on the species composition of the different habitats a Detrended Correspondence Analysis (DCA) was applied on the presence-absence-data of the vegetation analysis.

Calculating difference in projection

We calculated the difference in model projections by subtracting binary presence-absence maps of model 1 (with variable "distance to nearest road") from model 2 (without variable "distance to nearest road") for every time step, model and RCP respectively. Binary presence-absence maps were created using the cloglog output of the Maxent projections: all values ≥ threshold were set to 1, while all values < threshold were set to 0. We used the Maximum training sensitivity plus specificity threshold (MTSS): $MTSS_{model\,1} = 0.531$, $MTSS_{model\,2} = 0.553$. All calculations were done in R.

$$difference\ in\ projection = binary\ output\ (model\ 2 - model\ 1)$$

Calculation of percentage cover

In R, we calculated the amount of habitat [%] currently 1) vegetated by native Icelandic plant species and 2) barren soil which is projected to be suitable lupine habitat under present day and/or future climate conditions. First, we created two binary land cover maps with 1 = vegetation or barren soil respectively and 0 = all other land cover classes. Second, we calculated the percentage of cells shared between the binary native vegetation/binary barren soil maps and the binary presence-absence maps for every time step, model and RCP respectively.

Results and Discussion

Species list

The most diverse ecosystem in Iceland is the heathland, which accommodates 40 different species on a plot size of 2 x 2 m. Species numbers of the grassland and woodland are similarly low with six and seven species respectively. In total we found 72 different species (Tab. A1). The main difference in species richness and diversity was found to be among habitats rather than lupine cover levels.

Table A1: List of taxa recorded in the course of the vegetation analysis and their occurrence in the respective habitats and lupine cover levels. Notation of habitats and levels: YXXX: the first letter stands for the habitat [Y], all following letters determine the respective lupine cover levels the taxa was found in [XXX]. Habitat: W = woodland, H = heathland, G = grassland; lupine cover level: N = no (0 %), L = low (10 - 50 %), H = high (51 – 100 %) cover. Different habitats and their levels are separated by comma. In total 72 different taxa were distinguished.

Taxa	Habitats and levels	Taxa	Habitats and levels
Agrostis capillaris	W(NL)	*Hieracium spec.*	H(NLH), W(H)
Agrostis spec.	H(LH)	*Hieracium thaectolepium*	H(NH)
Agrostis stolonifera	G(NH), H(N), W(H)	*Juncus trifidus*	H(NL)
Agrostis vinealis	G(NL), H(NLH), W(H)	*Juncus triglumis*	H(N)
Alchemilla alpina	H(L)	*Kobresia myosuroides*	H(N)
Angelica archangelica	G(NLH)	*Lathyrus japonicus*	H(NLH), W(L)
Angelica sylvestris	G(H), H(N), W(NLH)	*Leontodon spec.*	H(N)
Anthoxanthum odoratum	H(N), W(NL)	*Listera cordata*	H(N)
Arctostaphylus uva-ursi	H(NLH)	*Lupinus nootkatensis*	G(LH), H(LH), W(LH)
Armeria maritima	H(N)	*Luzula multiflora*	G(L), H(NLH), W(NL)
Bartsia alpina	H(NL), W(N)	*Luzula spec.*	H(NLH)
Betula nana	H(NLH)	*Luzula spicata*	H(N)
Betula pubescens	G(H), H(NLH), W(NLH)	*Myosotis arvensis*	G(N)
Bistorta vivipara	H(NLH), W(NL)	*Parnassia palustris*	H(NH)
Calluna vulgaris	H(NLH)	*Pinguicula vulgaris*	H(NLH)
Campanula rotundifolia	H(NLH), W(LH)	*Platanthera hyperborea*	H(N)
Carex capillaris	H(N)	*Poa annua*	W(N)
Carex maritima	H(N)	*Poa glauca*	H(LH), W(L)
Cerastium fontanum	H(L), W(L)	*Poa pratensis*	G(NLH), W(L)
Cyperaceae	H(L)	*Poaceae*	H(NLH)
Dactylorhiza maculata	H(N)	*Potentilla crantzii*	H(NH)
Deschampsia flexuosa	G(LH), H(NLH), W(NLH)	*Ranunculus acris*	G(H), W(N)
Dryas octopetala	H(NL)	*Rhinanthus minor*	H(N)
Empetrum nigrum	H(NLH)	*Rubus saxatilis*	H(H), W(NLH)
Equisetum arvense	W(NLH)	*Rumex acetosa*	G(NLH), W(NLH)
Equisetum hyemale	W(NLH)	*Salix herbacea*	H(N)
Equisetum pratense	W(NLH)	*Salix lanata*	H(NL)
Equisetum variegatum	W(NLH)	*Salix phylicifolia*	G(L), H(N), W(NL)
Erigeron spec.	H(NLH)	*Selaginella selaginoides*	H(N)
Euphrasia frigida	H(LH)	*Silene acaulis*	H(N)
Festuca richardsonii	G(N), H(NLH), W(NLH)	*Taraxacum spec.*	G(L), W(H)
Festuca spec.	H(NLH)	*Thalictrum alpinum*	H(NLH)
Festuca vivipara	G(NL), H(NLH), W(NLH)	*Thymus arcticus*	H(NLH)
Galium normannii	H(LH), W(LH)	*Tofieldia pusilla*	H(NLH)
Galium verum	G(NL), H(NH), W(NLH)	*Trisetum triflorum*	G(L), H(NH)
Geranium sylvaticum	G(H), W(NLH)	*Vaccinium uliginosum*	H(NLH), W(NL)

