Interacting climate change pressures drive temporal dynamics of mountain plant communities

Dissertation

zur Erhaltung des akademischen Grades
Doctor rerum naturalium (Dr. rer. nat.)

an der Fakultät für Biologie, Chemie und Geowissenschaften der
Universität Bayreuth

Vorgelegt von

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Geboren in Breisach am Rhein, Deutschland
Bayreuth, im September 2022

‘The mountains are calling, and I must go.’

- John Muir, botanist and mountaineer

Die Vorliegende Arbeit wurde in der Zeit von März 2019 bis September 2022 in Bayreuth an der Professur für Störungsökologie und Vegetationsdynamik unter Betreuung von Frau Professorin Dr. Anke Jentsch angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erhaltung des akademischen Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.)

Dissertation eingereicht am: 08.09.2022
Zulassung durch die Promotionskomission: 21.09.2022
Wissenschaftliches Kolloquium: 15.12.2022

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Content

Glossary

AGB	Aboveground biomass
ANPP	Aboveground Net Primary Production
BBCH	The BBCH-scale is used to identify phenological stages of plants.
Climate tracking	A species ability to adapt to experimentally altered climatic conditions (i.e. warming) by shifting phenological cues such as advancing the date of flowering. Intraspecific trait variation is crucial for plastic responses within a local species pool.
Extinction debt	Extinctions that are expected to occur as consequence of climate change that have not yet occurred.
Flowering onset	The opening of the first flower (BBCH 60+; visible stamen)
ITV	Intraspecific trait variation; the variation in specific plant functional traits within a local species pool
LA	Leaf area
LDMC	Leaf dry matter content; a higher LDMC indicates a more conservative plant growth strategy
LMA	Leaf dry mass per area
Leading / trailing range edge	A species distribution range is confined between the leading and trailing range edge. In the special case of mountain plant communities, the leading range edge is at the highest elevation while the trailing range edge is at the lowest elevation. Novel biotic interactions occur at both range edges under climate change. At its trailing edge, a species that fails to migrate upslope to track climate change will compete with native community members or with novel species migrating upslope. At its leading edge, a species will compete with species of a higher elevation community or its current competitors that simultaneous track climate to higher elevations.
MAP	Mean annual precipitation
MAT	Mean annual temperature
Migration failure	If a focal species is not able to ‘track’ climatic change to higher elevation or a close micro refugia. Migration failure is often

	simulated by planting single focal mountain species into existing lowland plant communities.
OTC	Open top chamber, plexiglas chamber to experimentally alter canopy temperature
PFT	Plant functional traits
Performance sensitivity	Proportional change in number of flowers (averaged across replicates where species occurred within each respective climate treatment) per degree warming.
Phenological sensitivity	Days shifted in species-specific flowering onset between the control and warming treatments, per degree warming.
Phenotypic plasticity	A measure of the ability to develop a rapid response to climate change within the same genotype. Phenotypic plasticity can weaken phylogenetic signals in plant functional traits; I refer to trait shifts upon translocation as 'plastic,' assuming that initial sampling started with plants of similar phenotypes (hence similar genetics)
SLA	Specific leaf area; ratio of leaf area to leaf dry mass; a higher SLA indicates a more opportunistic plant growth strategy
Translocation experiment	Down- or upslope translocation of intact plant-soil units (plant communities including roots and substrate) to simulate changes in climate and matrix vegetation If translocated downslope, plant communities get exposed to novel climate (warmer and most of the times dryer) and, if reburied into an existing lowland plant community (matrix), the in nature still existing dispersal barrier of lowland species into high-elevation plant communities is actively removed. If translocated upslope, the climate change-induced upward migration of lowland species is simulated to explore the influence of novel lowland species on native high-elevation plant communities. In the latter case, the common approach is to plant single focal lowland species into existing high elevation plant communities – simulating the upward-migration of that particular species.

1 Summary

Mountain ecosystems and high latitudes are especially prone to pronounced temperature increases (Appenzeller et al., 2008; Box et al., 2019; Pepin et al., 2015; Schickhoff et al., 2022). Extreme weather events such as heatwaves and droughts are rarely observed in high-elevation, alpine ecosystems (Körner, 2021) but will likely become more frequent at mid elevations in the subalpine and montane belt (IPCC, 2021; Spinoni et al., 2018; Stephan et al., 2021). Thus, subalpine plant communities' vulnerability to future climate change is raised, and the same will likely be true for alpine plant communities at higher elevations by the middle of the current century. Increased sensitivity to climate change becomes especially important, as various experimental studies (Alexander et al., 2015; Berauer et al., 2019; Cui et al., 2018; De Boeck et al., 2016, 2018; Haider et al., 2022; Nomoto & Alexander, 2021) and modelling approaches (Engler et al., 2011; Hülber et al., 2016; but see Dagnino et al., 2020) have found the highest species turnover and local extinction rates of various mountain species at the trailing range edge (often the subalpine belt) or under the most severe experimental climate treatments (often warming interacting with either drought or soil disturbances). So far, many studies have focused on climate warming effects on mountain tops only (Steinbauer et al., 2018), creating a knowledge gap for novel biotic outcomes for species and plant communities growing at lower elevations.

Interestingly, evidence of local extinctions in natural mountain plant communities is almost lacking. Most long term observational studies have only found an increase in species richness (Steinbauer et al., 2018), a thermophilisation of species (Lamprecht et al., 2018) and sometimes tendencies of native species abundance to decrease (Rumpf et al., 2018; Steinbauer et al., 2020). The lack of local extinctions creates the so called 'extinction debt', which describes an expected local extinction due to climate change and novel biotic interactions that has not yet occurred (Alexander et al., 2018).

Through a combination of various experimental setups across the European Alps created by the Disturbance Ecology team of the University of Bayreuth, I address critical gaps in the knowledge of climate change-induced novel biotic interactions in mountain plant communities. We have implemented a downslope translocation experiment (SusAlps) along an elevational gradient in the German Alps to investigate shifts in mountain plant species phenologies in response to changing climate (Manuscript 1). Furthermore, we have exposed mountain plant communities originating from a subalpine grassland just below treeline (Stubai, Kaserstattalm,

Austria, 1850 m a.s.l) and an alpine pasture just above treeline (Furka AlpFor, Switzerland, 2440 m a.s.l) to interacting climate change stressors by translocating them down to Bayreuth (Germany, 350 m a.s.l). Our aim was to push those high-elevation plant communities beyond their resistance thresholds, in order to explore novel biotic interactions under severely changing climate (TransAlps ; Manuscripts 2 and 3).

The five manuscripts of this thesis aim to:

i) contribute to the understanding of the interactive effects of warming and drought on various ecological parameters such as plant phenology and reproductive output (Manuscript 1), community composition and temporal turnover (Manuscript 2, 3, 4, 5), as well as niche dynamics and novel biotic interactions (Manuscript 2 & 3).

ii) link the insights of the presented experimental evidence as well as conclusions of various other translocation experiments to partly contrasting observations in unmanipulated, natural mountain plant communities (i.e. ‘extinction debt’).

Key-findings of my lead-authorship manuscripts:

- All subalpine plant species were able to track climate warming by advancing green-up and flowering under the respective warming treatments (Manuscript 1).
- Plant investments into reproductive organs (i.e. flowers) increased with temperature but were dependent on sufficient water availability, highlighting threshold dynamics in the presence of two interacting climate change drivers (Manuscript 1).
- ANPP and species richness showed comparable threshold dynamics in response to interacting warming and drought along the downslope elevational gradient (Manuscript 1).
- Local loss of native mountain species due to experimentally induced abrupt climate change was followed by the colonization of novel lowland species, particularly after a severe Central-Europe-wide drought year, highlighting the interaction of climate change drivers (Manuscript 2).
- The temporal lag between local losses of native mountain species and colonization by novel lowland species indicated direct ‘environmental filtering’ as opposed to the assumed ‘biotic competition’ (Manuscript 2).
- Plant functional traits in translocated mountain plant communities shifted from resource-conservative growth towards resource-acquisitive growth (Manuscript 3).

- Mountain plant community native species lacked the plant functional traits (e.g. taller growth, fast reproduction) to quickly fill drought-induced, unoccupied niche space, instead allowing the colonization of novel species (Manuscript 3).
- Measures such as ‘functional richness’ should be handled with care, as the observed increases in functional richness were mainly attributable to the plant functional trait values of novel lowland species of likely threatening pristine mountain plant communities (Manuscript 3).

Zusammenfassung

Berg-Ökosysteme und die hohen geografischen Breiten der nördlichem Hemisphäre sind besonders stark und schnell vom global beobachteten Temperaturanstieg betroffen (Appenzeller et al., 2008; Box et al., 2019; Pepin et al., 2015; Schickhoff et al., 2022). Extremwetterereignisse wie lang anhaltende Dürren sind bisher seltene Phänomene in der alpinen Stufe (Körner, 2021), während diese in den Höhenlagen der montanen und subalpinen Stufe in Zukunft zunehmen werden (IPCC, 2021; Spinoni et al., 2018; Stephan et al., 2021). Deshalb sind Pflanzengemeinschaften der subalpinen Stufe besonders vulnerabel gegenüber dem zukünftigen Klima. Die Vulnerabilität der alpinen Stufe wird sich bis Mitte dieses Jahrhunderts sehr sicher auch erhöhen (IPCC, 2021).

Die Ergebnisse verschiedener Verpflanzungs-Experimente (Alexander et al., 2015; Berauer et al., 2019; Cui et al., 2018; De Boeck et al., 2016, 2018; Haider et al., 2022; Nomoto & Alexander, 2021) und Modellierungen (Engler et al., 2011; Hülber et al., 2016; aber siehe Dagnino et al., 2020) deuten darauf hin, dass ein starker Artenwechsel und lokaler Artenverlust der Bergpflanzen unter einer Klimaerwärmung stattfinden wird. Dies ist insbesondere verstärkt, wenn Erwärmung mit Dürre oder einer mechanischen Störung des Oberbodens einhergeht. Bisher haben viele Studien ein besonderes Augenmerk auf Berggipfel gelegt (Steinbauer et al., 2018), was dazu führte, dass Ergebnisse zu neuen biotischen Interaktionen in niedrigeren Höhenlagen in der Literatur unterrepräsentiert sind.

Unter natürlichen Bedingungen, also ohne experimentelle Manipulation, wurden jedoch bisher keine lokalen Artenverluste in Berg-Ökosystemen beobachtet. Die meisten Langzeit-Beobachtungen haben bisher einen Anstieg der Artenzahl (Steinbauer et al., 2018), eine Thermophilisierung der Arten (Lamprecht et al., 2018) und selten einer Abnahme der Abundanzen heimischer Arten (Rumpf et al., 2018; Steinbauer et al., 2020) aufgezeigt. Dieses durch den Klimawandel und neue biotische Interaktionen erwartete, jedoch ausbleibende Aussterben von heimischen Arten wird als 'Aussterbe Schuld' (engl. 'extinction debt') beschrieben (Alexander et al., 2018).

In dieser Arbeit behebe ich kritische Wissenslücken in Bezug auf durch den Klimawandel bedingte neuartige biotische Interaktionen in Bergpflanzengemeinschaften. Wir haben ein Verpflanzungsexperiment entlang eines Höhengradienten in den deutschen Alpen durchgeführt (SusAlps), um Verschiebungen in der Phänologie von Bergpflanzenarten zu untersuchen (Manuskript 1). Darüber hinaus haben wir Bergpflanzengemeinschaften aus dem Stubai Tal,

gerade unterhalb der Baumgrenze (Österreich, Kaserstattalm, 1850 m ü. M.) und dem Furka Pass, gerade oberhalb der Baumgrenze (Schweiz, AlpFor, 2440 m ü. M.) in einem Verpflanzungsexperiment nach Bayreuth (Deutschland, 350 m ü. M.) verwendet, um Artengemeinschaften über ihre Resistenzschwelle hinaus zu bringen und neuartige biotische Interaktionen unter dem Einfluss von Klimawandelstressoren zu untersuchen (TransAlps ; Manuskript 2 und 3).

Die hier vorgestellten Manuskripte tragen bei:

i) zum Verständnis der interaktiven Wirkung von Erwärmung und Trockenheit auf verschiedene ökologische Parameter wie Phänologie und Reproduktionsleistung (Manuskript 1), Gemeinschaftszusammensetzung und zeitliche Stabilität (Manuskript 2, 3, 4, 5) oder Nischendynamik und neuartige biotische Wechselwirkungen (Manuskript 2 &3).

ii) die Erkenntnisse der vorgestellten Manuskripte und die Schlussfolgerungen verschiedener anderer Verpflanzungsexperiment mit kontrastierenden Beobachtungen in natürlichen, unmanipulierten Bergpflanzengemeinschaften zu verknüpfen (‘extinction debt‘).

Meine Hauptergebnisse der verschiedenen Erstautoren-Manuskripte sind:

- Alle subalpinen Arten konnten sich auf die experimentell manipulierten Klimaveränderungen anpassen (`climate tracking`) indem sowohl die Blattentwicklung als auch die Blüte früher einsetzte (Manuskript 1).
- Investitionen in die Fortpflanzungsorgane nahmen mit der Temperatur zu, waren aber von der Wasserverfügbarkeit abhängig - was die Schwellendynamik in Gegenwart von zwei interagierenden Faktoren des Klimawandels (Erwärmung und Dürre) verdeutlichte (Manuskript 1).
- Produktivität und Artenzahl zeigten eine vergleichbare Schwellendynamik bezüglich der Interaktion von Erwärmung und Dürre entlang des Höhengradienten (Manuskript 1).
- Auf den lokalen Verlust einheimischer versetzter Arten folgte nach einem schweren mitteleuropäischen Dürrejahr die Ansiedlung neuer Arten aus dem Tiefland. Dies

verdeutlicht abermals die Wechselwirkung zwischen Erwärmung und Dürre (Manuskript 2).

- Die zeitliche Verzögerung zwischen den lokalen Verlusten einheimischer versetzter Berg-Arten und der Besiedlung durch neue Tieflandarten deutet auf eine direkte Umweltfilterung im Gegensatz zur angenommenen biotischen Konkurrenz hin (Manuskript 2).
- Bergpflanzengemeinschaften verlagerten ihre traits von ressourcenkonservativen Wachstumsstrategien hin zu ressourcenfordernden Wachstumsstrategien (Manuskript 3).
- Einheimischen, versetzten Bergpflanzengemeinschaftsarten fehlten die traits (z.B. höheres Wachstum, hohe Reproduktion), um trockenheitsbedingte unbesetzte Nischen schnell zu besetzen, was zur Einwanderung neuer Arten führte (Manuskript 3).
- Messgrößen wie "funktionelle Diversität" sind mit Vorsicht zu genießen, da die beobachtete Zunahme des "funktionellen Reichtums" hauptsächlich auf die traits neuartiger eingewanderter Tieflandarten zurückzuführen ist. Dies ist für die unberührten Bergpflanzengemeinschaften im Gebirge sehr wahrscheinlich bedrohlich (Manuskript 3).

1.1 Future directions

Future studies in the field should focus on:

- The long term (10yrs +) effect of experimentally altered climate conditions on mountain plant communities as many experimental studies only capture initial responses while long term effects may be contradicting to initial responses (see chapter 4 for more details).
    - Assumption to be tested: depending on experimental severity, initial responses (e.g. species turnover, changes in AGB production, plastic trait response) are strong while long term effects may either saturate or become accumulative.

- The interaction of climate change drivers (warming and drought) in carefully planned experimental setups to disentangle the individual effects (i.e. control vs warming vs. drought vs warming * drought ; see chapter 4 for details).
    - Assumption to be tested: The so far underexplored interaction of warming and drought in mountain plant communities will lead to highest difference in a given response variable (e.g. species turnover, species specific AGB, leave Nitrogen content, seedmass) compared to the respective control treatment.

- The trailing edge of species in the subalpine belt where climatic stressors, their interactions and novel biotic interactions are expected to be the most severe.
    - Assumption to be tested: Species originating from the subalpine belt are more competitive in upward migration than alpine species as subalpine plant communities have a legacy of higher intra-community competition than alpine plant communities which have a rather facilitative community legacy. Thus, range size compression of alpine plant species is more likely than that of subalpine species.

- The temporal stability of micro habitats in natural mountain plant communities to explore buffering capacities.
    - Assumption to be tested: The temporal stability of alpine micro habitats is too low to buffer climate change permanently - especially once novel lowland species occupy such ‘safe-sites’ and more frequently occurring droughts disrupt the particular microclimatic regime.

- Expanding the insights of accelerated phenology (Manuscripts 1) and local species loss of mountain community native species followed by the colonization of novel lowland species upon downslope translocation (Manuscript 2) by exploring natural dispersal barriers of lowland species into mountain plant communities (i.e. planting focal lowland species or sowing seeds of lowland species into existing mountain plant communities). Ideally, the latter approach is combined with a climate change treatment (e.g. drought shelter) to simulate realistic future scenarios (i.e. novel climate interacting with novel biotic competition). Furthermore, such an experimental setup could include microtopographical features (i.e. hollows and hillocks) and differing number of native species present (i.e. different levels of facilitation ; differing species richness or differing functional diversity) to test particular buffering capacities of mountain slopes. An important asset to such an experimental approach would be take the special role of graminoids vs. forbs during the colonization process into account, as many graminoids in our experiments have shown to draw significant benefits (e.g. high seed output, high survival rate, high plasticity) from downslope translocation.
    - Assumption to be tested: Climate change induced gaps in mountain plant communities will be filled by novel lowland species more successfully as their dispersal and growth traits are more competitive than those of community native mountain species. In particular, species with high seed output (such as graminoids and cosmopolitan forbs) will be most successful in a permanent establishment in mountain plant communities. Furthermore, it is likely that microtopographical heterogeneity will decrease dispersal barriers and thus facilitate establishment for such opportunistic novel species.