Based on the Venn-Diagrams and the mean species abundance (Fig. A1), community composition changed the most in the grassland and the least in the heathland due to the presence of *L. nootkatensis*. In the grass- and woodland, lupine invasion increased the number of level-unique-species (species which are only present in one of the respective lupine cover levels). Lupine level "none" of the grassland showed a proportionally low number of species, which were not present in the other two levels, while level "low" and "high" had rather high numbers of level-unique-species (Fig. A1, a-c). In the woodland, the number of level-unique-species were rather equally distributed (Fig. A1, a-c). Level "none" in the heathland had a proportionally high number of level-unique-species, while the lupine cover levels "low" and "high" comprised a significantly lower number of level-unique-species (Fig. A1, a-c).

Heathland species composition was, compared to the woodland and grassland, not remarkably altered by the introduction of new species with advancing lupine invasion but by a relatively high species loss (Fig. A1, a – c). For typical heath species (Fig. A1, d) a slight decrease in abundance was found with a simultaneous increase in *Betula pubescens*. Woodland species showed very different changes in abundance with the invading lupine (Fig. A1 e). Remarkably, the cover of *Betula pubescens* increased with invader presence. The abundance of one of the most notable species of the woodland community *Geranium sylvaticum*, however, decreased drastically with invading lupine density while the abundance of *Angelica archangelica* increased.

However, the ordination graphic (Fig. A2) showed distinct differences of species composition with ongoing invasion in the heathland. Plots of level "high" and "low" generally reach higher values on the invasion-axis (DCA2), while plots of the level "none" were allocated to lower values on the invasion-axis.

The DCA-analyses (Fig. A2) showed that, heathland community composition endured a strong negative alteration by the invading lupine: decrease in species richness, decrease in the abundance of typical heath species, increase in tree cover (e.g. *Betula pubescens*). The plant community of the heath was reorganized: a vegetation type which is mainly characterized by dwarf growth changed to a vegetation type characterized by tall growing plant e.g. trees. Thus, *L. nootkatensis* alters the functional integrity of the heathland community.

L. nootkatensis changes the composition of the woodland shrub community as well as species abundances. For example, the abundance of *G. sylvaticum* declined and *R. acris* disappeared completely, while new nitrophilous shrub species (*Taraxacum spec*) arrived. Those effects might be related to additional shading effects as well as nitrogen enrichment of the soils invaded by the lupine. Native species of the grassland disappeared, leading to great dissimilarities between plots with and without *L. nootkatensis*. The invader transformed the plant community from a grassland to a vegetation with tall growing shrubs and small trees. Thus, the lupine induces succession.

The differences between the habitats are much more distinct than between the lupine cover levels and community composition did not converge among the three habitat types with increasing lupine cover level (Fig. A2).