- Expanding the insights of morphological plant traits (SLA, LDMC, vegetative Height ; Manuscript 3) with a detailed analysis on individual-specific leaf-stoichiometry (i.e. C:N:P of warmed and control plant individuals). Such an approach would offer a mechanistic understanding on leaf economics and would thus provide evidence for a potential abiotic niche expansion for warmed mountain plant communities (see chapter 4.1 for details).
    - Assumption to be tested: Besides changing their morphological plant traits towards a more resource acquisitive growth, species of warmed mountain plant

communities also make use of an abiotic niche expansion by changing their physiology (e.g. higher leave C:N due to higher soil nutrient availability).

2 Thesis background

In this introduction I will first describe the effects of climate change on plant communities in mountain regions, with special focus on the European Alps. Second, I will discuss the known and controversial effects of climate change on mountain plant communities with special regards to insights from experimental translocation studies simulating potential future climate, followed by insights from observational studies in natural mountain plant communities.

2.1 Climate change in mountain regions

Recent temperature increases within the central European Alps mirror the pronounced temperature increases in high latitudes of the northern hemisphere (Box et al., 2019). In both these regions, various studies have shown a mean annual temperature increase of two to three times higher than the global average (Appenzeller et al., 2008; Brunetti et al., 2009; Pepin et al., 2015) and distinct spatial and seasonal patterns (Hock et al., 2019). Since the early 1980s, but particularly since the 1990s, a substantial warming of 0.5°C per decade has been documented in central European mountain regions (Schickhoff et al., 2022). In the Swiss Alps, a strong warming of 1.8°C has been observed since the temperature minimum during the Little Ice Age in the mid-nineteenth century (Begert et al., 2005). Pepin et al. (2015) reviewed mechanisms leading to elevation-dependent warming and identified various challenges in gaining accurate measures across larger scales, such as the lack of long-term data at high elevation and landscape heterogeneity.

Moreover, the cautious use of the term ‘temperature’ needs to be highlighted. Deviations in measurement locations (e.g. the ‘gold standard’ at 2m above ground, canopy- level, or leaf-level) can cause significant differences in measured and reported temperatures. Furthermore, the temporal reference period of measurements matters (e.g. mean annual temperature (MAT) versus growing season temperature). Thus, determining the ‘temperature a plant experiences’ *sensu* Körner (2021) and Körner & Hiltbrunner (2018) becomes very important but difficult when discussing climate change effects on different mountain plant communities (for example varying in canopy structure) across different experimental sites (for example varying in growing season length) like those presented in this thesis. We decided to use ‘growing season temperatures’, measured at 2m height in the years of experimental exposure for all of the here reported findings (presented manuscripts) as this is the ecologically most meaningful and was the most consistent dataset across sites.

Temperature increases will drive changes in snow cover, mainly its onset in autumn and snowmelt in spring. Changes in snow cover duration can affect mountain ecosystems indirectly by changing the seasonal water budget (Wieser et al., 2008), or albedo feedback loops affecting the surface energy balance (Harte, 2005). The most obvious direct effect of a shorter snow cover is an earlier onset of phenological cues and therefore an extension of the growing season. Changes in growing season length are expected to be most pronounced in regions with strong interannual seasonality (Pau et al., 2011). Higher winter and spring temperatures have been shown to advance phenological cues (Zhao et al., 2020) leading to an earlier start of the growing season, while warmer autumns delay the end of the growing season (Box et al., 2019; Inouye, 2008); both processes elongate the theoretically possible window of growth. Late frost events may counterbalance the benefits of a longer, temperature-induced growing season (Liu et al., 2018; Wipf et al., 2009). However, most high elevation plant species, such as *Geum montanum* L., have adapted to late frost events by spreading vulnerable phenological stages (i.e. the open flower; BBCH 60+) across time among individuals of the same species to ensure that only a minority of individuals are affected by sudden cold spells in the spring (Körner, 2021).

Growing season precipitation and especially the precipitation regime (i.e. not the total amount (MAP) but the temporal distribution) are benchmarks for studying a mountain plant communities' vulnerability to climate change (Müller & Bahn, 2022). Extreme weather events, such as heatwaves and droughts, are rarely observed in alpine ecosystems (Körner, 2021), while they will likely become more frequent at mid elevations in the subalpine and montane belt (IPCC, 2021; Spinoni et al., 2018; Stephan et al., 2021). The study $\mathrm{EDII}_{\mathrm{ALPS}}$ (European Drought Impact report Inventory) by Stephan et al., 2021 is one of the first transnational central European studies researching the impact of drought in mountain ecosystems. It has reported a substantial increase in drought vulnerability in the last two decades. The study focused on productivity and crop cultivation and exposed the need for a similar approach to study grassland communities and their temporal stability. Moreover, experimental evidence has shown that drought effects during the mid-season may suppress plant growth of mountain plant communities (Liu et al., 2012; Yang et al., 2018; Zeiter et al., 2016) and may decrease the reproductive fitness of mountain species (Cornelius et al., 2013; Dunne et al., 2003; Manuscript 1).

Yet, most of the climate change drivers described above are already affecting species specific abundances and will likely affect competitive outcomes of biotic interactions in the near future. Mountain plant communities' vulnerability to climate change-induced species turnover, namely the colonization of novel lowland species, is still under debate with contrasting conclusions.

2.2 Effects of climate change on mountain plant communities

In the last 3.5 years, I have found a strong discrepancy between the findings of experimental studies (e.g. translocation experiments), mountain species distribution modelling, and field surveys in mountain plant communities. It is possible that there are even two 'schools' of scientists looking at mountain plant communities from different spatial and temporal angles or across scales, using different methodologies, and thus finding contrasting signals. In the following three chapters I would like to expose these contrasting findings, followed by a discussion on experimental artifacts. I will highlight the demonstrated insights and expose discrepancies in a later chapter of this thesis (see Chapter 4, 'Synopsis, research gaps and upcoming research frontiers').

2.2.1 Insights from experimental studies with special focus on translocation experiments

Early climate change manipulation studies at the end of the last century have found significant shifts from forb dominated to shrub dominated subalpine Rocky Mountain meadows under experimental warming (Harte & Shaw, 1995). Their study at the *Rocky Mountain Biological Laboratory* was followed by various studies building on the initial warming manipulation by adding a gradient analysis and snowpack manipulations (see Methods in Dunne et al. (2003)) to study flowering phenology (Dunne et al., 2003) or various ecophysiological and diversity metrics (Harte, 2005) under experimental warming. At the same time increasing computational power allowed first attempts of species distribution modelling under climate change (Austin, 1987) which revealed detailed species' sensitivity to climate change (Thuiller, Lavorel, et al., 2005) and novel biotic interactions (Thuiller, Richardson, et al., 2005). Such models, built to predict future outcomes, quickly offered findings showing a high rate of replacements for mountain community native species by novel species migrating upwards from lower elevations under climate warming (Engler et al., 2011; Hülber et al., 2016; but see Dagnino et al., 2020).

These findings from early climate manipulation studies and species distribution models are generally supported by numerous, recent case studies using various experimental approaches to simulate climate change (e.g. warming, drought or the interaction of both). There are various approaches to increase temperature in experimental setups. Common approaches are to use open top chambers (OTC, i.e. ITEX, 1990) or heat radiating devices (i.e. IR heating lamps above ground, i.e. Kreyling et al. (2019). Another approach is a 'space-for-time' approach, which is either implemented by translocation experiments (intact 'turfs', 'plant-soil monoliths' or 'mesocosms') or experiments being set up along elevational gradients with the same treatment on different elevations ('experimental macroecology'). In the following, I will review and summarize key insights from manipulative experiments exploring the impact of climate change on mountain plant communities.

In a short-term downslope translocation experiment in the Swiss Alps from above treeline to below treeline, heat spells in combination with drought had strong effects on the aboveground productivity of alpine plant communities, while heat spells alone had no significant impact (De Boeck et al. 2016). These observations match my own results from Manuscript 1 & 4 of this thesis (see further down). Cui et al. (2018), Haider et al. (2022) and Volk et al. (2020) found that increase in aboveground productivity correlated with increase in temperature and peaked at sites with medium temperature increase and no water limitation. These insights highlight the adaptation of high elevation species to high canopy temperatures at daytime and the often-ignored atmospheric decoupling of air and tissue temperature (*sensu* Körner & Hiltbrunner, 2018). Further De Boeck et al. (2016) demonstrated that proportional contributions to above ground biomass (AGB) increased for graminoid species, while it decreased for forbs under warming interacting with drought, the discrepancy likely due to dissimilarities in leaf anatomy (forbs with higher SLA compared to graminoids suffered more from drought because water and nutrient economy was too acquisitive in forbs exposed to drought while a conservative leaf-economy in graminoids led to post-drought survival). A follow up study by De Boeck et al. (2018) (see also Collins et al. 2022; Klanderud et al. 2015; Rosbakh et al. 2017) exploring legacy and recovery effects of the same translocated plant communities found a forb-depressed-state dominated by graminoid species; this highlighted species turnover and dominance shifts among community native species driven by interacting climate stressors.

An open-top chamber-based study took temporal species turnover (three consecutive years) into account and found that experimental warming of mountain areas (White Mountains, California, USA) resulted in less diverse plant communities and dominance of thermophilic species (Oldfather & Ackerly (2019). In another study, competitive pressure among southern Norwegian plant communities increased with increasing temperatures, leading to the survival of dominant, mostly graminoid species and loss of subordinate, mostly herbaceous species (Olsen et al. 2016). Cui et al. (2018) highlighted that climate change beyond a species' present climatic range (i.e. +4K as the strongest translocation treatment for the focal species *Viola biflora* L.) significantly constrained population growth rates and led to mortality rates of 90-100% in the Tibetan Plateau. Here, the main reason for the local extinction of *V. biflora* was competitive pressure of both the native and the novel plant community that both were able to draw significant benefits from a warmer climate (i.e. dense AGB). A strong negative relationship was found between climate warming and population growth of four focal species (*Plantago alpina* L., *Anthyllis alpestris* L., *Trifolium badium* SCHREB. and *Campanula scheuchzeri* VILL.) in a downslope translocation experiment in the Swiss Alps (Nomoto & Alexander 2021). If warming and novel competitor presence interacted in the latter study, the negative effect on population growth was even stronger. These findings are supported by species' tendencies found in a previous study, where four different alpine forb species (Anthyllis vulneraria ssp. *Alpestris* L., *Plantago atrata* HOPPE*, Pulsatilla vernalis* L. and *Scabiosa lucida* VILL.) experienced increased competition within their maternal community under various experimental warming scenarios (Alexander et al. 2015). Furthermore, changes in biotic interactions among native species would likely be disrupted by the presence of novel lowland species under climate change. Alexander et al. (2015) exposed the above mentioned four alpine forb species to a combination of a warmer climate and the presence of novel competitors (a lowland plant community), simulating a species inability of climate tracking to higher elevations ('migration failure'). In this scenario, there was a strong effect of novel competitors on the overall performance of native species, indicated by a reduction in native species survival, productivity, and flowering. These effects were mainly explained by a strong functional dissimilarity (SLA, LDMC, LA, LMA & height) between the low and mid elevation community, demonstrating the important role of functional richness in addition to species richness. This finding aligns with model-derived insights (Urban et al., 2012) that predict the strongest increases in competitive pressure for species with low phenotypic plasticities occupying narrow abiotic and biotic niches – species such as those from high elevation plant communities (Körner, 2021). Additionally, leaf economic theory suggests that leaf investments that are not economically competitive will be eradicated through time (Reich, 2014; Wright et al., 2004). Several experimental studies (Manuscript 3 of this thesis; de Bello et al. 2013; Rixen et al. 2022; Stanisci et al. 2020; van Zuijlen et al. 2021) found empirical evidence of shifts in resource-use strategies towards a more opportunistic, resource acquisitive growth (i.e. higher stature, decreased LDMC, increased SLA) under an abiotic niche expansion as a result of climate change in mountain plant communities. Shifts in resource-use strategies of the above mentioned studies were found to be due to plastic responses of native species (Rixen et al., 2022; Stanisci et al., 2020; van Zuijlen et al., 2021) or species turnover (i.e. the colonization by novel species ; Bjorkman et al. (2018)). Henn et al. (2018) emphasized high plasticity in leaf functional traits as mechanistic basis for persistence, as high plasticity enabled species to converge their trait values towards a recipient plant community's mean value in a translocation experiment. They also highlighted that the high degree of phenotypic plasticity found in single PFTs (e.g. LA. SLA, LDMC, N:P and C:N) of alpine species did not correlate to intraspecific variation of the same PFT at a regional scale (Henn et al., 2018).

Even though many species of high elevation plant communities reproduce clonally (Körner, 2021), sexual reproduction of plants is evolutionary crucial to adapt to novel climates and biotic interactions. It has been shown that climate warming can indirectly affect plant reproduction through changes in plant-pollinator interactions (Richman et al., 2020) or through divestments into reproductive output once warming passes a temperature threshold (Manuscript 1 and Cornelius et al. 2013; Dunne et al. 2003). Another study explored the impact of novel competitors on native plant communities, focusing on shifts in phenological cues of the model species *Lactuca serriola* L. (Alexander & Levine 2019). They found the presence of the species *L. serriola*, a ruderal cosmopolitan species with high phenotypic plasticity, to be decisive whether or not native species survived. The strong adaptive capacity of *L. serriola* to a warming climate led to advanced phenologies compared to native species and showed a strong neighbor suppression potential (see also Giejsztowt et al. 2020). The study highlighted the importance of considering phenological plasticities to understand future outcomes of species competition, as novel, highly plastic species are more likely the suppressors of native species. This is in line with a translocation experiment in alpine and subalpine grassland turfs in southern Norway, where native species that had adapted to colder temperatures lacked PFT expressions to effectively compete with the increasing seedling emergence of novel species (Meineri et al. (2020). However, a translocation study in the European Alps found that climate warming alone did not result in an increased invasibility of an alpine plant community under the presence of a lowland colonizer (*Senecio inaequidens* DC. ; Haider et al. (2022)). Rather, it was the combination of soil disturbance and climate warming that favored the survival, growth and reproduction of the colonizing species (Haider et al. (2022). Similar results of soil disturbances favoring the colonization of novel species have been found in subarctic meadows (Milbau et al. (2013) and Lembrechts et al., (2016, 2018)). The MIREN network (Mountain Invasion Research Network; www.mountaininvasions.org) concluded that oftentimes, colonization resistance was not explained by extreme conditions in mountain sites (e.g. ‘unfavorable’ climate or substrate) but rather by pathways such as soil disturbances, as novel species in their study were cosmopolitan species with broad climatic tolerances (Alexander et al., 2011).

Overall, the studies reviewed above support the conclusion that high elevation plant communities are vulnerable to climate warming with respect to productivity and species turnover. Most notable is the importance of interacting climate change drivers, i.e. warming in combination with drought or with soil disturbances.

2.2.2 Insights from long-term field surveys in mountain plant communities

In a large scale synthesis study across the tundra biome, including European and North American alpine sites, Bjorkman et al. (2018) observed temperature-related plant functional trait shifts towards taller and more resource acquisitive plant communities. The observed shifts were mainly due to species turnover (i.e. particularly the colonization by novel species from warmer environments). In contrast to this large-scale study, there are only a few detailed case studies reporting the expected species replacement in natural (not experimentally altered) mountain plant communities by novel species from lower elevations under a warming climate. A study by Kudo et al. (2011) found that the colonization of a community-novel dwarf bamboo negatively influenced grassland species richness in the Taisetsu Mountains, Japan. Rumpf et al. (2018) found species-specific results in a large scale historical relevés study across 183 plant species present on 1.576 plots in the European Alps. While the majority of species in the latter study (n=51) experienced both an increase in range size and abundance during the last decades (first survey before 1970; resurvey in 2014 & 2015), range size and abundance decreased for 33 species (~ one fifth of total species present). Interestingly, these 'losing' species were cold-adapted species, while the 'winning' species were thermophilic and thus better adapted to changes in climate. Further, the strongest changes in range shifts and species abundances were found at lower elevations, suggesting that the trailing range edge was most vulnerable to novel competitive interactions and climate change – yet not experiencing local extinctions.

At the GLORIA (Global Observation Research Initiative in Alpine Environments) site Schrankogel in Austria, Steinbauer et al. (2020) observed a decline in native species cover and native species richness over time. Importantly, they found that open spaces due to native species loss were not filled immediately, indicating abiotic factors dominating biotic interactions: climatic unsuitability was driving the loss of native species, rather than competitive pressure by novel species. Interestingly, there was a shift towards warmth-demanding and drought-tolerant species (thermophilisation), especially at the trailing range edge at lowest elevation (see also Lamprecht et al., 2018). Across 302 European mountain summits part of the GLORIA network, Steinbauer et al. (2018) found contrasting signals. The meta study found strong increases in mountain top species richness during the last 145 years that correlated with a simultaneous temperature increase, which had not yet reduced native species richness. Here, the authors concluded that a potential explanation of increasing species richness on Europe's mountaintops might be a ‘transient phenomenon’, so far hiding an important aspect of climate change in high elevation ecosystems. The lack of expected native species loss due to abiotic (mainly temperature and precipitation regimes) and biotic (novel-competitor interactions) changes is currently discussed as the so called ’extinction debt’ (see Tilman et al. 1994 and Figueiredo et al. 2019).