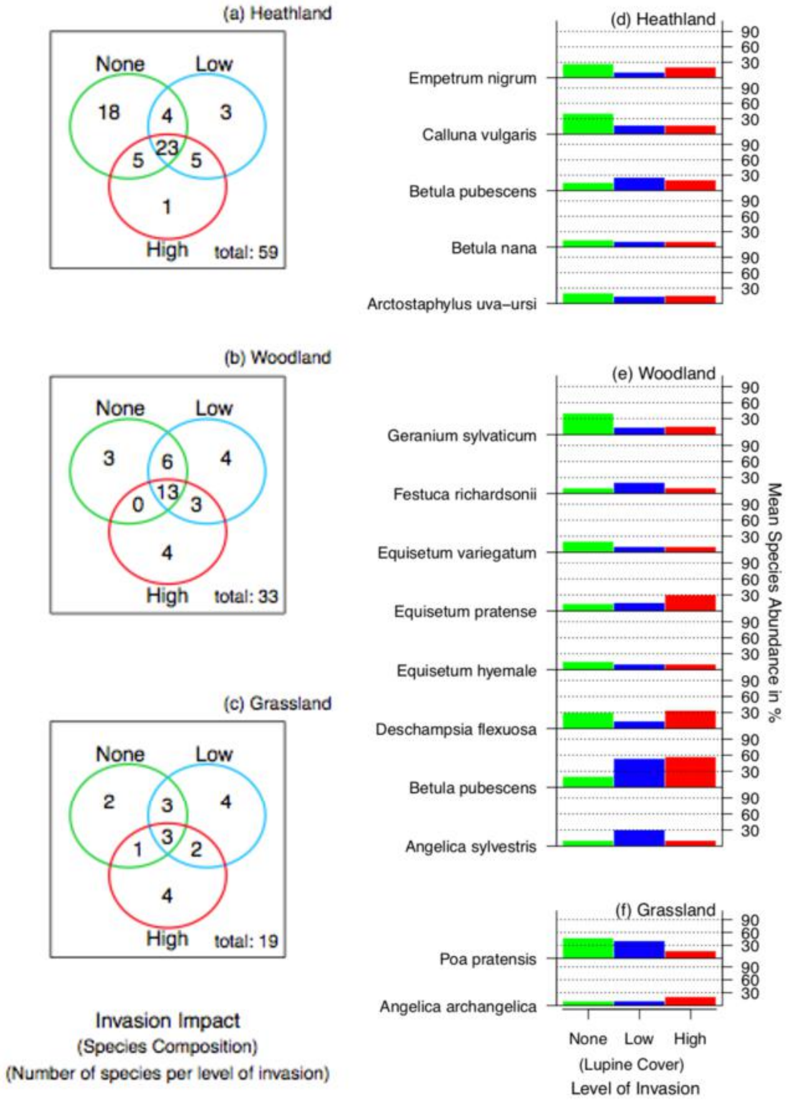


Figure A1: Impact on lupine invasion on species composition and abundance. (a – c) Venn-Diagrams visualize the impact of invasion on the species composition of the community. Number of species exclusive for or shared by the different stages of lupine invasion are indicated by the numbers in the respective (inter-)sections. (d – f) Mean abundance of species affected by different levels of lupine invasion. Level of lupine invasion was measured in the lupine cover classes "no" (0 %), "low" (< 50 %) and "high" (51-100 %).

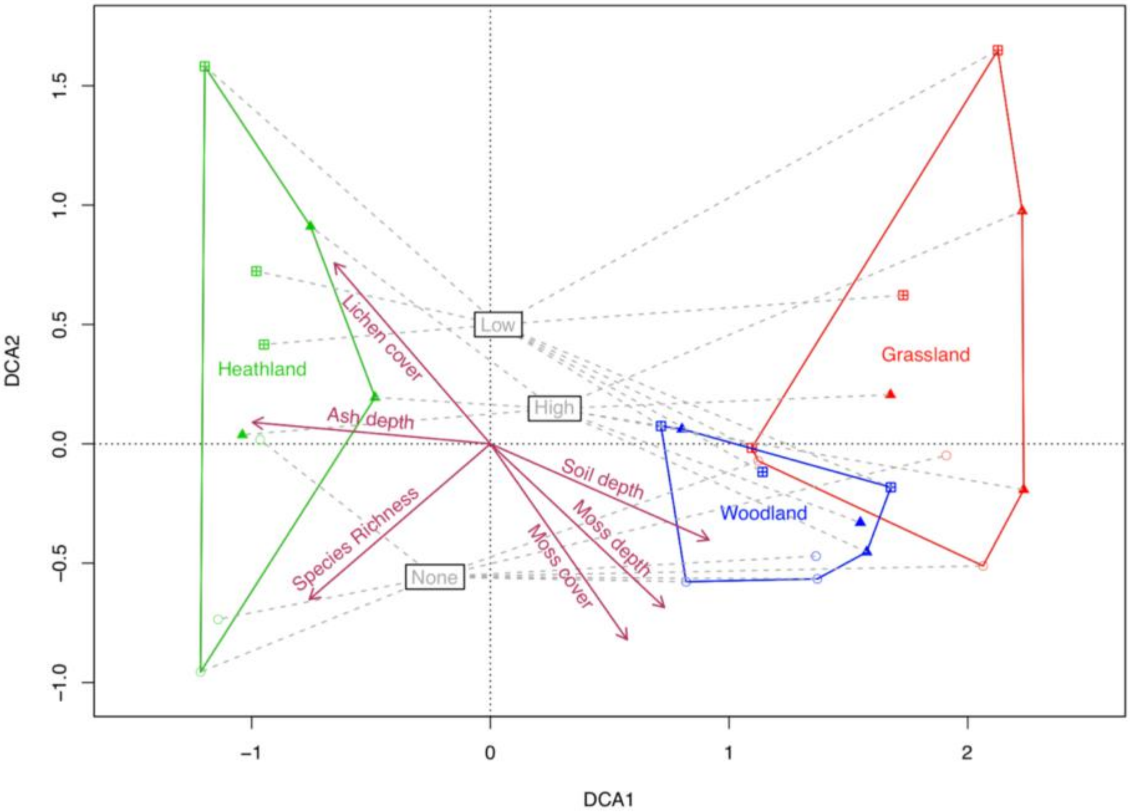
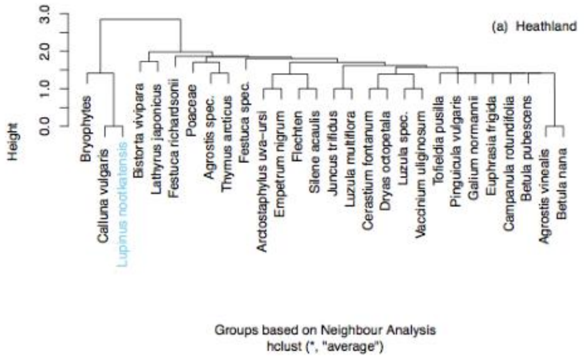