2.2.3 Extinction debt

The concept of ’extinction debt’ is associated with local species extinctions expected to happen as consequence of climate warming (as suggested by various experimental studies and species distribution modelling) but not happening yet (see Alexander et al., 2018). The extinction debt observed in mountain regions may be explained by the following four aspects:

I. **Time lags in dispersal and establishment of novel lowland species:** Rumpf et al. (2018) observed that range shifts of all 183 plant species present on 1.576 plots in the European Alps lagged behind climate warming. Further, they found that the strongest changes in range shifts and increases in species abundance were at lower elevations, highlighting the vulnerability of areas with interacting climate stressors and novel biotic competitors (and human disturbances as occasional additional stressors). Dispersal lags describe a species limitation in keeping track with changing climates. The ability to track climatic changes varies across species, likely even across individuals, and is not necessarily binary (in the sense of ‘able to track’ vs. ‘unable to track’) but rather complex and dependent on PFTs such as reproductive output, seed size and seed dispersal (see manuscript 1 of this thesis; Parolo & Rossi, 2008). Establishment lags describe the lag between novel species’ propagule presence at higher elevation and successful establishment. It has been shown that outside its maternal environment, mountain species establishment is almost neglectable (Basto et al., 2018; Haynes et al., 2021) because of high mortality rates (Milbau et al., 2013) and novel species abundances being very likely far away from ‘carrying capacities’. Thus, local extinctions hinge on the competitive success of novel lowland species.

II. **Demographic inertia resulting in extinction lags:** De Witte et al. (2012) presented the longevity of clonal mountain specialists in combination with sexual reproduction as a key aspect of high mountain species inertia and resilience to today’s climate change. The study identified genets older than 4000 years (e.g. *Carex curvula* All. and *Dryas* *octopetala* L.) that have been exposed to strong climatic fluctuations (such as the 17th century little Ice Age and current anthropogenic warming) and demonstrate a high level of inertia and persistence. Furthermore, demography of the studied species was skewed towards younger individuals, indicating successful sexual reproduction (De Witte et al., 2012). These findings align with various modelling approaches (Dullinger et al., 2012; Hülber et al., 2016) and point towards lags in extinction, mainly at the trailing range edge, due to the long lifespan of an individual. While generalities on mountain plant species cannot be drawn from results of the above mentioned species (e.g. opposing results for *Ranunculus glacialis* found in Prock & Körner 1996), these findings nevertheless provide a reasonable explanation for lags in extinction.

III. **Topography-driven isolation:** Topographic isolation likely influences the colonization success of novel lowland species into mountain plant communities. Due to the conical shape of mountains, habitat connectivity is limited (Elsen & Tingley, 2015; Jentsch & Beierkuhnlein, 2003). As an example: a lowland novel species tracks climate change by migrating to higher elevations and either finds an unoccupied niche or co-exists with native species (e.g., through facilitative amelioration). Further upward migration, however, could be a constraint, as similar habitat niches (with similar temperatures and substrate) may only be found on the opposite side of the valley, resulting in a migratory dilemma (topography-driven isolation *sensu* Steinbauer et al. 2016). This assumption is supported by studies showing that a majority of mountain species did not successfully fill their potential abiotic niche post glaciation (Dullinger, Willner, et al., 2012) or the monotonic increase in percent endemism with increasing elevation (Steinbauer et al., 2016).

IV. **Landscape heterogeneity in high elevation ecosystems:** The decoupling of surface temperatures and atmospheric conditions has been shown by Körner & Hiltbrunner (2018). This becomes particularly important in mountain grasslands with small, statured species growing close to the ground. Scherrer & Körner (2011) have shown that the variation in mean seasonal temperatures of plant meristems can be up to 8-9K within one alpine slope. Consequently, nearby thermal niches in the alpine environment exceed the worst climate change scenarios. These insights are fundamental in understanding species responses to climate change and likely offer a potential explanation for the observed high resilience (‘extinction debt’) of natural mountain plant communities.

Körner & Hiltbrunner (2021) have addressed the ‘robustness’ of the alpine flora under climate change by placing special emphasis on the high variability in micro-environmental conditions in proximity to an individual’s current location. They concluded that the strong landscape heterogeneity in high elevations ‘make the alpine world one of the safest for plants when the climate changes’, as individuals will have the opportunity to migrate into a nearby escape habitat. This is novel and in contrast to the generally presumed and very simplified assumption of a species’ upward migration, which is, at some point, limited in case of mountainous regions.

2.2.4 Experimental constraints and possible artifacts in manipulative studies with a special focus on translocation experiments

Non-manipulative experiments, such as repeated vegetation surveys, can give valuable insights about natural changes of the past but do not offer the possibility to simulate future climate conditions. Furthermore, observations from the past cannot easily be translated into future scenarios, since underlying causes of observed changes cannot be derived due to the lack of true controls, plus due to future environmental changes being potentially different from past environmental changes.

One powerful way of investigating future plant community responses to climate changes and their underlying mechanisms is by using manipulative experiments (Kreyling & Beier, 2013) such as downslope translocation experiments (Yang et al., 2018), which passively simulate the warming of plant communities. In such experiments, scientists make use of so-called ‘control treatments’, which receive no alteration in the respective treatment, and compare them to similar plant communities receiving a particular treatment (e.g. warming, drought or both). Nevertheless, translocation studies are constrained to a smaller scale compared to vegetation surveys carried out under natural conditions, as manipulative treatments cannot be applied on larger scale grasslands or entire mountain slopes, for instance. Thus, conducting manipulative ecological experiments like translocation experiments is always constrained by tradeoffs between logistical limits, feasibility (e.g. manpower and money) and ecological realism. Five of the major constraints of translocation experiments are outlined below:

I. The most important consideration in setting up a manipulative experiment, particularly a translocation experiment, is the imagination of the planning scientists to avoid pitfalls. For example, in a recent meta-analysis of various drought experiments, Kröel-Dulay et al. (2022) depicted how drought simulated through manipulated experiments had weaker effects on plant communities than naturally occurring droughts in observational studies. Results from small-scale drought treatments of many studies are likely affected by the surrounding landscape not receiving a drought treatment (‘island effect’ *sensu* De Boeck et al. 2015) and the fact that drought severity is not only influenced by the reduction in precipitation but also influenced by temperatures, canopy humidity and cloud cover (Kreyling et al., 2017).Yang et al. (2018) found strong differences in species richness and dominance shifts within the same plant communities when using open top chambers (OTCs), downslope translocations, or observations along an elevational gradient, demonstrating the importance of choosing the appropriate experimental setup to tackle particular research questions.

II. Translocating focal species or entire plant communities up- or downslope affects several abiotic and biotic factors. Not only are abiotic factors such as temperature, precipitation, or photoperiod changed, but so are biotic factors such as intraspecific and interspecific competition and interactions with pollinators or herbivores. If experimental setups do not account for the single effects (fully crossed, multifactorial setups), disentangling cause and effect becomes problematic.

III. Responses of plant communities will likely vary with experimental duration (Chapin III & Shaver, 1996; Kröel-Dulay et al., 2022; McLaren & Turkington, 2011, Manuscript 4). While short-term experiments (e.g. three years due to funding constraints) may yield insights to direct effects of translocation, ecologically important, long-term effects such as resilience or legacy effects (Scheffer & Carpenter, 2003; Walter et al., 2013) may go undetected. This is particularly important as previous-year precipitation and productivity of grasslands have shown to control a significant fraction of current-year production in long-term drought manipulation experiments across the globe (Isbell et al., 2015; Sala et al., 2012). The results of short term studies can therefore only be interpreted as ‚transient results‘ that depict snapshots in time.

IV. Species climate tracking naturally occurs on an individual species level (Ammann, 1995) or even on the level of single genotypes (Alexander et al., 2015; Haider et al., 2022). Thus, the common approach to translocate entire plant communities (which includes translocating maternal soil and its microbiota) is a rather unrealistic approach to simulate climate change. Another approach involves planting single focal species into novel plant communities, either upslope to simulate species-specific climate tracking, or downslope to simulate the inability to migrate due to lowland species interference (Alexander et al., 2015). However, this experimental setup lacks the natural temporal dynamics of native and novel species migration, including all competitive establishment and persistence pressures. Additionally, conclusions made on single focal species cannot easily be applied to the responses of other species, leading to the inability to form generalizations (Nomoto & Alexander, 2021).

V. Sexual reproduction of mountain plant species can vary significantly from year to year (Diemer, 1992; Dunne et al., 2003; Körner, 2021), once again demonstrating the importance of long-term experiments to account for interannual variation in response variables. Furthermore, downslope translocation studies simulate the abrupt absence of maternal species seed rain due to the lack of such species in the novel matrix. Thus, sexual reproduction is constrained to the reproductive output of translocated individuals growing on a small scale (e.g. a mesocosm 30cm in diameter) in comparison to novel climate native plant communities with larger population sizes in the matrix. This is especially important since establishment of community native seedlings may be low due to highly competitive lowland species with a higher reproductive output (Alexander & Levine, 2019; Guittar et al., 2020; Meineri et al., 2020).

On one hand, insights derived from manipulative experiments hinge on the above-mentioned aspects, often unintentionally affecting findings and thus complicating a direct transfer of conclusions to natural plant communities. On the other hand, such manipulative experiments provide the unique opportunity to simulate future climate scenarios without waiting until such climatic changes occur under natural conditions. Ultimately, translocation studies offer a great tool to test future outcomes for plant community dynamics experiencing climate change as long as results are interpreted with caution (see Nooten & Hughes 2017 for a detailed review on 'the power of the transplant').

In the next chapter, I will describe the experimental design of the presented studies, introduce my objectives, and summarize all included manuscripts. In Chapter 4 I will detail upcoming research frontiers derived from the presented manuscripts in this thesis and explain how these knowledge gaps may be filled with insights from carefully planned future experiments in mountain ecosystems.

3 Outline and main findings of the studies of this thesis

In the following section, I will first describe the experimental design and detail climatic parameters of the underlying studies. Second, I will present the objectives of this thesis and establish the experimental approach to tackle the objectives and generate fundamental insights for the scientific community and our society. Third, I will summarize the five manuscripts presented in this thesis. Fourth, I will demonstrate the main insights of all five manuscripts followed by a conclusion that leads to the next chapter on upcoming research frontiers.

3.1 Experimental design of presented studies

For the here presented first author papers and Manuscript 4 and 5, I used subsets of the entire SusAlps translocation experiment (‘Sustainable use of alpine and pre-alpine grassland soils in a changing climate’; Grant: Jentsch 2015, 2018 and 2021 UBT: FKZ 031B0516C) illustrated in Fig. 1.

In 2016, we have taken a total of 126 intact plant-soil mesocosms from native grasslands by inserting PVC tubes (⌀=30cm) with a modified jackhammer. Sampling depth was variable depending on soil depth and varying bedrock. Replicates (each n=9) from Furka (Switzerland) and Stubai (Austria) were taken with a depth of 25cm while mesocosms from the other sites were taken with a depth of 40cm. Nine replicates from Furka and Stubai have been reburied at site of origin as climatic control and translocated downslope to Bayreuth. Mesocosms originating from experimental sites in Germany have been translocated to each site with a lower elevation in addition to a climatic control remaining at site of origin.

We have chosen 6 grassland sites across Germany, Austria and Switzerland spanning a vast climatic gradient to explore mountain plant communities and single species response to a novel climatic exposure within and beyond their natural distribution range. Furthermore, these sites have had research infrastructure (e.g. meteorological towers) already established. All sites beside Furka which is an alpine pasture are semi-natural grasslands sites with species adapted to an extensive land use regime (i.e. one to two cuts per year). Geographic and climatic parameters in addition to detailed information on dominant species can be found in Table 1 and the respective manuscripts.

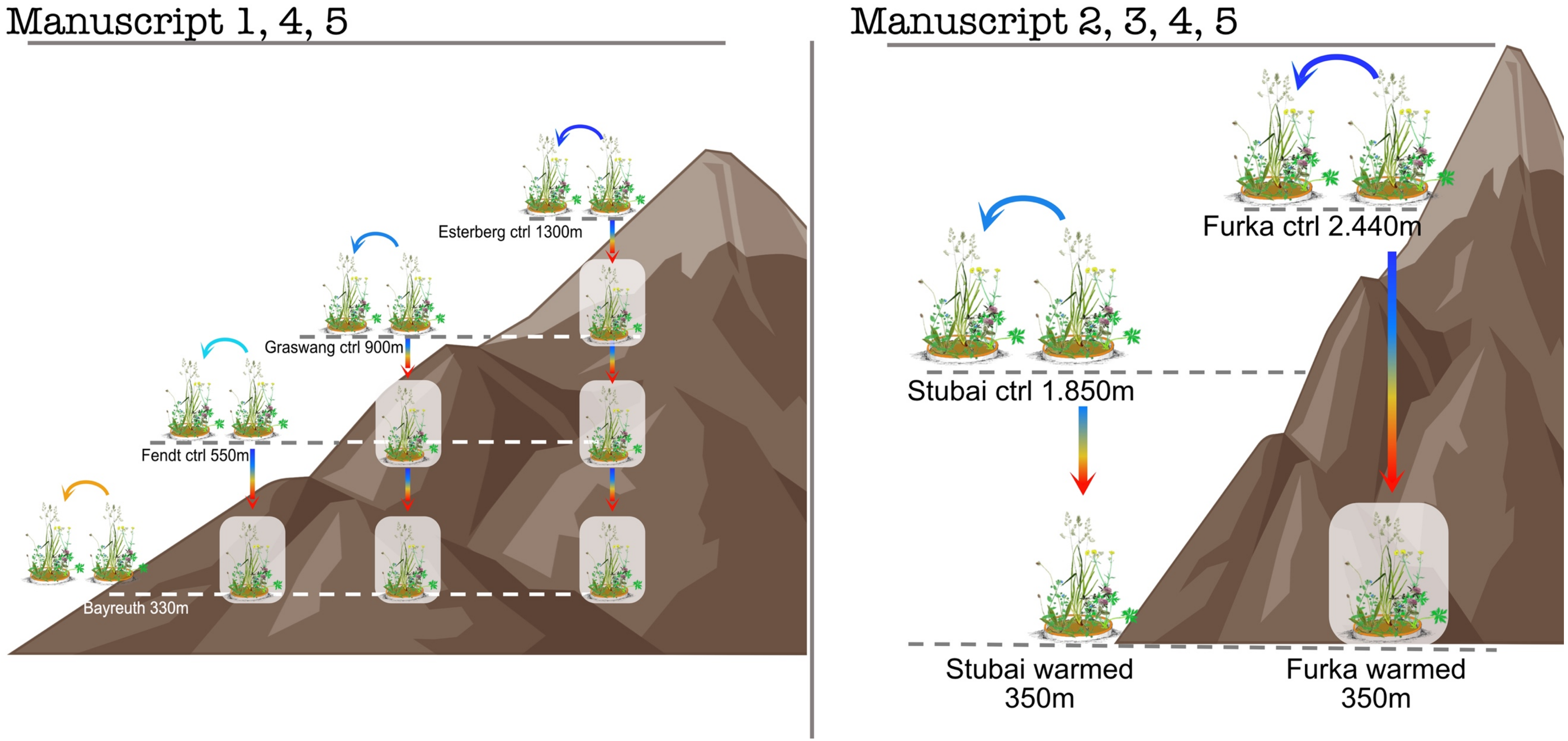

Figure 1 Experimental setup of the research project SusAlps ('Sustainable use of alpine and pre-alpine grassland soils in a changing climate'; Grant: Jentsch 2015, 2018 and 2021 UBT: FKZ 031B0516C) along the elevational gradients. In particular Manuscript 1 used only the elevational gradient of Esterberg downslope to Bayreuth (4 sites) ; Manuscript 2 and 3 used replicates of the two sites Furka (Switzerland) and Stubai (Austria) and their respective warmed plant communities translocated to Bayreuth ; Manuscript 4 used all climatic controls and all translocated plant communities ; Manuscript 5 used only the climatic controls of all sites of origin except Fendt and the respective warmed replicates growing in Bayreuth. Each set of mesocosms is replicated nine times.

Table 1 Geographic, climatic and plant sociological characteristics of the SusAlps study sites in the European Alps. Order from low (Bayreuth) to high (Furka) elevation. Growing season length was site specific. Data shown was calculated from on-site weather station data, with exception of Esterberg.

			Site (Country)					
			Bayreuth (D)	Fendt (D)	Graswang (D)	Esterberg (D)	Stubai (A)	Furka (CH)
Geography	Elevational belt		Colline	Montane	Montane	Subalpine	Subalpine	Alpine
	Coordinates		49°55′16″N 11°34′55″E	47°49′44″N 11°03′58″E	47°34′11″N 11°01′51″E	47°30′59″N 11°09′28″E	47°07′44″N 11°18′19″E	46°34′36″N 08°25′17″E
	Elevation [m a.s.l.]		350	550	900	1300	1850	2440
Climate	Long-term mean	MAT [°C]	8.2	8.6	6.6	NA	3.0	-0.5
		MAP [mm]	724	959	1285	NA	1097	1600
	Ø Growing Degree days [heat sum]	Total	2155	1919	1611	1288	1344	403
		Growing season	885	829	713	549	623	210
	Ø MAT [°C] Exposure	Total	9.6	9.1	7.1	5.7	6.9	0.3
		Growing season	13.2	12.1	11.3	10.7	9.9	8.8
	Ø MAP [mm] Exposure	Total	608	948	1306	1095	1031	1096
		Growing season	166	392	503	424	397	181
Common plants	Plant sociology		Arrhenatheretum elatioris	Arrhenatheretum elatioris	Trisetetum flavescentis	Cynosuretum cristati	Trisetetum flavescentis	Caricetum curvulae
	Common species		*Agrostis capillaris* *Anthoxanthum odoratum* *Festuca rubra* *Achillea millefolium* *Hieracium pilloselloides* *Plantago lanceolata* *Rumex acetosa*	*Alopecurus pratensis* *Dactylis glomerata* *Elymus repens* *Lolium perenne* *Poa pratensis* *Taraxacum sect. Ruderalia*	*Dactylis glomerata* *Festuca pratensis* *Festuca rubra* *Trisetum flavescens* *Pimpinella major* *Plantago lanceolata* *Trifolium pratense*	*Anthox. odoratum* *Cynosyrus cristatus* *Elymus repens* *Festuca pratensis* *Festuca rubra* *Lolium perenne* *Trifolium pratense*	*Agrostis capillaris* *Trisetum flavescens* *Dactylis glomerata* *Carum carvi* *Scorzo. helvetica* *Leontodon hispidus* *Rumex acetosa*	*Carex curvula* *Helict. versicolor* *Nardus stricta* *Luzula lutea* *Campanula barbata* *Homogyne alpina*

3.2 Objectives

As discussed in the introduction, various previous studies have found contrasting signals in natural mountain plant communities compared to experimental studies simulating climate change in mountain plant communities. While strong effects on productivity and species turnover have been observed in experimental studies, natural mountain plant communities have only shown a thermophilisation of species without the loss of native species - likely due to the various demonstrated ‘lags’. So far, most studies have focused on mountain tops and high elevation, alpine plant communities with a lack of knowledge on subalpine plant communities undergoing climate change.

Until now, there is no general agreement on how climate change will affect mountain plant communities in the future. Will mountain plant communities withstand future climate change due to their ‘robustness’ (*sensu* Körner & Hiltbrunner 2021), or will they, as suggested by various experimental approaches, experience tremendous species turnover and loss of native species once a certain threshold is crossed? Adding to the knowledge of mountain plant community dynamics under climate change by performing various experiments and discussing these insights in the light of knowledge derived from natural plant communities is the conceptual framework of this thesis.

The two main objective of this thesis are:

I. to explore the effects of interacting climate change drivers, namely warming and drought, on mountain plant communities using intact plant-soil-mesocosms originating from various experimental grassland sites across the European Alps. Experimentally induced warming via downslope translocation, with the underlying idea of a space-for-time approach, is a great opportunity to simulate future climates and thus study the potential changes in productivity and species community dynamics of tomorrow. Other than biomass production as a main ecosystem function, a special focus was drawn to species-specific reproductive output in addition to the temporal species turnover driven by the loss of native species and the colonization by novel lowland species. Moreover, we measured various plant functional traits (PFTs) of all species within these translocated mountain plant communities to explore a single species’ ability of plastic responses to interacting climate change drivers – a completely underrepresented field of study. Aside from one alpine site (Furka), we translocated various subalpine plant communities (Stubai, Esterberg, Graswang) since many previous studies only focused on mountain tops (above the tree line). This is especially important and fills a knowledge gap, as the most severe climatic and biotic changes are expected at the trailing range edges of many species – which is the subalpine belt in mountain systems.

II. to link insights from various translocation experiments to contrasting observations in natural mountain plant communities ('extinction debt') by using insights of published studies.

To address these objective and advance our understanding of interacting climate change effects on mountain plant communities and novel biotic interactions, we used:

a) a downslope translocation experiment of natural (not planted) plant-soil mesocosms originating from five different sites across an elevational gradient in the European Alps. In this experimental setup, mountain plant communities were exposed to five different climate warming scenarios, mainly varying in temperature and precipitation regimes. The results are presented in Manuscripts 1 through 5, with each manuscript using a different experimental site and exposure time to answer the respective questions. The experiment was established and funded within the framework of the SusAlps project, 'Sustainable use of alpine and pre-alpine grassland soils in a changing climate'; Grant: Jentsch 2015, 2018 and 2021 UBT: FKZ 031B0516C.

3.3 Summaries of manuscripts

In this chapter I will briefly summarize the experimental approach and key insights from the five manuscripts building the core of the presented thesis.

Manuscript 1:

Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming (2021; *Ecosphere* ; doi: 10.1002/ecs2.3661)

Max A. Schuchardt, Bernd J. Berauer, Andreas von Heßberg, Peter Wilfahrt, Anke Jentsch

In Manuscript 1, we monitored a subalpine plant community translocated downslope along an elevational gradient throughout one growing season. We simulated 3 warming scenarios to investigate plant species' abilities to leverage earlier leaf unfolding and flowering into increased aboveground biomass and increased investments into reproductive organs under a warmer climate. We found that advanced phenology at lower elevations, thus under warmer temperatures, led to increased productivity and reproductive performance as long as water limitations did not prevail. Furthermore, we detected biotic competition mechanisms that resulted in a shift towards forb-depressed mountain plant communities, with graminoids benefitting most from increased temperatures and reduced precipitation during the growing season.

Our findings suggest that mountain plant communities' productivity and sexual reproduction are conditional on drought stress, and individual species can draw benefits out of a warming climate as long as a temperature threshold is not crossed and water resources are not severely reduced. Moreover, this study highlights the vulnerability of species rich mountain grasslands to the interaction of two climate change drivers, namely warming and drought.

Manuscript 2:

Drought erodes mountain plant community resistance to novel species under a warming climate (2022, *Arctic, Antarctic and Alpine Research* ; doi: 10.1080/15230430.2023.2174282)

Max A. Schuchardt, Bernd J. Berauer, Justyna Giejsztowt, Andreas v. Heßberg, Yujie Niu, Michael Bahn, Anke Jentsch

In Manuscript 2, we monitored two downslope translocated mountain plant communities for four years with special focus on their novel competitor interactions and found that species turnover increased with time. The local loss of native species was followed by novel species colonization after a year of severe natural drought in 2018. We observed a time lag between the local loss of native species and the colonization of novel species, indicating that abiotic factors (i.e., the interaction of warming and drought) rather than biotic interactions (i.e., interspecific competition) were driving threshold dynamics in mountain communities' resistance to colonization. Moreover, we found stable contributions of single plant functional groups to aboveground biomass: a key measure of ecosystem functioning through time, despite strong changes in species identity that likely indicate compensatory effects of species filling a similar functional niche.

This study highlights environmental filtering as a key mechanism facilitating novel species colonization into mountain plant communities. We showed that climatic extreme events, in addition to the already present warming, destabilized mountain plant communities' structure and provided windows of opportunity for novel species to become established. Our study suggests that colonization by novel species will occur quickly and severely once a threshold of community resistance is crossed.

Manuscript 3:

Increases in functional diversity of mountain plant communities under warming is mainly driven by species turnover under warming (2023, *OIKOS* ; doi: 10.1111/oik.09922)

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Manuscript 3 explores the functional diversity of two mountain plant communities after four years of experimental warming via downslope translocation. One plant community originated from a high elevation alpine pasture Furka (Switzerland, 2440 m a.s.l), while the other plant community originated from the subalpine grassland Stubai (Austria, 1850 m a.s.l). Thus, the experimental treatments differed in climate change intensity and species composition. The experimentally induced climate change scenarios led to an abrupt expansion of the abiotic niche, consequently creating unoccupied niche space. To investigate both single species and plant community responses to the abiotic niche expansion, 1951 species specific leaf trait samples were measured *in situ*.

The growth of plant communities shifted from rather resource conservative to resource acquisitive under both climate change scenarios. Mountain plant communities' adaptive abilities to fill unoccupied niche space was lower for the alpine plant community compared to the subalpine plant community. Moreover, functional richness of both plant communities increased while functional evenness decreased. For the high alpine plant community, shifts in functional richness and evenness were mostly attributable to species turnover, namely the colonization by novel lowland species bringing along plant functional traits of a wider resource use range. For the subalpine plant community, shifts in resource use strategy were partially explained by species specific adaptation (plasticity) to novel climates towards a faster, more opportunistic growth, in addition to novel species colonization. Interestingly, small statured species with a rather conservative resource use strategy were lost under both climate change scenarios because they lacked the competitive ability (PFT expressions such as high stature, high seed-output) to persist.

This manuscript highlights the lack of competitive ability (PFTs) present in mountain plant communities to persist in function and structure under climate change. High colonization susceptibility, in addition to an abiotic niche expansion through global warming, is likely increasing mountain plant communities' vulnerability to climate change. Even though we found increasing functional richness upon downslope translocation, the observed trends should not necessarily be interpreted as advantageous for mountain ecosystems. Underlying functional traits driving the patterns were mainly species turnover driven, consequently threatening mountain plant communities and questioning indices such as functional diversity without linking them to ecosystem functioning and species identity.

Manuscript 4:

Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes (2019; *Arctic, Antarctic and Alpine Research* ; doi: 10.1080/15230430.2019.1618116)

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Manuscript 4 is of particular interest for this thesis since it only builds upon initial responses of the mountain plant communities to abrupt temperature changes, which are studied in more detail and over a longer time span in Manuscripts 1, 2 and 3.

Manuscript 4 explored the initial species and plant community responses to an abrupt, experimentally induced climate change. Herein, we have investigated the aboveground productivity and species composition of 5 mountain plant communities in a downslope translocation experiment after one year of novel climate exposure. We found that changes in aboveground productivity were dependent on the precipitation regime and that dryness

presented the most limitations to productivity. Additionally, we found a consistent pattern of decreasing species richness with increasing climatic distance to the site of origin.
This study emphasizes the extremely low initial resistance of mountain plant species to warming interacting with drought stress, resulting in tremendous decreases in species richness. Surviving native species did not show the ability to compensate for lost native neighbors as indicated by decreases in community aboveground biomass.

Manuscript 5:

Stable plant community biomass production despite species richness collapse under lasting extreme climate – (2022, *Science of the Total Environment* ; doi: 10.1016/j.scitotenv.2022.161166)
Yujie Niu, **Max A. Schuchardt**, Andreas von Heßberg, Anke Jentsch

In manuscript 5, we used a five-year multisite translocation experiment to actively push mountain plant communities past their ecological thresholds to explore communities' temporal stability of productivity. We found that productivity did not change significantly over time despite a strong native species loss. Compensatory growth of persisting native species has been shown to make up for the loss of AGB from native neighbors under all warming and droughting scenarios. However, an exception occurred at the high elevation site, Furka, where only two native species survived until the end of the experiment and novel colonizing species increased their contributions to AGB. Our data suggests that when focusing only on above ground biomass production as a major ecosystem function, most investigated mountain plant communities were stable across time irrespective of the number and types of species in the community. The debate on climate resilience of mountain plant communities should not only focus on simple measures like productivity, since species identity and their respective PFTs (e.g. leaf nutrients indicating fodder quality; reproductive output indicating plant-pollinator interactions and evolutionary adaptation) have shown to change tremendously upon translocation.

3.4 Summarizing discussion and conclusion

The presented thesis aims to explore effects of interacting climate change drivers on mountain plant communities originating from various elevations in the European Alps (objective I) and discuss the insights from various translocation experiments and field surveys in the light of the extinction debt debate (objective II).

I. Effect of interacting climate change drivers on mountain plant community dynamics

Manuscript 1 of this thesis presents evidence of a clear response threshold along the elevational gradient. While mountain plant communities experiencing a +1K temperature increase were able to leverage earlier phenologies (leaf unfolding and flowering) to increase investments into reproductive organs and ANPP, plant communities translocated further downslope, which thus experienced higher temperatures and increasing water limitations, showed the opposite trend. These findings highlight that the combination of warming and drought pushed mountain plant communities past a threshold of resistance, resulting in decreased performances in reproductive output and productivity.

Manuscript 2 found a time lag in the loss of native species and the establishment of novel species upon downslope translocation. While mountain plant communities, irrespective of species composition and site of origin, showed initial resistance to colonization by novel species, the central Europe-wide drought in 2018 led to the thinning of mountain plant communities and created a ‘window of opportunity’ for novel species to colonize. This time lag in novel species colonization demonstrates that abiotic factors, namely the interaction of persistent warming and drought as an extreme weather event, rather than primarily biotic interactions (i.e. competition), can lead to strong and quick changes in mountain plant community composition and dominances. As long as abiotic factors are not creating such ‘windows of opportunity’, inert mountain plant communities show a certain ‘robustness’ to novel competitors.

Manuscript 3 of this thesis demonstrates competitive outcomes after 5 years of novel climate exposure using *in situ* measured plant functional traits (PFTs). We found that only few native species were able to survive for several years until the end of the experiment and that the surviving species showed some plastic capacity to adapt to novel climates. Such surviving species adapted towards a faster, more opportunistic growth strategy to fill available biotic niche space. In addition to the few plastic native species, the gaps in plant canopy were filled by novel, highly competitive species, as illustrated in Manuscript 2, after the drought year 2018.

The strong colonization by novel species led to an increase in functional richness under both warming treatments, because novel species brought along PFTs not present in the native mountain communities (e.g. larger leaves, higher stature).

Manuscripts 1 and 2 demonstrated the importance of interacting climate change drivers pushing mountain plant communities beyond thresholds of resistance, or 'robustness' (sensu Körner & Hiltbrunner 2021). The findings align with other translocation studies that found high mortality rates of native species and legacy effects under the strongest climate change scenarios when plant-available water is limited (Cui et al., 2018; De Boeck et al., 2018; Nomoto & Alexander, 2021). Manuscripts 3, 4, and 5 highlighted that simple measures of ecosystem functioning (e.g. 'productivity') or upcoming and novel measures of functional diversity based on PFTs (e.g. 'functional richness') should be interpreted and handled with caution, as these measures ignore a species' origin (e.g. native or novel to a community) – a fundamental criteria to explore future competitive outcomes under climate change.

Ultimately, our results of all presented manuscripts add to a growing body of literature highlighting the need to transfer insights from small scale experimental studies of various plant communities and ecozones to larger scale (long-term) field experiments focusing on the compound effect of interacting climate change drivers (warming and drought) and disturbances (e.g. soil erosion). An attempt to find such evidence across ecozones is tackled by the 'TransPlant Network' consisting of 17 experiments distributed throughout the Northern Hemisphere, exploring the underlying mechanisms of local extinctions and the colonization by novel lowland species in 88 different subsites of which 5 experimental sites are the once presented in the here presented Manuscripts.

II. Linking insights from translocation experiments to contrasting observations in mountain plant communities

Natural mountain ecosystems have experienced an enrichment in species, mainly due to novel species colonization from lower elevations as the climate has gradually warmed in the past decades. So far, no definite negative effects on native species (i.e. local extinctions) have been observed, creating the 'extinction debt'. Various ideas to explain 'extinction debt' have been explained in a previous chapter (see Chapter 2.2.2). The combination of species longevity and nearby microsite refugia is likely blurring patterns we observe as 'reality' in nature – besides the fact that there is no such thing as a 'control landscape' not affected by climate change. Additionally, establishment lags of lowland novel species colonizing higher elevations enable native species persistence until today. As demonstrated in the chapters above, various modelling approaches and experimental studies have shown tremendous range size compressions and native species losses that are contrasting results to processes happening in nature.

Experimental approaches likely bring the risk of overestimating patterns (see Chapter 2.2.4 on experimental artifacts and constraints), as various response 'lags' prevent observing the real-time impact of climate warming in natural mountain plant communities. Nevertheless, interacting global change drivers (e.g. climate warming and drought in combination with atmospheric nitrogen input, or propagule vectors and soil disturbances from tourism (Liedtke et al. 2020)) will likely push mountain plant communities beyond their thresholds. This is especially threatening at the trailing range edge, which is most exposed to simultaneously occurring global change drivers. To my knowledge, there are no studies on the effect of interacting climate stressors on landscape heterogeneity either in subalpine or alpine plant communities, exposing a major novel research frontier.

The idea of microclimatic heterogeneity creating nearby escape habitats seems to be a promising mountain landscape attribute that increases mountain species' 'robustness' to climate change. Nevertheless, this idea hinges on several criteria with high uncertainties under climate change. First is the question of temporal stability of microhabitats (Lenoir et al., 2017). Assuming that a particular species tracks its optimal abiotic niche into a nearby refuge, such a refuge needs to be climatically stable for several years, if not decades, to ensure enough time needed to establish and reach carrying capacity. The presence of similar microhabitats in close proximity allows for gene flow (niche connectivity), which is the deciding factor for a persistence throughout time or a time lag in local extinction (i.e. short-term climate buffering). Second, the opportunity for alpine species to migrate to a 'refuge' is based on the assumption that there are either unoccupied habitats in close proximity or that such habitats are only occupied by species that do not show a niche overlap with the migrating species, resulting in a weak biotic filter. The latter point is especially crucial to successful migration, as mountain species have been shown to lack competitive trait expressions such as tall stature, fast and opportunistic growth, or a high rate of seed production (see Manuscript 3 and Alexander & Levine 2019). However, interspecific competition within the same abiotic niche (microhabitat) can be counterbalanced by facilitative processes that promote co-existence, which is often found in mountain plant communities (Callaway et al., 2002; Körner, 2021).

Third, important factors influencing a mountain community's 'robustness' in the future include not only the climatic niche (*sensu* Scherrer & Körner 2011 and Körner & Hiltbrunner 2021) of a microhabitat, but also the availability of suitable substrate in suitable climate niches. The shortage of organic soil with increasing elevation has been shown to be a strong limiting factor for species migration (Kulonen et al., 2018). Soil formation processes in higher elevations lag behind climate change simply because soil forming processes are comparatively slow to the pace of anthropogenic climate change (Hagedorn et al., 2019). This constrains the substrate niche for alpine species at the leading range edge towards scree fields or rocky habitats on mountain tops. Moreover, subalpine grassland species are likely establishing at warmer and fertile microhabitats at their leading range edge, taking advantage of the low competition potential of alpine species at their trailing range edge. Thus, mountain species dependent on organic substrate will likely experience the strongest competitive pressure from upward migrating species.

In summary, the entire debate of micro refugia *sensu* Körner & Hiltbrunner (2021) in natural mountain plant communities focuses on high elevation alpine plant communities (above tree line) and assumes temporal stability to create and ensure ‘robustness’. However, the strongest effects on plant-plant competition are expected to occur at the species’ more vulnerable trailing range edge, located at lower elevations where interacting climatic stressors will likely become more important in the near future (IPCC, 2021; Spinoni et al., 2018). Moreover, it has been shown that responses to climate change are species specific resulting in species specific migratory processes (Rixen et al., 2022) with highest turnover rates and local losses of native species at the trailing range edge - experimentally simulated by the strongest climatic treatment (i.e. the lowest elevation recipient site of translocation experiments) (Alexander et al., 2015; Cui et al., 2018; De Boeck et al., 2016; Haider et al., 2022; Nomoto & Alexander, 2021; Olsen et al., 2016). Overall, we lack empirical evidence on temporal plant community stability (with regards to productivity and, more importantly, species persistence) in the transition zones between the montane, subalpine and alpine belt. There is a need for long-term monitoring approaches that consider microhabitats and their temporal stability. On the other hand, waiting for insights from long-term monitoring bears the risk of a major reduction in scope of action as we know that many processes in nature are threshold dependent and irreversible once a threshold is crossed. Thus, to best simulate climate change’s future impact on mountain plant communities, it is crucial to conduct detailed and carefully planned experiments exploring such threshold dynamics of interacting global change drivers. Two fundamental steps into this direction are (i) using standardized protocols (de Bello, (2021); Halbritter et al. (2020); Pérez-Harguindeguy et al. (2013); used in Manuscript 3 of this thesis) and (ii) teaming up in networks such as the TransPlant Network that use synthesis studies across continents, countries and experimental translocation setups to create a general understanding of the underlying drivers of species turnover, local extinctions, and colonization.