Figure A2: Detrended correspondence analysis (DCA) on presence-absence-data of the vegetation analysis including an environmental fit of background data. DCA1 = habitat-axis: differences in the species composition between the habitats; DCA2 = invasion-axis: differences among lupine cover level ["none" (0 %), "low" (10 - 50 %), "high" (51-100 %)]. Single plots of the three habitat types are displayed using different symbols in the respective color of the habitat (green: heathland, blue: woodland, red: grassland). Plots belonging to the same lupine cover level are displayed in the same symbol (circle: "none", square: "low", triangle: "high") and are linked by a grey ordispider. The centroids of the ordispiders are labeled with the respective lupine cover level. The significant environmental parameters are indicated by maroon arrows.

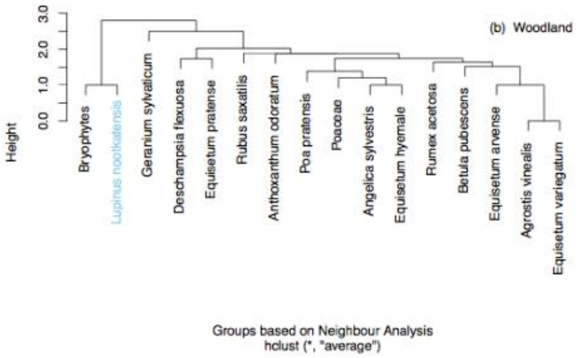
Nearest neighbor growth pattern

Analysis of the nearest neighbor growth patterns did not indicate any vascular plant species to have interspecific interactions with *L. nootkatensis* (Fig. A2). Only bryophytes in general were able to grow closest to the stem basis of *L. nootkatensis*. In all habitats, a positive interaction between lupine and the bryophytes were indicated. In the heathland an additional indication for a positive interaction with *Calluna vulgaris* was found and a negative interaction with *Agrostis vinealis* and *Betula nana*. Indication for negative interactions with *Agrostis vinealis* and *Equisetum variegatum* were found in the woodland, while a minor positive interaction of the lupine with *Poa pratensis* was found in the grassland.

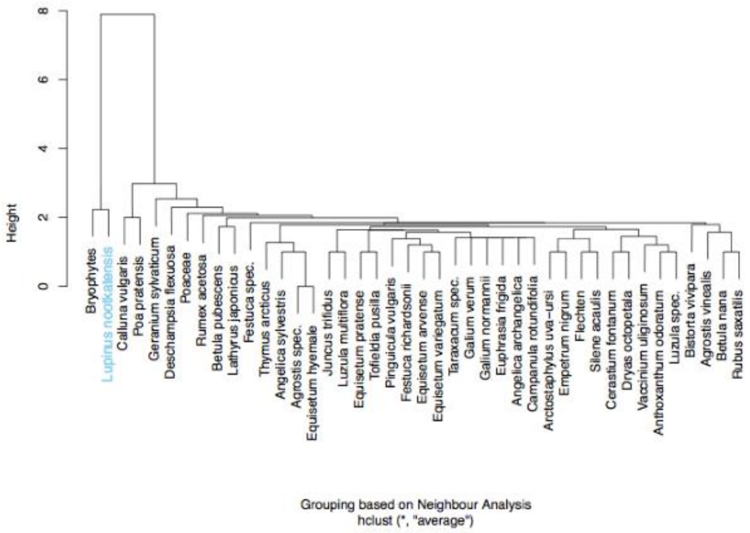
a)