In the next chapter I will detail upcoming research frontiers in experimental translocation experiments tackling the inertia of mountain plant communities.

4 Synopsis, research gaps and upcoming research frontiers

In the following chapter I will first portray emerging research frontiers for the presented first-author manuscripts. Second, I will briefly connect insights from the various presented manuscripts and observational studies and end with a concluding remark on the extinction debt debate, as well as the need to synthesize across study contexts like in the TransPlant Network approach.

4.1 Emerging research frontiers of single manuscripts

Manuscript 1: *Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming* (2021; *Ecosphere*; doi: 10.1002/ecs2.3661)

We found that advanced flowering phenology at lower and warmer elevations translated into increased reproductive performance but was dependent on drought stress. Similar to flower abundance, ANPP and species richness showed similar thresholded responses with benefits at a 1K temperature increase. Furthermore, they showed divestments into reproductive organs and aboveground biomass under stronger climate scenarios with interacting warming and drought. We also demonstrated that graminoid species best took advantage of warming interacting with drought, which led to forb-depressed mountain plant communities.

To disentangle warming and drought effects, a subset of translocated mesocosms was watered bi-weekly at the lowest experimental site. We found that alleviating water stress at the lowest experimental site led to delayed phenological flowering onset (compared to the non-irrigated mesocosm) but did not significantly prevent native species loss or decreases in ANPP irrespective of plant functional groups. It is likely that a full factorial experimental setup, with water addition replicates at all elevation sites, would have yielded even more interesting threshold responses – warming greater than 1K and sufficient water supply may ameliorate phenologies and plant growth. Unfortunately, we have been constrained to low replicate numbers due to the fragile mountain plant community at the site of origin (Esterbergalm). Additionally, this study consisted of phenological data of only one growing season. The major drought in 2018 was likely affecting the phenological outcomes monitored in 2019, highlighting the need for more long-term studies.

Another interesting yet unexplored research frontier emerging from this experimental setup is how reproductive success, not just flower abundance, is impacted by climate change-induced advanced phenologies. Other than counting filled seeds (BBCH 80+), future research should focus on the seedling emergence and establishment in translocated mountain plant communities. Due to the management practice of the semi-natural subalpine grassland of the site of origin (two cuts per year), we were not able to collect seeds, as biomass was harvested at peak biomass in the beginning of July when most seeds had not ripened. Nevertheless, studying the sexual reproduction, seedling emergence, establishment, and persistence of mountain plant communities under interacting climate change drivers is a valuable part of this thesis, not only because of its importance for fitness and population demography, but also because many mountain species lack competitive trait expressions to persist under novel biotic interactions (Alexander et al., 2015; Alexander & Levine, 2019; Meineri et al., 2020).

Manuscript 2: *Drought erodes mountain plant community resistance to novel species under a warming climate* (2022, *Arctic, Antarctic and Alpine Research* ; doi: 10.1080/15230430.2023.2174282)

We found that species turnover increased with time under two warming-droughting scenarios. First, the local loss of native species was followed by the colonization of novel lowland species after a severe central Europe wide drought year. Second, the interaction of lasting warming interacting with a severe drought pushed mountain plant communities beyond a threshold of persistence, leading to the window of opportunity for novel species colonization.

Like Manuscript 1, this study highlighted that mountain plant communities have a certain resistance to warming alone and that community responses are highly dependent on native species adaptive capacities (e.g. plastic phenological responses like advanced flowering onset or early leaf senescence) to the interaction of warming and water limitations.

An undiscussed factor facilitating the colonization of novel species is the comparatively short annual above ground life circle of mountain plant species (Körner, 2021). While the growing season of mountain species is sometimes constrained to 6-8 weeks, from leaf unfolding to senescence, most lowland species are adapted to growing season lengths of 5-7 months with multiple formations of reproductive outputs (e.g. *Taraxacum* sect. *Ruderalia* L. or *Rumex acetosa* L.). This implies that if native species in a nearby mesocosm have already reproduced in early season, and the native community is not competitively active anymore during local peak biomass, it is possible for a novel species to easily colonize the mountain plant community. Therefore, mountain plant communities are vulnerable to colonization by highly competitive, novel lowland species because of these species‘ heavy seed rain (Alexander et al., 2015; Alexander & Levine, 2019) and faster, more opportunistic growth (Manuscript 3 of this thesis; Bjorkman et al., 2018; Stanisci et al., 2020). It is also unclear which native mountain plant community species are able to extend their annual life cycle due to growing season elongation – a crucial trait for persistence under climate change.

Furthermore, we found that seed rain from the matrix was a major driver of temporal mountain plant community dynamics. Mesocosms at the lowest recipient experimental site were exposed to the seed rain of local, novel species, while the seed rain of native species was negligible due to the low number of surviving individuals and limited fecund reproductive output. Thus, open niches in downslope translocated mountain plant communities – created by the severe drought in 2018 – were colonized by novel, lowland species simply because this was the only seed input available. Future studies should include native species seed addition (simulating seed rain at the site of origin) to explore the competitiveness of focal mountain plant species under climate change drivers and novel biotic interactions. Another approach would be to sow novel lowland species seeds into existing mountain plant communities at various elevational levels to test the upward migration of lowland species and competitive outcomes. In particular, different levels of species richness and functional richness of such mountain plant communities should be considered to test for facilitative processes among native species that will likely have a buffering effect on novel species establishment. Furthermore, experimental plots in varying microtopographical exposition should be considered to also test for the influence of such ‘micro-refugia’.

The occurrence of the central Europe-wide drought in 2018 was an ideal natural coincidence to study the interaction of warming and drought. For future studies, the interference of the natural drought highlights the importance of additional irrigated replicates of the two mountain plant communities to disentangle single effects of warming versus drought, as mentioned in the summary of Manuscript 1.

Another insight of Manuscript 2 is that the two strong climatic treatments (Furka-to-Bayreuth, -2090m elevation, + 8.7K MAT, -876mm MAP & Stubai-to-Bayreuth, -1500m elevation, +5.2K MAT, -373mm MAP) were ‘strong enough’ to push most species across their threshold of resistance, but they lacked the spatial resolution (along the translocation gradient) to draw insights of exact tipping points that created the tremendous species colonization. This dilemma originates from nonlinearities in ecological responses to interacting climate responses. One emerging research frontier involves studying tipping point dynamics in more detail (Turner et al., 2020) by using a ‘true’ experimental gradient instead of the design used here (with n=9 mesocosms per site). It has been shown that nonreplicated sampling (e.g. one mesocosm with a particular mountain plant community) at a maximum number of sampling locations (e.g. elevational steps) maximizes prediction accuracy (Kreyling et al., 2018). Besides funding constraints, this sampling method is favorable for future studies because replicate number of fragile and diverse mountain plant communities is additionally constrained to a certain maximum to keep the disturbing impact at excavation sites as low as possible. Combining results from our replicated design (n=9; two sites) with a future gradient design (n=1; nine sites along a single, but long, mountain slope) will be a great asset to future studies.

Manuscript 3: *Increases in functional diversity of mountain plant communities is mainly driven by species turnover under warming* (2023, *OIKOS*; doi: 10.1111/oik.09922)

We found that mountain plant community-averaged PFTs shifted from resource conservative growth strategies towards rather resource acquisitive growth strategies. Mountain plant communities from the high elevation site Furka shifted to higher productivity, higher stature and increased SLA mainly because of novel species colonization. Meanwhile, PFTs of species of the subalpine site Stubai indeed showed similar shifts, but this was attributable to a plastic response of some native species (mainly graminoids) in combination with the colonization of novel species. Along with the expansion of the abiotic niche upon downslope translocation, we observed (i) a strong increase in functional richness through novel species colonization (and thus utilization of the increased range of resource availability), (ii) a decrease in functional evenness, and (iii) varying responses of functional divergence, depending on the degree of niche differentiation among species.

While Manuscript 2 looked at the temporal species turnover of the two mountain plant communities from subalpine versus alpine origin (native species loss and novel species colonization with a significant time lag), Manuscript 3 aimed to understand the observed species turnover from a functional trait perspective by exploring niche dynamics in functional space. We tested various functional diversity measures with state of the art protocols (de Bello, 2021; Halbritter et al., 2020; Pérez-Harguindeguy et al., 2013) and R-packages (Magneville et al., 2022) contributing to easily reproducible analyses. We demonstrated that only a few native graminoid species of the Stubai community were able to shift their leaf economy towards a more opportunistic growth upon downslope translocation. Other small statured species in both warming scenarios were lost in earlier years, most likely due to the interacting climate change drivers (see Manuscripts 1 & 2). Ultimately, our translocation experiment mirrored the effects of climate change (see Bjorkman et al. 2018) by likely increasing the abiotic niche of mountain plant communities. Native species lacked the functional trait expressions or ability (e.g. taller growth, high reproductive output) to quickly fill the unoccupied niche space, allowing for the colonization of novel species. Moreover, one of our key insights was that measures such as functional richness should be handled with care, as the observed increases in functional richness were mainly attributable to the PFTs of novel lowland species that were new to mountain plant communities (similar to findings across the entire 'tundra biome' in Bjorkman et al. 2018). These novel PFTs do not necessarily translate into 'desirable' community composition: the novel species found in Manuscripts 2 and 3 consisted of annual cosmopolitan species (e.g. *Lactuca serriola* L., *Senecio vulgaris* L. or *Festuca rubra* L.) that likely do not benefit other ecosystem services, but rather threaten pristine mountain plant communities. As we did not measure the influence on ecosystem services, such as plant pollinator interactions or nutritious values (i.e. leaf stoichiometry), I would like to highlight this as an important additional measure for future research to gain a deeper insight into mountain ecosystem change beyond plant species composition. Additionally, the temporal dynamic of measured PFTs and subsequently derived functional diversity measures in translocation experiments is a major research frontier emerging from our study insights. As PFTs were only measured once, in the fifth year of the experiment after 4 years of climatic exposure, our insights are only a snapshot in time of potential outcomes that lack the important long-term temporal aspect. Mesocosms in and from Furka and Stubai were destructively harvested in 2020 to measure belowground traits (e.g. root biomass) and various soil parameters for future analyses linking below- to aboveground processes. These future studies are set up to get a more mechanistic understanding of abiotic niche expansion that can only be evidenced by increases soil nutrient availability in warmed replicates and increased C:N leaf-levels in warmed individuals.

Having more replicates (despite funding constraints and fragile mountain habitats) at single sites or evenly distributed along a 'true' elevational gradient needs to be highlighted again as a key insight for future studies. Having the possibility to measure PFTs and (destructively) harvest a second set of mesocosms after a longer climatic exposure (i.e. after 10 years) would yield unknown results and likely help to identify non-linear responses in mountain plant community ecology. This is especially important as various translocation studies (performed by the TransPlant Network) point towards strong initial responses (i.e. species turnover) followed by an equilibrium state.

Insights from all three manuscripts demonstrate the need to disentangle the effect of warming and drought in translocation experiments by using a carefully planned experimental setup. One highly promising approach to simulate the interaction of both climate change drivers is to set up larger scale drought shelters and add water (e.g. a sites long term weekly mean) to a subset of 'droughted' plots. The advantage of such a setup is that scientists are in full control of drought severity and duration, so they avoid interfering natural droughts or extreme precipitation events. Moreover, having both treatments ('warming only' and 'warming interacting with drought') underneath the same drought shelter creates exactly the same warming treatment. Rainout shelters have shown to increase canopy temperatures and decrease canopy moisture levels (Hoover et al., 2018; Kreyling et al., 2017; Kröel-Dulay et al., 2022; Vogel et al., 2013) that complicate a comparison between plant community responses in- and outside a shelter.

Additionally, I suggest the use of a mixture of several replicates per experimental site (to account for individual responses) and a fine scale resolution in translocation steps (e.g. every 400m with less replicates instead of one elevational step of 2090m with nine replicates like in our most severe climate treatment) for future studies (see the advantages mentioned above *sensu* Kreyling et al. 2018) to increase our knowledge on tipping point dynamics in mountain plant communities. Using a fine scale gradient in translocation experiments will address the microclimatic refugia idea – that small-scale temperature differences in heterogenous landscapes may buffer climate change – as there is currently a lack of empirical evidence to support the theory. Since there is little to no knowledge on refugia persistence under interacting climate change drivers (see Chapter 3.4), studying the temporal stability of abiotic niches and novel biotic interactions in microsites presents a major research frontier (see, 'MICROCLIM,' (Dullinger & team) that explores climate buffering capacities of European high-mountain floras; https://www.mountainresearch.at/microclim/).

Furthermore, synthesis studies, such as the TransPlant initiative, across various continents, countries, different experimental approaches (e.g. mesocosms and turfs), and severities of climate change yield great insights into mountain plant communities' vulnerabilities in a changing climate. Additionally, synthesizing studies are of great value for gaining a general understanding of underlying drivers of species turnover, local extinction, and colonization. This is a particularly important aspect in a scientific world full of small-scale insights and a lack of attempts to sum up conclusions of the various smaller-scale experiments. Ultimately, such synthesis studies may have a large impact and offer a great opportunity to transfer general insights to action (e.g. conservation and protection).

4.2 Concluding remark to the extinction debt debate and future steps

My research in this thesis was motivated by a desire to contribute to the knowledge of climate change impacts of mountain ecosystems, particularly mountain grasslands. I performed various translocation experiments and discussed the insights in light of the observed ‘extinction debt’ in natural mountain plant communities.

In particular, I explored reproductive outputs and temporal species turnover of mountain plant communities in addition to their temporal stability in productivity. Furthermore, I investigated the degree of plastic responses in PFTs of two different mountain plant communities originating from a subalpine and an alpine grassland site. Overall, I found clear threshold responses in each experiment. Once a threshold of resistance was crossed, either induced by the interaction of warming and drought or the occurrence of a natural severe drought, native species reproductive output and productivity was reduced, native species loss increased, and the colonization of novel species was launched once mountain plant communities were thinned. Moreover, preliminary results from the TransPlant Network (*in prep.*) have shown that patterns observed in my smaller-scale studies within the SusAlps and TransAlps framework, in addition to other previously published studies, can be confirmed by patterns found across 88 sites consisting of 50922 unique observations. Namely, these are: (i) high local extinction and colonization rates in warmed mountain plant communities; (ii) a decrease in turnover with experimental exposure time, highlighting the system’s initial vulnerability; and (iii) no general turnover dependency on temperature alone, but rather on the amount of growing season precipitation and interaction with novel lowland species pools.

My findings and preliminary insights from the various translocation experiments within the TransPlant Network are contributing to a growing body of literature highlighting the vulnerability of our European mountain plant communities, especially contributing to a lack of knowledge for the trailing range edge of many species (often the subalpine belt). Furthermore, these findings align to the various above-mentioned modelling approaches (Dullinger et al., 2012; Engler et al., 2011; Hülber et al., 2016) that expect strong range size compressions within the next decades. A recently published study by Rumpf et al. (2022) found that 77% of the European Alps above the tree line experienced greening (e.g. due to a reduction in snow cover) in the past four decades, which in turn impacts the life cycle of all living organisms by controlling growing season length (Körner 2021). Further, their study stressed that glaciers and snow provide half of the world’s freshwater resources. Ultimately, these insights reveal experimental, observational, and modelled evidence of climate change threatening mountain plant communities and all the linked ecosystem functions and -services— not only in mountain regions, but also in the respective lowlands. In contrast to observational studies, which only take advantage of non-manipulated climate change and thus create a major time lag in response, experiments and modelling approaches seek to simulate the future. Bringing these two ‘schools’ of scientists together will be a major challenge for the future to provide society with a uniform message of mountain ecosystems' vulnerability to the future climate. This becomes particularly important in a world of 'alternative facts' and a decreased trust in scientific findings.

Besides the lack of evidence of local extinctions in natural mountain plant communities, the greening and observed thermophilisation of many mountain tops is enough of an early warning signal, as native species already undergo novel biotic (and abiotic) interactions that will not become ameliorating in the near future.

Thus, based on my experimental insights, I hypothesize another additional mechanism becoming important to explain the observed pattern of a lack of 'payment' to the 'extinction debt' in natural plant communities under increasing anthropogenic pressures: while mountain plant communities have some resistance to warming *per se*, warming reduces resilience to subsequent disturbances. Events like drought can create windows of opportunity that lead to novel species colonization and 'payment' of the 'extinction debt'.

It is very likely that various previous experimental studies exploring mountain plant community dynamics and 'extinction debt' did not use strong enough treatments and that interacting climate change drivers have not been strong and persistent enough under natural conditions to launch the payment of extinction debt. While most translocation experiments have moved species within the species current distribution range (see Nooten & Hughes 2017 for a detailed review), few studies have used strong climatic scenarios pushing mountain plant communities or single focal species beyond their current distribution range and thus beyond the historically experienced climate (see Knapp et al., 2018 for 'a reality check for climate change experiments'). This is important since novel biotic interactions become very likely favored by pathways such as soil disturbances or windows of opportunity created by interacting climate change drivers, namely warming and drought.

The climate is predicted to globally warm at least ~2.5K within the current century, with an even higher temperature increase predicted for mountain regions and high latitudes (IPCC, 2021; Spinoni et al., 2018). Additionally, the frequency of extreme weather events is likely increasing for most of the land area in central Europe (Cook et al., 2020), potentially limiting windows for plant comminuties' recovery. Further, the interaction of climate change drivers (i.e. warming and drought; see Manuscripts 1, 2 & 4 in addition to De Boeck et al. 2016) or the interaction of single climate change parameters and soil disturbances (Meineri et al., 2013, 2020) will likely push mountain plant communities beyond thresholds, crossing a tipping point of resilience (Jentsch & White, 2019). The promoted 'robustness' of high elevation ecosystems *sensu* Körner & Hiltbrunner (2021) might be true as long as the highest elevations of our mountains will not experience interacting stressors (warming, drought, human disturbances, novel biotic interactions). For lower elevations, especially the montane and subalpine belt, the vulnerability to the mentioned stressors will likely increase and lead to fundamental changes in ecosystem structure (e.g. species turnover) and functioning (e.g. productivity, fodder provisioning, water provisioning, slope stability, recreation), as shown by my presented first author studies. To gain more knowledge on future climate change impacts of mountain regions, we as scientists need to develop experiments that expose single focal species or entire plant communities to climates (and more importantly climate regimes and interacting disturbances) likely to prevail in the second half of this century. This is the only opportunity to provide our society and legislature with the scientific insights that may hopefully be considered important enough to preserve our beloved mountain landscapes with the unique biodiversity as we find them today.

5 List of Manuscripts and declaration of personal contribution

Concept: study idea, development of experimental design

Data acquisition: organization, execution and conduction of data acquisition and processing together with the help of colleagues, students and interns

Data analysis: statistical analysis of data and their illustration in tables and figures

Writing: writing the manuscript, including literature research

Editing: proof-reading and grammar editing, including comments and inputs from co-authors and their integration in the manuscript and preparation for resubmissions after the manuscript was reviewed by the journals' referees

Manuscript 1

Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming (2021; *Ecosphere* ; doi: 10.1002/ecs2.3661)

Max A. Schuchardt, Bernd J. Berauer, Andreas von Heßberg, Peter Wilfahrt, Anke Jentsch

Concept: 10%
Data acquisition: 80%
Data analysis: 80%
Writing: 75%
Editing: 70%

Manuscript 2

Drought erodes mountain plant community resistance to novel species under a warming climate (2022; *Arctic, Antarctic and Alpine Research* ; doi: 10.1080/15230430.2023.2174282)

Max A. Schuchardt, Bernd J. Berauer, Justyna Giejsztowt, Andreas v. Heßberg, Yujie Niu, Michael Bahn, Anke Jentsch

Concept: 10%
Data acquisition: 65%
Data analysis: 85%
Writing: 80%
Editing: 70%

Manuscript 3

Increases in functional diversity of mountain plant communities is mainly driven by species turnover under warming (2023; *OIKOS* ; doi: 10.1111/oik.09922)

Max A. Schuchardt, Bernd J. Berauer, Anh Le Duc, Johannes Ingrisch, Yujie Niu, Michael Bahn, Anke Jentsch

Concept: 10%
Data acquisition: 65%
Data analysis: 85%
Writing: 80%
Editing: 70%

Manuscript 4

Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes (2019; *Arctic, Antarctic and Alpine Research* ; doi: 10.1080/15230430.2019.1618116)

Bernd J. Berauer, Peter A. Wilfahrt, Mohammed A. S. Arfin-Khan, Pia Eibes, Andreas von Heßberg, Johannes Ingrisch, Michael Schloter, Max A. Schuchardt, Anke Jentsch

Concept: 5%
Data acquisition: 15%
Data analysis: 5%
Writing: 5%
Editing: 5%

Manuscript 5

Stable plant community biomass production despite species richness collapse under lasting extreme climate – (2022, *Science of the Total Environment* ; doi: 10.1016/j.scitotenv.2022.161166)

Yujie Niu, **Max A. Schuchardt**, Andreas von Heßberg, Anke Jentsch

Concept: 5%
Data acquisition: 50%
Data analysis: 5%
Writing: 15%
Editing: 40%

6 Appendix

6.1 Participation at conferences

Talks

Increases in functional diversity are mainly driven by species turnover under warming.
Schuchardt M, Berauer B, Anh Le Duc, Niu Y, Jentsch A (2022): International Mountain Conference 2022, Innsbruck, Austria

Drought increases local extinction and erodes mountain plant community stability.
Schuchardt M, Berauer B, Giejstowt J, Niu Y, Jentsch A (2022): World Biodiversity Forum 2022, Davos, Switzerland

ENSO driven vegetation dynamics in Northwest Peru.
Schuchardt M, Rodríguez Arismendiz R, Schweiger A, von Heßberg A, Richter M, Jentsch A (2018): DETOCC (Dryland Ecosystems: Threats and opportunities associated with climate change) 2020, Piura, Peru [online participation and presentation]

Phenological responses in a changing climate.
Schuchardt M, Berauer J, Wilfahrt P, von Heßberg A, Jentsch A (2019): International Mountain Conference 2019, Innsbruck, Austria

Phenological responses in a changing climate.
Schuchardt M, Berauer B, Wilfahrt P, von Heßberg A, Jentsch A (2019): Bayceer colloquium 2019, Bayreuth, Germany

El Niño Southern Oscillation (ENSO) Dynamics in Northwest-Peru over 2 Decades - Desert and Dry Forest Response to extremely fluctuating resources.
Schuchardt M, Rodríguez Arismendiz R, Schweiger A, von Heßberg A, Richter M, Jentsch A (2018): Jahrestagung AK Biogeographie 2018, Bonn, Germany

Poster

Increases in functional diversity are mainly driven by species turnover under warming.
Schuchardt M, Niu Y., Jentsch A. (2022): Frontiers in Exp. Ecol. on Changing Environments, UFZ Leipzig, Germany

Temperature sensitivity of soil respiration changes with long-term warming and cooling of grassland soils – a question of carbon stability?
Schierling L, Pausch J, Abdalla K, Sun Y, Schuchardt M, Jentsch A, Lehndorff E, Meyer N: Bayceer Workshop 2021, Bayreuth, Germany

Phenological responses in a changing climate 2.0.
Schuchardt M, Bernd J. Berauer, Peter Wilfahrt, Andreas von Heßberg, Jentsch A. (2019): BonaRes Status Seminar 2020, UFZ Leipzig, Germany

Phenological responses in a changing climate.
Schuchardt M, Berauer B, Wilfahrt P, von Heßberg A, Jentsch A (2019): International Mountain Conference 2019, Innsbruck, Autria

Flowering phenology of sub-alpine grasslands and potential shift under warmer conditions.
Eibes P, Schuchardt M, Wilfahrt P, Berauer B, von Hessberg A, Jentsch A (2018): SusAlps Conference, Garmisch-Partenkirchen, Germany

El Niño Southern Oscillation (ENSO) Dynamics in Northwest-Peru over 2 Decades - Desert and Dry Forest Response to extremely fluctuating resources.
Schuchardt M, Rodríguez Arismendiz R, Schweiger A, von Heßberg A, Richter M, Jentsch A (2018): Jahrestagung AK Biogeographie 2018, Bonn, Germany

6.2 Activity in networks

TransPlant Network

The TransPlant Network aims at synthesizing insights from various translocation experiments executed across three continents in the Northern Hemisphere (17 replicated experiments, 88 subsites and 50922 unique observations).

The team of Disturbance Ecology has contributed to this network with biomass data from the SusAlps project (6 out of 88 sites for 5 years; see Manuscripts 1, 2, 4, 5) and PFT data from 3 experimental sites in the year 2020 (see Manuscript 3). Active participation in a meeting of the TransPlant Network and various discussions with network members on patterns found across experimental setups and continents (first network manuscript currently in preparation).

DragNet

DragNet (Disturbance and Resources Across Global Grasslands) aims at assessing the generality and site-specificity of factors influencing disturbance recovery and community assembly in herbaceous dominated ecosystems (https://nutnet.org/dragnet).

In February 2020, I was a central actor of the Disturbance Ecology team setting up the DragNet experiment at our research facilities in the botanical garden of the University of Bayreuth. Since then the team of Disturbance Ecology is annually contributing data to the network (PAR measurements, vegetative height measurements, soil samples, cover estimates and biomass). Furthermore, I actively participated in an annual meeting of DragNet as breakout parts of the Nutrient Network annual meeting in 2021. I offered exchange on experimental designs, first insights on treatments in Bayreuth as one of the first sites established globally and the first site established in semi natural grasslands of central Europe. Insights from the Bayreuth site and protocol improvements (how to practically execute the disturbance part in semi natural grasslands, estimates on hours etc.) were shared among the network.

6.3 Teaching

Type	Title	Contribution	Year	Semester
Field course	Experimental Ecology	Introductory lecture (90min), Supervision of groups working along in ongoing global change experiments	2022 2021 2020	Summer
Field course	Projektseminar Landschaftsökologie	Supervising two students collecting data and writing a ‘mini paper’ in the SusAlps experimental research project	2020	Summer
Seminar	Natural risks and Hazards	Preparation and execution of 3-day weekend seminar including 4 topic-presentations (each 15 min)	2020	Winter
Seminar	Stability, Resilience and Inertia	Preparation and execution of 3-day weekend seminar including a ‘keynote’ of 40mins on ‘alternative biome states in terrestrial ecosystems’ and ‘the global tree restoration potential’	2021	Winter
Seminar	Fundamentals in Biodiversity research	Co-supervising master students of various study programs to write a draft on recent topics of biodiversity research, acting like a journal editor to handle students reviews on course manuscripts.	2018	Winter
Lecture	Disturbance Ecology	Preparation and execution of 2 ‘guest lectures’ on ‘Fire Ecology’ and ‘Disturbance interactions, loops and cascades’	2021 2020	Winter

6.4 Co-supervision of Master thesis

Rüthers J. (2021) Effects of reciprocal translocation of montane and alpine plant-soil monoliths on above- and belowground plant performance.

6.5 Co-authorships in various manuscript initiatives

Berauer, B. J., Wilfahrt, P. A., Arfin-Khan, M. A. S., Eibes, P., Von Heßberg, A., Ingrisch, J., Schloter, M., **Schuchardt, M. A.**, & Jentsch, A. (2019). Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes. *Arctic, Antarctic, and Alpine Research*, *51*(1), 215–231. https://doi.org/10.1080/15230430.2019.1618116

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8 Manuscripts

Manuscript 1

Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming (2021; *Ecosphere*, doi:10.1002/ecs2.3661)

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Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming

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Citation: Schuchardt, M. A., B. J. Berauer, A. von Heßberg, P. Wilfahrt, and A. Jentsch. 2021. Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming. Ecosphere 12(7):e03661. 10.1002/ecs2.3661

Abstract. Warming due to climate change is generally expected to lengthen the growing season in areas of seasonal climate and to advance plant phenology, particularly the onset of leafing and flowering. However, a reduction in aboveground biomass production and reproductive output may occur when warming is accompanied by drought that crosses critical water deficit thresholds. Tracking warmer temperatures has been shown to be species-specific with unknown impacts on community composition and productivity. The variability in species' ability to leverage earlier leaf unfolding and flowering into increased aboveground net primary production (ANPP) or increased investments into reproductive organs has heretofore been poorly explored. We tested whether phenological sensitivity to temperature, as a result of experimental warming, directly translated into increased plant performance, as measured by ANPP and flower abundance. In order to experimentally simulate climate warming, we translocated a total of 45 intact soil–plant communities downslope along an elevational gradient of 900 m within the European Alps from 1260 to 350 m asl and weekly recorded flower abundance and total green cover as well as cumulative biomass production at peak growing season. We found that advanced phenology at lower elevations was related to increased reproductive performance and conditional on whether they experienced drought stress. While a temperature increase of +1K had positive effects on the amount of reproductive organs for species with accelerated phenology, temperature increase going along with drier conditions resulted in plants being unable to sustain early investment in reproduction as measured by flower abundance. This finding highlights that the interaction of two climate change drivers, warming and drought, can push communities' past resistance thresholds. Moreover, we detected biotic competition mechanisms and shifts toward forb-depressed states with graminoids best taking advantage of experimentally altered increased temperature and reduced precipitation. Our results suggest that while species may track warmer future climates, concurrent drought events post a high risk for failure of temperature-driven improvement of reproductive performance and biomass production in the European Alps.

Key words: alpine; Bavarian Alps; climate change; phenological sensitivity; plant community; plant functional type; plant reproduction; translocation experiment; transplant.

Received 23 March 2021; accepted 30 March 2021; final version received 19 May 2021. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Climate change will affect plant community dynamics and functions by unevenly altering species' phenologies (CaraDonna et al. 2014, Alexander and Levine 2019, Giejsztowt et al. 2020). Temperature increase due to climate warming in mountain regions is expected to be two to three times higher than the global average (Appenzeller et al. 2008, Pepin et al. 2015). The potential positive effect of warming in mountain regions on plant growth via longer growing seasons (Gobiet et al. 2014) and increased metabolic rates (Larcher 2003, Körner 2006) can be counterbalanced by late frost events (Inouye 2008, Wipf et al. 2009) or drought effects (Jentsch et al. 2009, Buchner et al. 2015, De Boeck et al. 2016, Berauer et al. 2019). Plant reproductive potential is tightly linked to phenological plant strategies such as the timing and abundance of flower production, making the sensitivity of phenology to climate warming a critical component of future plant community dynamics and ecosystem service provisioning in mountain regions.

Warming is expected to generally advance flowering onset (Menzel and Fabian 1999, Cornelius et al. 2014, Munson and Sher 2015). Long-term monitoring has shown that species that declined in abundance over time showed little or no ability to track warmer local climate and did not advance their flowering phenology (Willis et al. 2008). Changes in flowering phenology are among the earliest observed reactions to changed environmental conditions (Inouye 2008, Box et al. 2019), responding to a variety of abiotic factors (such as photoperiod, above- and below-ground temperatures, soil moisture and snow cover, in other words vernalization cues) and in turn steering biotic interactions (Jentsch et al. 2009, Zhao et al. 2020). Responses to warmer climate have been shown to vary between early- and late-flowering species, with early-flowering species tending to benefit most from increased spring temperatures (Moore and Lauenroth 2017, Arfin Khan et al. 2018). Despite this general trend, late-flowering species can match (Miller-Rushing and Inouye 2009) or exceed (Carbognani et al. 2016) the benefits early-flowering species receive, potentially pointing to deleterious effects of early flowering such as pollinator desynchronization. On a community level, changes in plant phenology can increase a niche overlap of species, decreasing phenological complementarity (Rathke and Lacey 1985). Decreasing phenological complementarity in turn may influence competition between species by increasing overlap in resource acquisition strategies (Nord and Lynch 2009, CaraDonna et al. 2014), plant–pollinator mutualism (Dyer et al. 2021), and trophic synchronization (Hegland et al. 2009, Schmidt et al. 2016) or windows of opportunity for non-native species to establish within the community (Wolkovich and Cleland 2011, Alexander and Levine 2019, Vetter et al. 2019, Giejsztowt et al. 2020).

Warming can also indirectly influence plant phenology by increasing water stress due to amplifying droughts, which will likely increase in abundance due to shifts in precipitation regimes (Gobiet et al. 2014, Spinoni et al. 2018). This is important, as water limitation may suppress both plant growth and reproductive fitness (Engler et al. 2011, Robinson et al. 2013, Leitinger et al. 2015, Dietrich and Smith 2016, Grant et al. 2017). Thus, phenological advancement can make early investments into reproductive organs followed by water stress potentially damaging to an individual. However, phenological responses to drought vary widely, having been shown to advance (Peñuelas et al. 2004, Jentsch et al. 2009, Bernal et al. 2011) or delay plant development (Nagy et al. 2013). Further, phenological response to drought may inert flowering onset, change abundance of flowers (Dunne et al. 2003, Saavedra et al 2003, Abeli et al. 2012, Cornelius et al. 2013) or reduce carbon allocation to reproductive organs (Barnabas et al. 2008, Liu et al. 2012, Zeiter et al. 2016, Kreyling et al. 2017), highlighting species-specific responses (Jentsch et al. 2009). Further, extreme summer conditions such as drought in the temperate zone are known to increase early leaf senescence (Kreyling et al. 2008, Benot et al. 2014, De Boeck et al. 2016), decrease plant vegetative growth, and reduce seed abundance and seed weight (Zeiter et al. 2016), indicating that plant stress reduces plant fitness (Walter et al. 2013). Ultimately, while warming may advance flowering, subsequent drought can interrupt or reverse this pattern as species divest from reproduction.

The effect of warming on the abundance of reproductive organs has shown to be highly species-specific and study system-dependent.

Moreover, it remains unclear whether advanced phenologies of species that are able to track climate change can draw benefits, namely increase in carbon allocation to vegetative biomass or reproductive organs, from these early investments. Increased temperature going along with drought stress can result in drought-induced divestments from reproductive organs (Saavedra et al. 2003, Giménez-Benavides et al. 2007, Abeli et al. 2012, Zeiter et al. 2016). When warming occurs without water stress, the investment into reproductive organs remains unclear. Thus, increasing temperature may reveal underexplored thresholds, where the warming effect on plant growth and reproductive organs changes from positive to negative (Scheffer and Carpenter et al. 2003, Turner et al 2020), which in turn may have strong long-term effects on community reassembly under future climatic conditions.

In this unique study, we explored how experimental warming by downslope translocation of entire plant–soil communities in the German region of the European Alps (Berauer et al. 2019) affected the onset and abundance of flowering in semi-natural grasslands along a temperature–precipitation gradient that ranged from benign to stressful water availability conditions. We additionally explored how different plant functional groups, namely early- vs. late-flowering species, graminoids, forbs, and herbaceous legumes, reacted to this temperature–precipitation change and the relationship to overall aboveground community biomass production. We hypothesize that (1) early-flowering species better track climate change by adjusting flowering onset to the novel climatic conditions as they rely on the higher resource availability of early spring; (2) species that advance their flowering phenology in response to a warmer climate increase their reproductive output as measured by the number of flowers; and (3) carbon allocation toward aboveground net primary production (ANPP) increases with warming.