(a) Heathland
Height
0.0
1.0
2.0
3.0
Bryophytes
Calluna vulgaris
Lupinus nootkatensis
Bistorta vivipara
Lathyrus japonicus
Festuca richardsonii
Poaceae
Agrostis spec.
Thymus arcticus
Festuca spec.
Arctostaphylus uva-ursi
Empetrum nigrum
Flechten
Silene acaulis
Juncus trifidus
Luzula multiflora
Cerastium fontanum
Dryas octopetala
Luzula spec.
Vaccinium uliginosum
Tofieldia pusilla
Pinguicula vulgaris
Galium normannii
Euphrasia frigida
Campanula rotundifolia
Betula pubescens
Agrostis vinealis
Betula nana
Groups based on Neighbour Analysis
hclust (*, "average")

b)


(b) Woodland
Height
0.0
1.0
2.0
3.0
Bryophytes
Lupinus nootkatensis
Geranium sylvaticum
Deschampsia flexuosa
Equisetum pratense
Rubus saxatilis
Anthoxanthum odoratum
Poa pratensis
Poaceae
Angelica sylvestris
Equisetum hyemale
Rumex acetosa
Betula pubescens
Equisetum arvense
Agrostis vinealis
Equisetum variegatum
Groups based on Neighbour Analysis
hclust (*, "average")

c)


Height
0
2
4
6
8
Bryophytes
Lupinus nootkatensis
Calluna vulgaris
Poa pratensis
Geranium sylvaticum
Deschampsia flexuosa
Poaceae
Rumex acetosa
Betula pubescens
Lathyrus japonicus
Festuca spec.
Thymus arcticus
Angelica sylvestris
Agrostis spec.
Equisetum hyemale
Juncus trifidus
Luzula multiflora
Equisetum pratense
Tofieldia pusilla
Pinguicula vulgaris
Festuca richardsonii
Equisetum arvense
Equisetum variegatum
Taraxacum spec.
Galium verum
Galium normannii
Euphrasia frigida
Angelica archangelica
Campanula rotundifolia
Arctostaphylus uva-ursi
Empetrum nigrum
Flechten
Silene acaulis
Cerastium fontanum
Dryas octopetala
Vaccinium uliginosum
Anthoxanthum odoratum
Luzula spec.
Bistorta vivipara
Agrostis vinealis
Betula nana
Rubus saxatilis
Grouping based on Neighbour Analysis
hclust (*, "average")

d)

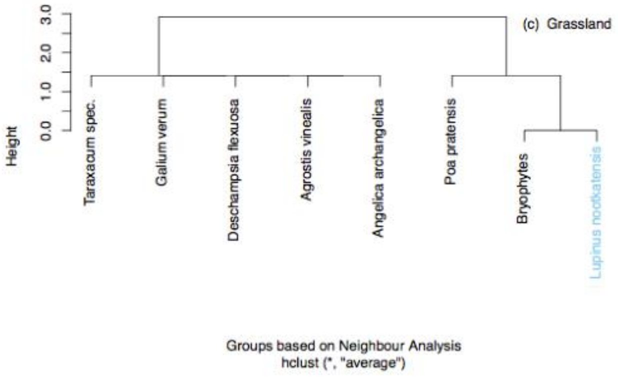

(c) Grassland
Height
0.0
1.0
2.0
3.0
Taraxacum spec.
Galium verum
Deschampsia flexuosa
Agrostis vinealis
Angelica archangelica
Poa pratensis
Bryophytes
Lupinus nootkatensis
Groups based on Neighbour Analysis
hclust (*, "average")

Figure A3: Indications for interspecific interactions with *Lupinus nootkatensis* – Cluster-analysis of the growth patterns around single lupine individuals in the primary stage of lupine invasion. Level of lupine invasion was measured in the lupine cover classes "no" (0 %), "low" (10 - 50 %) and "high" (51 - 100 %). The analysis is based on an Euclidean matrix combined with a cluster analysis with mode "average". a) No distinct indication for facilitative or inhibitive inter-habitat interactions with the lupine were found, except for the Bryophytes. b) Positive interaction with *Calluna vulgaris*; c) negative interaction with *Agrostis vinealis* and *Equisetum variegatum*; d) minor positive interaction with *Poa pratensis*. b-c) positive interaction with Bryophytes.

No indication was found that a universal vascular plant interspecific interaction existed in all three habitats. Bryophytes were able to grow close to the lupine indicating positive interactions as previously found by Magnusson et al. (2008)

Calluna vulgaris was found growing closest to the lupine in the heathland. However, this is not surprising as the *C. vulgaris* is the predominant heath species. Thus, this might not necessarily be an indication for a positive interspecific interaction, especially as the general abundance of *C. vulgaris* was greatly reduced by the invading lupine.