METHODS

Experimental setup

In the summer of 2016, 45 intact plant–soil monoliths were extracted from semi-natural montane grasslands in an extensively managed meadow at 1260 m asl. Monoliths were 30 cm in diameter and 40 cm in depth, representing an area shown to be sufficient to study community responses and interactions in small statured grasslands (Milbau et al. 2007) while maintaining belowground processes. After excavation, monoliths were translocated downslope and reburied flush with the ground at four target sites along an elevational gradient ranging from 1260 m asl (Esterberg; climatic control and recipient site of nine replicates) to 860 m asl (Graswang; +1K) to 600 m asl (Fendt; +3K) to 350 m asl (Bayreuth; +3.5K; for additional details on the study design, see Berauer et al. 2019).

At each climate treatment—including the site of origin—nine replicates were exposed to local climatic conditions. At the lowest climate treatment, an additional set of nine replicates was installed and received an irrigation treatment twice a week starting in spring 2018 (Fig. 5). The irrigation treatment was designed to alleviate communities' water limitation at the lowest elevation climate treatment caused by a sharp decrease in annual precipitation at this experimental site and clear signs of water stress in 2017 (Berauer et al. 2019). The amount of added water was mimicking a subalpine precipitation pattern (in amount and frequency) being calculated as the difference between monitored precipitation at the lowest climate treatment and the long-term monthly average of the subalpine Stubai Valley (1850 m asl, Austria), a higher elevation climate treatment of this project that was not used in this study, corresponding to a mean of 12.35 mm precipitation, twice a week.

The elevational gradient represents an increase of MAT by 3.5K between the highest and lowest experimental site with intermediate steps at +1K and +3K. This experimental setup tests a range of simulated climate change scenarios, with the maximum values representing IPCC Scenario A1B with a mean air temperature rise of 3–4K until 2100 (Körner 2003, IPCC 2007).

Environmental parameters

In spring 2017, a sensor for soil temperature and moisture (EcH2O 5-TM; Decagon Devices, Pullman, WA, USA) was installed horizontally at 5cm depth together with data loggers (EcH2O Em50; Decagon Devices) in one monolith at each climate treatment.

The start of growing season was defined as the first day where daily mean soil temperature was above 5°C for five consecutive days (Table 1; Appendix S1: Fig. S1; Zhang et al. 2011). This temperature threshold describes site-specific energy availability at ground level controlling both biological and biochemical processes (Jentsch and White 2019), which in turn are primarily driving the green-up and onset of flowering of grassland species (Scherrer and Körner 2009, Guo et al. 2018). Moreover, using soil temperature data allowed us to infer site-specific snowmelt regimes, which is especially important at montane sites, where growing season start is often determined by loss of snow cover rather than air temperatures above a certain threshold (Shaver and Kummerow 1992, Oberbauer et al. 2013).

Flowering phenology

Flowering phenology was monitored weekly at each climate treatment along the downslope translocation experiment in 2019, from the beginning of the growing season until peak biomass harvest (for an overview of defined growing season start and peak biomass, see Table 1). We monitored species-specific onset and duration of flowering plus number of flowers or inflorescences. Flowering was defined as the first open flower with visible stamen (Meier 2018). Once multiple individuals of a species in one monolith started flowering, we flagged the first flowering individual to monitor throughout the growing season; the number of flowers was counted from the flagged individual. For all graminoid species, the number of inflorescences was used as the flower unit, so that graminoid species were recorded as flowering once the first anthers were visible (Meier 2018). Due to graminoid's potential vegetative reproduction, all inflorescences of a given species per monolith were counted. We used mean number of flowers (individual-specific over the growing season) for further analysis (Hollister et al. 2005, Cleland et al. 2012). According to Jäger and Rothmaler (2017), we classified species starting to flower before or during May as early-flowering species, whereas species that started flowering after May were classified as late-flowering species. Furthermore, we visually estimated the percent of green cover of each monolith as a proxy for environmental stress (De Boeck et al. 2016, Stampfli et al. 2018, Berauer et al. 2019). Even though monitoring at the control and +3K climate treatment started slightly after local growing season start, we captured initial flowering onset of all present species.

Phenological sensitivity was calculated as the number of days shifted in species-specific flowering onset between the control and warming treatments, per degree warming (Cleland et al. 2012) averaged across all replicates where the species occurred within each respective climate treatment. The control treatment corresponds to the highest experimental site used in this study, which is the site of origin from where all translocated monoliths were excavated. Warming treatments correspond to the experimental sites along the downslope translocation gradient.

$$S_{\text{phen}} = \frac{\text{Onset}_{\text{warm}} - \text{Onset}_{\text{ctrl}}}{T_{\text{warm}} - T_{\text{ctrl}}}$$

Table 1. Site names of translocated plant–soil monoliths with elevation, climate treatment intensity, average annual precipitation of years of experimental exposure 2016–2019 (MAP_{exp}), total seasonal precipitation between 15 May and 31 July 2019 ($\text{Precip}_{\text{seas}}$), average air temperature at 2m unventilated between 2016 and 2019 ($\text{AirTemp}_{\text{exp}}$), average seasonal air temperature between 15 May and 31 July 2019 ($\text{AirTemp}_{\text{seas}}$), local growing season (Start_{GS}), phenological monitoring ($\text{Start}_{\text{mon}}$), and peak biomass harvest (PBH).

Locality	Elevation (m asl)	Climate treatment	MAP_{exp} (mm)	$\text{Precip}_{\text{seas}}$ (mm)	$\text{AirTemp}_{\text{exp}}$ (°C)	$\text{AirTemp}_{\text{seas}}$ (°C)	StartGS (DOY)	$\text{Start}_{\text{mon}}$ (DOY)	PBH (DOY)
Esterberg	1260	ctrl	1797	584	5.6	13.7	121	135	190
Graswang	860	+1K	1349	443	6.8	15.4	87	83	189
Fendt	600	+3K	1015	276	8.8	17	60	76	189
Bayreuth	350	+3.5K	630	114	9.6	18.03	60	62	175

Performance sensitivity was calculated species-specific as the proportional change in number of flowers (averaged across replicates where species occurred within each respective climate treatments) per degree warming. This value indicates if a translocated species is producing more or less flowers compared to the higher elevation climatic control treatment, which is the site of origin.

$$S_{\mathrm{perf}} = \frac{(\mathrm{n.\ flowers}_{\mathrm{warm}} - \mathrm{n.\ flowers}_{\mathrm{ctrl}})/\mathrm{n.\ flowers}_{\mathrm{ctrl}}}{T_{\mathrm{warm}} - T_{\mathrm{ctrl}}}$$

Aboveground biomass and species richness

Aboveground biomass of each monolith was harvested 3cm above the ground at site-specific peak biomass (Table 1). Biomass was sorted to species, dried at 60°C for 48 h, and weighed. Species richness at each climate treatment was calculated as the sum of all flowering species recorded during the phenological monitoring plus all additional non-flowering species found during the biomass harvest (detailed species lists in Appendix S1: Table S3). This approach captured early-flowering species (e.g., *Veronica chamaedrys* L.) that would otherwise be undetected at the peak biomass harvest, as they had already senesced by then.

Statistical analysis

We first tested whether (1) early-flowering species would better track climate change by adjusting flowering onset to the local growing season compared to late-flowering species. For a response variable, we calculated an average flowering onset day for each species in each climate treatment by taking the mean flowering onset day of all monoliths within a climate treatment where a given species was found. We conducted linear mixed-effect models using the nlme package in R (Pinheiro et al. 2021) with mean species-level flowering onset dates as the response variable (n = 9 for each climate treatment) and flowering time (two-level factor: early- vs. late-flowering species), climate treatment, and their interaction as explanatory variables. As many species occurred at multiple climate treatments, we used species as a random effect. We examined multiple Tukey-adjusted comparisons to calculate groups with significant differences in flowering onset using the emmeans package (Lenth 2020).

Next, we tested (2) whether performance sensitivity increased with phenological sensitivity. We averaged species-specific onset of flowering and number of flowers across replicates within each climate treatment and calculated sensitivities according to Cleland et al (2012; see section *Flowering phenology* above). Then, we used a linear mixed-effects model to test whether the interaction of phenological sensitivity and flowering onset (levels: early; late) predicted performance sensitivity with species ID as a random effect as species may have occurred at multiple climate treatments. Additionally, we used linear models to test whether phenological sensitivity predicted performance sensitivity for each climate treatment.

We investigated how (3) the production of aboveground plant biomass (ANPP) changed with warming. We used linear models to test whether differences in ANPP were predicted by climate treatments relative to climatic controls and how these differences varied by functional groups. We repeated this process using species richness as a response.

Lastly, we used generalized additive models (GAMs, mgcv package) with treatment as a factor to model and compare the observed green cover vs. days of the year due to non-linearities and potentially important declines in green cover in mid-season. GAMs were fit using restricted maximum likelihood (REML) to identify optimum smoothing parameters and a Gaussian error distribution. We used AIC to verify that our GAM improved the fit relative to a simple linear model. All model residuals were checked for normality and homoscedasticity. All analyses were performed in R Studio version 4.0.3 (R Core Team 2018).

RESULTS

Shifts in onset of flowering

The translocated plant–soil monoliths were able to track experimentally induced climate warming by modulating plant species' flowering onset to local climates ($P < 0.001$; Fig. 1). The mean flowering onset between earliest (lowest = warmest) and latest (highest = coolest) climate treatment differed by 34 d averaged across all species, corresponding to 3.14 d advancement per 100 m elevational change (see Table 2).

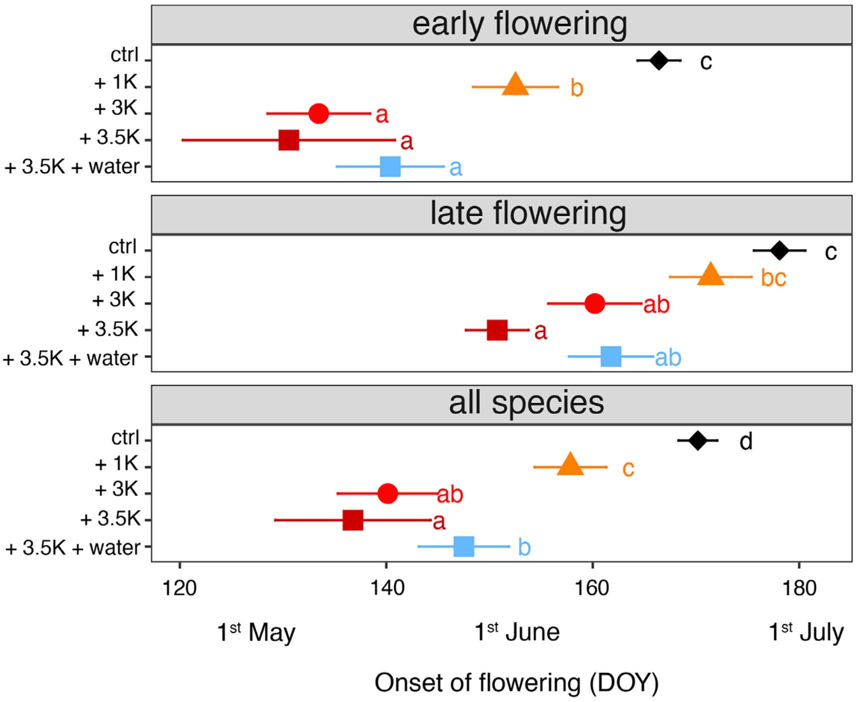

Fig. 1. Flowering onset of translocated plant–soil monoliths along an elevational gradient splits into groups of early- and late-flowering and all present species. Onset of flowering as measure of DOY follows the elevational gradient with earliest flowering onset at lowest elevation. Water addition at the lowest recipient climate treatment led to a shift back in flowering onset, likely indicating drought stress in plant communities without water addition. Letters indicate significant differences between climate treatments. Mean flowering onset between early- and late-flowering species differed marginally, indicating a phenological divergence between these two groups ($P = 0.056$).

Early-flowering species showed a mean advancement of 3.81 d per 100 m elevational change, while late-flowering species showed a mean advancement of 2.3 d per 100 m across all climate treatment (early vs. late: $P = 0.056$). The factors early and late were not confounded with growth form (Appendix S1: Table S3).

Phenological sensitivity and performance

Increased advancement of flowering phenology was correlated with increased investments into reproductive organs, as indicated by a negative relationship between flowering onset advancement and number of flowers produced ($P = 0.007$; Fig. 2). This relationship was consistent for both early- and late-flowering species ($P = 0.912$), indicating that both groups respond similarly to climate warming. The relationship between phenological sensitivity and performance sensitivity did not hold true for all climate treatments (Fig. 3). At the most moderate climate treatment of +1K, the trend was highly significant ($P < 0.001$) and mainly driven by forbs and legumes. The same trend was observed at the strongest climate treatment of +3.5K receiving water addition ($P = 0.039$), although a majority of species in this climate condition produced less flowers relative to the control and the pattern was mainly driven by an important indicator graminoid species *Poa pratensis* (L.) ($P = 0.169$ excluding *P. pratensis*). For the strong climate treatments +3K and +3.5K without watering, this trend was inverted, but non-significant ($P = 0.199$ and $P = 0.068$, respectively). Except for *Plantago lanceolata* (L.) in the +3.5K water addition

Table 2. Mean start of flowering along the elevational gradient with climate treatment intensity, flowering group, number of present species across all nine replicates (*N*), mean start of flowering, standard deviation (SD), standard error (SE), confidence interval (CI), elevational change, and day shift in mean flowering onset per 100 m elevational change.

Climate treatment	Flowering	*N*	Start (DOY)	SD	SE	CI	Elevational change (m)	Days per 100 m
Ctrl	Early	21	166.4	9.5	2.1	4.3	0	NA
+1K	Early	23	152.5	19.8	4.1	8.5	400	−3.48
+3K	Early	12	133.5	17.2	5	10.9	660	−4.98
+3.5K	Early	9	130.6	30.8	10.3	23.7	910	−3.93
+3.5K +water	Early	12	140.4	17.9	5.2	11.4	910	−2.86
Mean								−3.81
Ctrl	Late	10	178.1	7.9	2.5	5.6	0	NA
+1K	Late	9	171.4	11.8	3.9	9.1	400	−1.68
+3K	Late	4	160.2	9	4.5	14.3	660	−2.71
+3.5K	Late	4	150.8	6.1	3	9.6	910	−3.0
+3.5K +water	Late	6	161.8	10	4.1	10.5	910	−1.79
Mean								−2.3
Ctrl	All species	31	170.2	10.5	1.9	3.8	0	NA
+1K	All species	32	157.8	19.7	3.5	7.1	400	−3.1
+3K	All species	16	140.1	19.4	4.8	10.3	660	−3.31
+3.5K	All species	13	136.8	27.1	7.5	16.4	910	−3.67
+3.5K +water	All species	18	147.5	18.5	4.4	9.2	910	−2.49
Mean								−3.14

Notes: Note that water addition delayed mean start of flowering for both early- and late-flowering species. Mean onset of flowering between early- and late-flowering species was marginally significant ($P = 0.056$; $F_{77} = 3.738$).

treatment, all monitored species experienced advances in the onset of flowering (Fig. 3).

Productivity and species richness

Community aboveground biomass production (ANPP) did not respond linearly to the experimental climate treatment (Fig. 4A). ANPP increased under modest climate change ($P_{+1K} = 0.025$) fitting findings from previous years (Berauer et al. 2019). Communities under more severe climate change scenarios decreased in ANPP, indicating threshold dynamics after three years of climatic exposure ($P_{+3K} = 0.061$; $P_{+3.5K} < 0.001$; $P_{+3.5K+water} < 0.001$). The significant increase in ANPP at the +1K climate treatment was due to increased biomass production of graminoid species ($P = 0.003$). The increased production of graminoid species is likely at the cost of forb species, which decreased in production under modest warming ($P < 0.001$; Fig. 4B and Appendix S1: Table S1).

Species richness of plant communities declined significantly upon downslope translocation along the elevational gradient (Fig. 4C; Appendix S1: Table S3). While we did not find a significant decline in mean forb richness between the control and +1K climate treatment, forbs declined at +3K ($P < 0.001$), +3.5K ($P < 0.001$), and 3.5K +water ($P < 0.001$). The higher number of recorded forbs at +3.5K compared to +3K and +3.5K with water addition is due to the invasion of new species (i.e., *Senecio vulgaris* (L.), *Pilosella piloselloides* (Vill.) Soják) from matrix vegetation. Graminoid species richness declined significantly at +3.5K ($P < 0.001$) and even at +3.5K with water addition ($P = 0.002$). We did not find any significant changes in legume species richness, despite their absence at +3.5K without water addition (Appendix S1: Table S2).