Species-rich habitats like the heathland show a loss of species diversity and loss in species richness as well as a change in community composition as soon as lupine invasion occurs, while species-poor habitats, e.g. grassland and woodland, show an increase. The highly competitive *L. nootkatensis* shows strong negative impacts upon small resident species – small rosettes, cushion plants and orchids – of the heathland. *L. nootkatensis* is able to outcompete native vegetation and to use the surplus of resources (Arnalds and Runolfsson, 2008). The nitrogen fixation of *L. nootkatensis* is possibly responsible for the opposing reactions of species-poor versus species-rich habitats. A slight increase in soil nitrogen of a nutrient-poor habitat, like the heathland, leads to a loss of those species, which are poor competitors and thus dependent on nutrient depletion. Elevated nutrient and especially nitrogen levels threaten the mutualistic ericoid mycorrhiza of the heath (Hofland-Zijlstra and Berendse, 2009; Lilleskov et al., 2002). This results in a loss of mycorrhiza diversity and a shift in the parasite-mutualism continuum between plant and fungi; both affects the aboveground vegetation (Hofland-Zijlstra and Berendse, 2009; Lilleskov et al., 2002). An increase of soil nitrogen availability combined with shading, furthermore decreases the production of phenols and tannins in heath, resulting in a reduction of the competitive ability of heathland plants (Hofland-Zijlstra and Berendse, 2009). Nitrogen enrichment in the soil of species-poor grass- and woodlands leads to a slight increase in the total number of species, while a drastic increase of soil nitrogen caused by high lupine covers leads to the loss of specialist species and to a replacement by widespread nitrogen-using plants (e.g. *Taraxacum spec.* in the woodland or *Geranium sylvaticum* in the grassland) and late successional species (e.g. *Betula pubescens* and *Angelica archangelica*). Tall nitrophilous plants outcompete small resident species of open habitats, *e.g. Salix herbacea*, via competition for light (Mueller et al., 2016). By altering plant community organization and by inducing succession (Tab. A1, Fig. A1 – A2) *L. nootkatensis* changes the functional integrity of the respective habitats.

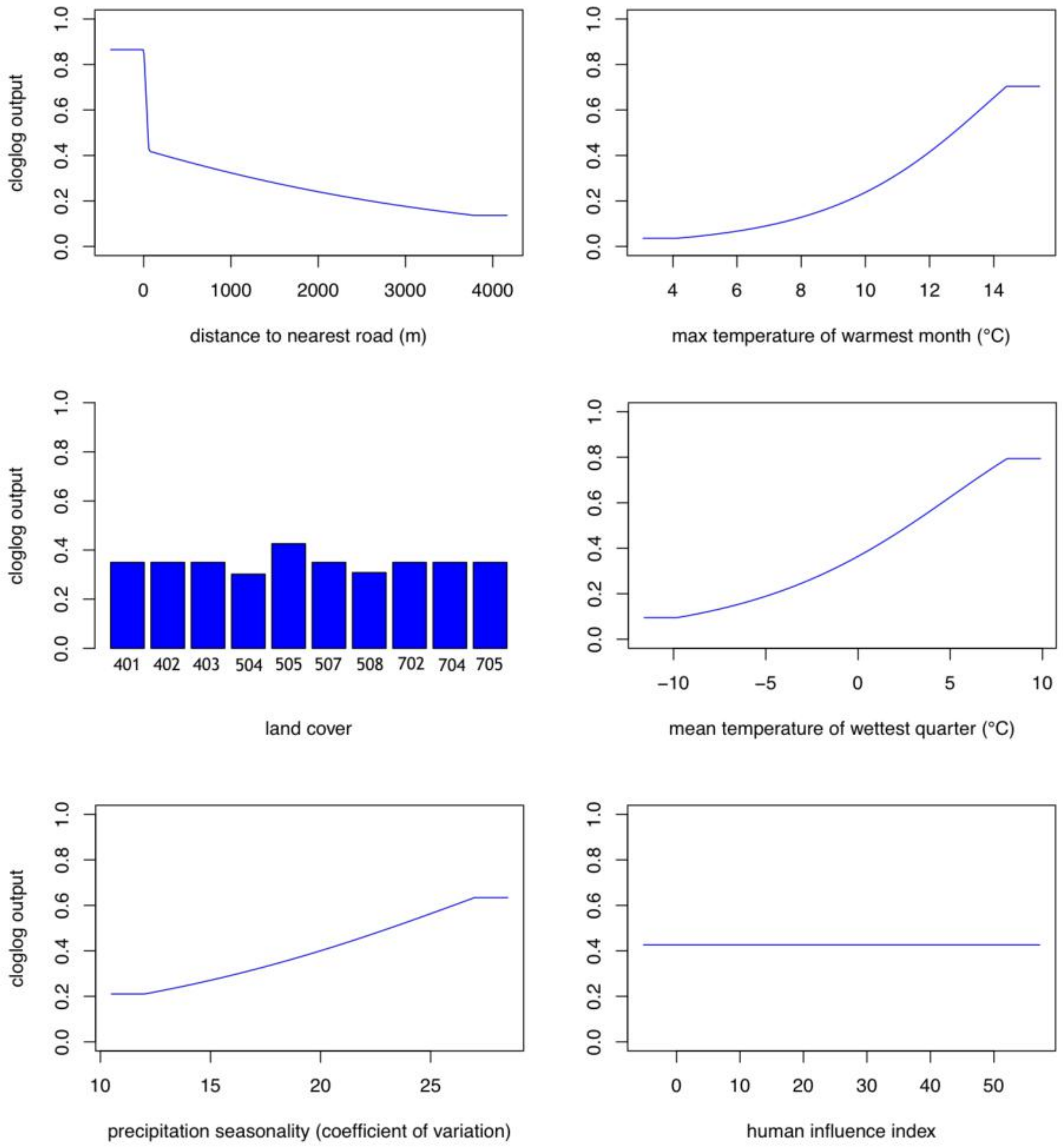


Figure A4: Marginal response curves of the environmental variables used to fit the final Maxent model 1. These response curves are fitted individually for each environmental variable, while the other predictors are kept at their average value. Environmental suitability (or the predicted probability of presence of the modeled species) ranges from: minimum = 0 to maximum = 1. Land cover categories: 401 = sand, 402 = lava, 403 = gravel plain, 504 = moss heath, 505 = grassland, heath, cultivated land, 507 = Birch woodland, 508 = wetland, 702 = rivers, 704 = water bodies, 705 = glaciers.

Table A2: Proportion of shared habitat between *L. nootkatensis* and the native vegetation of Iceland as well as proportion of bare soil projected to be covered by *L. nootkantensis* within the different time scales. Total area of Iceland covered by native vegetation: 45.9%, total area covered by bare soil: 41.3%.

Time scale	**Concentration pathway**	**Total area covered by *L. nootkatensis* [%]**	**Proportion of covered native vegetation**	**Proportion of covered bare soil**
current	-	13.3	24.1	26.8
MPI_ESM-LR	**RCP 4.5**	39.1	61.3	68.0
MPI_ESM-LR	**RCP 8.5**	61.7	86.9	96.4
NorESM1-M	**RCP 4.5**	50.1	74.5	82.6
NorESM1-M	**RCP 8.5**	58.0	81.3	90.2

In current as well as in future climate conditions, the amount of projected suitable habitat for *L. nootkatensis* will mainly cover areas without native vegetation (Tab. A2). However, in future climate conditions, up to 86.9% of the area currently domicile to the native vegetation of Iceland is projected to become suitable lupine habitat and thus 87% of the vegetation ecosystems of Iceland will be at risk of being permanently changed to a secondary vegetation due the invasive ecosystem engineer. In addition, 96.4% of the currently vegetation-free areas of Iceland were projected to become suitable lupine habitat in future climate conditions. This might eventually lead to a massive transformation of the majority of Icelandic ecosystems, especially under the assumption that nowadays barren soils (especially in the high elevation ecosystems) might become important refuges for native species in the context of climate change. However, if these high altitudinal refuges have already been altered by *L. nootkatensis*, colonization of indigenous species might no longer be possible. Subsequently, this could lead to the accelerated extinction of indigenous species in the context of climate change.

References

Arnalds, A., and Runolfsson, S. (2008). “The role of Nootka Lupin (Lupinus nootkatensis) for revegetation in Iceland,” in *Lupins for health and wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds. J. A. Palta and J. D. Berger (Canterbury, New Zealand: International Lupin Association).

Fremstad, E., and Elven, R. (2008). “Perennial Lupins in Fennoscandia,” in *Lupins for health and wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds. J. A. Palta and J. D. Berger (Canterbury, New Zealand: International Lupin Association).

Hofland-Zijlstra, J. D., and Berendse, F. (2009). The effect of nutrient supply and light intensity on tannins and mycorrhizal colonisation in Dutch heathland ecosystems. *Plant Ecol.* 201, 661–675. doi:10.1007/s11258-008-9554-3.

Lilleskov, E. A., Fahey, T. J., Horton, T. R., and Lovett, G. M. (2002). Belowground Ectomycorrhizal Fungal Community Change Over a Nitrogen Deposition Gradient in Alaska. *Ecology* 83, 104. doi:10.2307/2680124.

Londo, G. (1976). The decimal scale for relevés of permanent quadrats. *Plant Ecol.* 33, 61–64.

Magnusson, B. (2010). NOBANIS - Invasive Alien Species Fact Sheet - Lupinus nootkatensis.

Magnusson B., Magnusson S.H., and Sigurdsson B.D. (2008). “Plant succession in areas colonized by the introduced Nootka Lupin in Iceland,” in *Lupins for health and wealth: 12th International Lupin Conference, Fremantle, Western Australia, 14-18 September 2008*, eds. J. A. Palta and J. D. Berger (Canterbury, New Zealand: International Lupin Association).

Mueller, I. B., Buhk, C., Lange, D., Entling, M. H., and Schirmel, J. (2016). Contrasting effects of irrigation and fertilization on plant diversity in hay meadows. *Basic Appl. Ecol.* 17, 576–585. doi:10.1016/j.baae.2016.04.008.

Ritchie, M. E., Phipson, B., Wu, D., Hu, Y., Law, C. W., Shi, W., et al. (2015). *limma powers differential expression analyses for RNA-sequencing and microarray studies.*

Wasowicz, P., Przedpelska-Wasowicz, E. M., and Kristinsson, H. (2013). Alien vascular plants in Iceland: Diversity, spatial patterns, temporal trends, and the impact of climate change. *Flora - Morphol. Distrib. Funct. Ecol. Plants* 208, 648–673. doi:10.1016/j.flora.2013.09.009.

11 ACKNOWLEDGEMENTS

I thank all those who have helped me with the completion of this dissertation, who supported me and accompanied me through this important time in my life.

First of all, I would like to thank my two supervisors, Prof. Dr. Anke Jentsch (Department of Disturbance Ecology University of Bayreuth) and Dr. Constanze Buhk (Department of Geoecology/Physical Geography, University of Koblenz-Landau, Campus Landau), for their support, motivation as well as consultation and guidance throughout the development of this dissertation.

Anke, you sparked my interest in science and invasive plant species in the first place. Starting as a student you kept encouraging me to participate in science and research, be it as an intern, Hiwi or later during my diploma thesis. Thank you for being very supportive to all of my research ideas, for always encouraging me and for giving me the freedom I needed to develop my own research interests and profile.

Constanze, thank you for your prudent, patient and critical advice and support, for your important impulses and food for thought. Thank you for your many years of accompaniment from the diploma thesis to the dissertation.

Many thanks go to all of my dear **colleagues** of the Department of Disturbance Ecology and the Department of Biogeography of the University of Bayreuth (of course including all the Hiwis as well as the DAAD Rise and IAESTE students that helped so diligently in the experiments) as well as the Department of Geoecology/Physical Geography of the University of Koblenz-Landau, Campus Landau. Working with you was a great pleasure and always a lot of fun! I am grateful for the valuable feedback, the suggestions as well as the food for thought. Thanks for the coffee breaks, the lunch conversations and the fun we had during field work and conferences. Thanks for being so supportive colleagues, for your collaboration, discussion and company. I had a great time working with you all.

Carl, thank you for providing me with a job in your working group during the last year of my PhD. The related teaching responsibilities have further deepened my understanding of species distribution modeling and thus strengthened my chosen profile and my way as a scientist.

I would like to thank all of the **co-authors** of my manuscripts who contributed to my personal development as a scientist. I deeply enjoyed all of the collaborations. Special thanks go to Dr. Anja Jaeschke and Nils Tjaden who patiently taught me all about modelling and Dr. Peter Wilfahrt who's skillful recommendations and corrections helped me a lot in improving my writing. Further, I would like to thank all the anonymous **reviewers** and their valuable and thoughtful recommendations and suggestions which helped to improve my manuscripts.

I am grateful for the feedback and comments of **Anja** and **Sonja** to the introduction and discussion of this thesis.

A big thank you to all of my dear friends and my parents. **Mum**, **Dad**, thank you for believing in me, for fostering my interest in nature (in general) and in environmental sciences (in particular) since my early childhood days and for being so supportive of whatever I do. **My friends**, who have given everything from proof reading, distractions and desecrating humor to encouragement, patience and understanding, all they could to accompany me through this time: thank you so much!

Last but not least I want to thank my husband **Stefan** for always believing in me and for supporting me unconditionally. I could not wish for or imagine a better partner than you.

12 DECLARATIONS

(Eidesstattliche) Versicherungen und Erklärungen

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.

(§ 8 Satz 2 Nr. 4 PromO Fakultät)

Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. –vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.

(§ 8 Satz 2 Nr. 7 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung der Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.

(§ 8 Satz 2 Nr. 8 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.

…………………………………………………………………………………………….

Ort, Datum, Unterschrift