Green tissue as a stress indicator

Our generalized additive model (GAM) analysis indicated that green tissue in the control, +1K, and +3K treatments plateaued and showed no stress from drought effects (ctrl, $F = 22.77$, df = 4.57, $P < 0.001$; +1K, $F = 77.24$, df = 4.60, $P < 0.001$; +3K, $F = 27.17$, df = 4.30, $P < 0.001$). Moreover, green tissue began senescing in the last week of May (DOY = 148) at the most intense climate treatment of +3.5K without water

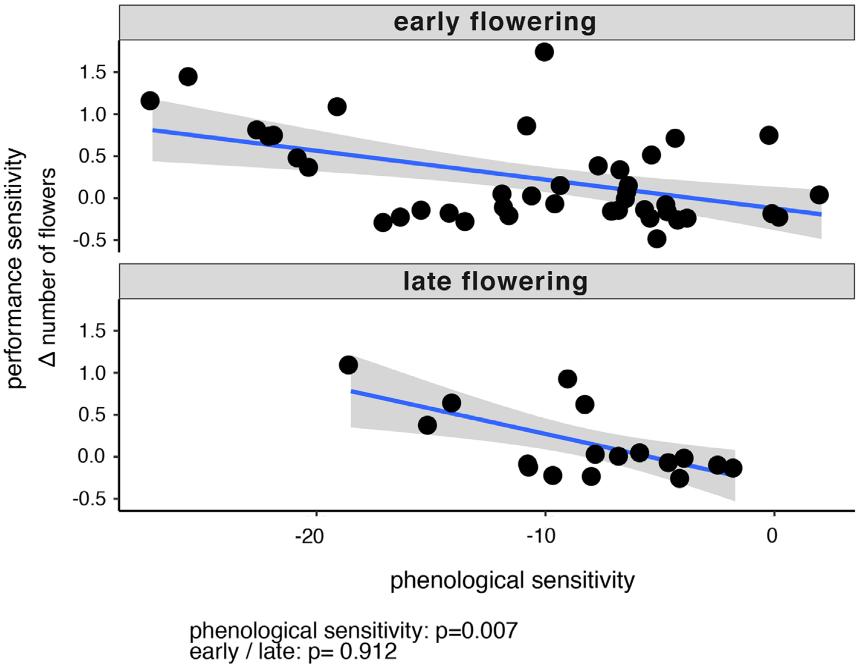

Fig. 2. Phenological sensitivity as a significant predictor of flowering performance. Species that tracked experimentally induced climate change by flowering earlier showed positive performance responses. This trend stayed consistent across early- and late-flowering species.

addition ($F = 18.35$, df = 5.79, $P < 0.001$; Fig. 5), likely as a result of depleted soil moisture by evapotranspiration. Conversely, no bimodality was observed in the +3.5K with water addition treatment (consistent water supply resulted in a linear increase of green tissue over time). The overall model D^2 was 71%, indicating that the GAM provided a good fit. The GAM indicated that smoothing functions were appropriate for all climate treatments excluding the +3.5K with water addition; model fit using smoothing parameters was better than when using a standard linear model, as evidenced by AIC ($\mathrm{AIC_{GAM}} = 6056$; $\mathrm{AIC_{lm}} = 6382$). Within two weeks from DOY = 142 to DOY = 155, soil moisture was reduced from 40% to 14% at +3K and 20% to 4% at +3.5K, respectively. Soil moisture values stayed low during the critical time of flowering until the harvest date in early July (i.e., soil moisture +3.5K ≤ 15% for 96 d). At the +3.5K climate treatment, monoliths receiving water addition corresponding to a mean of 12.35 mm precipitation twice a week were able to sustain green tissue. Orographic rainfall in combination with frequent morning dew at the +1K climate treatment continuously provided water to the translocated plant–soil monoliths.

Discussion

As hypothesized, nearly all species in downslope translocated monoliths were able to track climate change by advancing onset of flowering under warmer conditions with early-flowering species seeming to have greater advancement than late-flowering species. Generally, species that were better able to track local climate in flowering phenology were also able to increase their investment into reproductive organs displaying more flowers. However, at climate treatments where precipitation declined with increased temperature, investment into reproductive organs did not increase with advanced flowering dates and even showed a tendency to decline. We found that responses were highly species-specific with the tendency toward

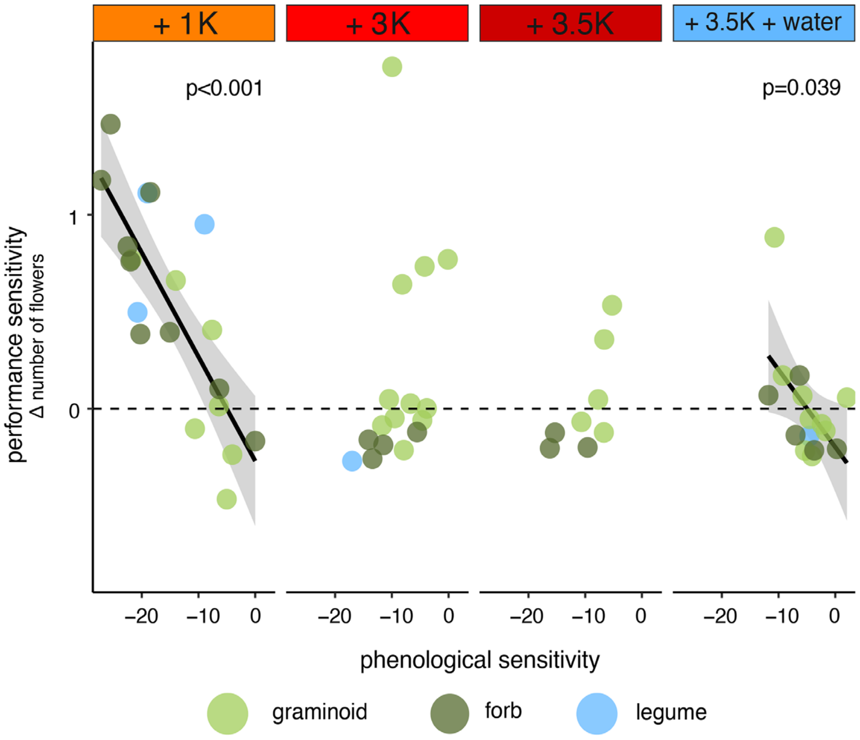

Fig. 3. Relative effect of passive warming on phenological sensitivity and performance sensitivity along the elevational gradient. Climate treatments at the more severe climate treatments of +3K and +3.5K suffering under drought effects reduce investments into reproductive organs. Some graminoid species show increased performance under drought.

increased graminoid reproductive performance at the expense of forb reproductive performance under dry conditions.

Phenological sensitivity predicts flowering performance

As per our hypothesis and in line with previous findings (Jentsch et al. 2009, Cleland et al. 2012), we found that with advancing flowering phenology, the amount of reproductive organs of species increased in general. While others have shown that late-flowering species may delay their flowering phenologies to avoid unfavorable conditions in the middle of summer (Taylor and Garbary 2003, Sherry et al. 2007, Munson and Sher 2015), all species in our study (except one), whether early or late flowering, showed an earlier flowering onset compared to the climatic control, which fits the general observations of advanced flowering under warming (Menzel and Sparks 2007, Moore and Lauenroth 2017).

Previous studies reported stronger responses to warming in early-flowering species compared to late-flowering species (Miller-Rushing and Inouye 2009, Moore and Lauenroth 2017, Arfin Khan et al. 2018), and we found a similar tendency for early-flowering species to advance flower onset to a greater degree than late-flowering species. We observed a similar, positive relationship between flower onset advancement and reproductive performance, measured as number of flowers per individual, in early- and late-flowering species, but due to the greater advancement potential of some early-flowering species, the greatest increase in investments into reproductive organs was seen in the early-flowering cohort. Graminoids dominated the late-flowering cohort (see Appendix S1:

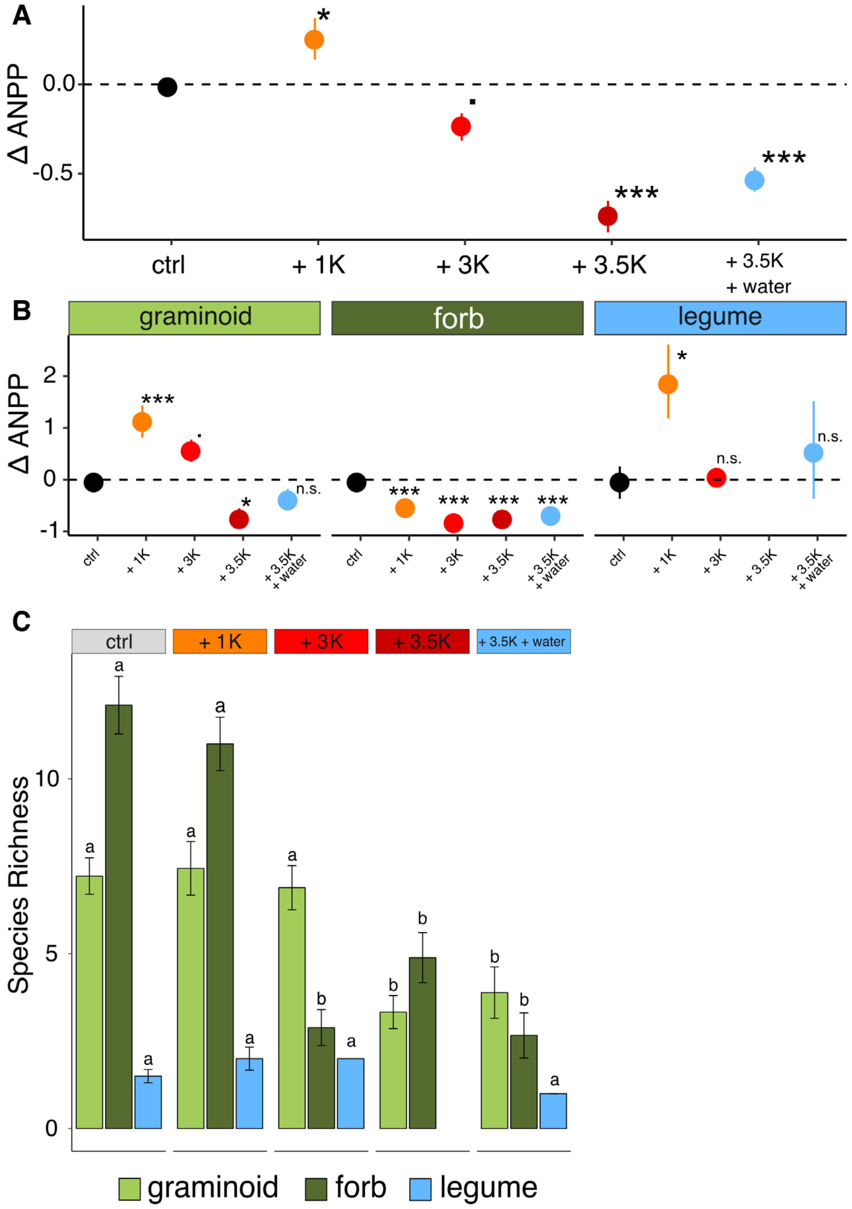

Fig. 4. Aboveground net primary production and species richness along the elevational gradient after three years of passive warming. (A) ANPP of all species present at climate treatments. (B) ANPP of three plant functional groups. Asterisks indicate levels of significance between each recipient climate treatment and the climatic control. (C) Species richness splits into three plant functional groups. For each plant functional group, letters indicate significant changes in species richness due to experimentally altered climate conditions.

Table S3). While most forbs such as *Myosotis sylvatica* ssp. *alpestris* (F.W. Schmidt) and legumes such as *Trifolium pratense* ssp. *pratense* (L.) suffered under water deficiency at the more severe climate treatments (+3K and +3.5K without water addition), certain graminoid species such

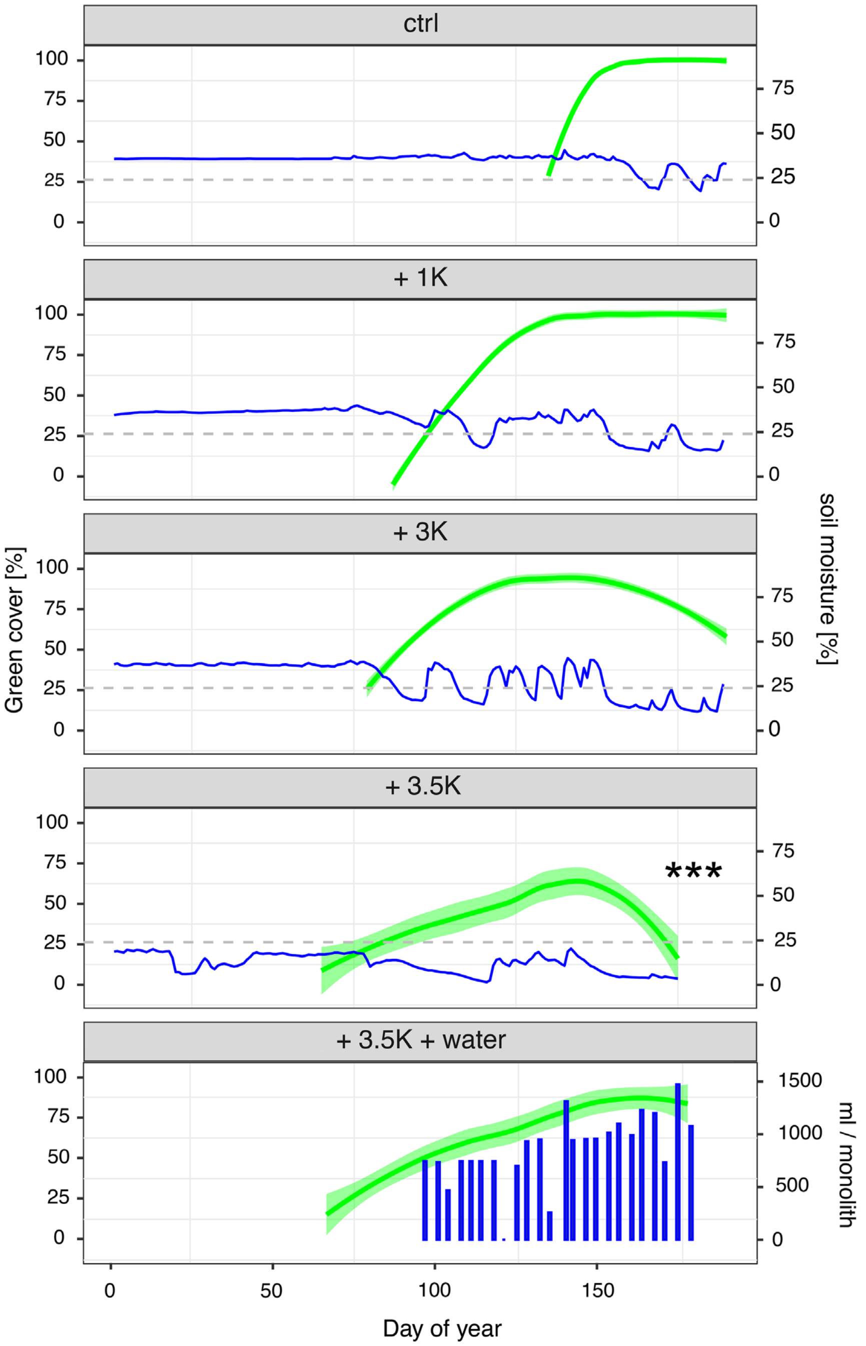

Fig. 5. Green cover of translocated plant communities along the elevational gradient modeled as GAM (solid green line) with 95 confidence interval (green ribbon). Early senescence of plant communities due to soil water depletion indicated as soil moisture at 5 cm (blue lines). Blue bars at the lowest climate treatment indicate biweekly water addition per plant–soil monolith to remove water limitation as soil moisture data were unavailable. Asterisks show significant differences in green cover relative to the control.

as *Elymus repens* (L. Gould) still increased performance compared to the climatic control treatment, potentially masking the signal of forb or legume performance declines in the group of late-flowering species.

Interestingly, the relationship of species-specific phenological sensitivity to climate warming and performance was not consistent along the entire climatic gradient indicating unknown threshold dynamics. Monoliths translocated to a warmer site with sufficient water availability throughout the season produced more flowers with advancing phenologies. This trend was also evident at the warmest site when water was experimentally supplemented, though this pattern was dominated by a single species, *Poa pratensis*. Consequently, the benefit of a species advancing its phenology in warmer environments appears to be dependent on water deficiency. Climate treatments experiencing drought stress even tended to show the reverse trend, with decreased flowering performance with higher climate sensitivity (Saavedra et al. 2003). Under drought conditions, competitive interactions between species of various growth forms have shown to alter species-specific onset and length of flowering period (Jentsch et al. 2009). Likely, this meant that plant communities under stressful, water-limited conditions were not able to sustain this early warming-driven investment in reproduction. Hence, advanced flowering does not necessarily translate into higher reproductive performance and can potentially result in wasted resource investments for a plant (Saavedra et al. 2003), highlighting the need to explore interacting climate change drivers to reveal where critical water deficit thresholds cause species performance to decline (Turner et al 2020).

At the lowest climate treatment receiving biweekly water addition, most present species produced less flowers compared to the climatic control treatment, but still showed a significant negative relationship between phenological sensitivity and flowering performance. Species highly sensitive to warming, thus accelerating their flowering onset, produced more flowers compared to species less sensitive to warming within the same climatic treatment. At +3.5K with water addition, this relationship was driven by *P. pratensis* (L.), a fairly durable and drought-resistant species, which may be an early indicator for community reassembly (toward graminoid dominance) after three years of climate exposure due to (1) increased investments into reproductive organs and (2) relative dominance in space (40% mean cover in 2019). Plants may shift their resources from reproduction to maintenance (Parsons 1990) or from aboveground to belowground productivity (Barnabas et al. 2008) under stressful conditions (Knapp et al. 2008, da Silveira Pontes et al. 2015). Our watering treatment began in 2018 after observing a sharp decline in community performance in the first year of study after downslope translocation (Berauer et al. 2019). It is likely, then, that even after alleviating water stress, these communities were still recovering from drought conditions, potentially explaining their poor performance relative to the wetter and cooler controls. Moreover, a severe and extended natural drought occurred in Central Europe in the summer of 2018 (Buras et al. 2019), potentially delaying recovery of these communities even with watering as evapotranspirative demand was severe. This finding suggests that plant communities in the +3.5K water addition treatment may be in an intermediate state between recently sufficient water supply and recovering from the 2018 natural drought, thus showing a single species-driven pattern.

Climate-dependent allocation strategies

Biomass production is often reduced under drought conditions, which may decrease overall fitness by reducing fecundity (Shipley and Dion 1992, Tracey and Aarssen 2011, Gellesch et al. 2017, Younginger et al. 2017). In our study, species under modest warming showed higher flower abundances mainly driven by forb and legume forb responses, while the species with the greatest ANPP gains were graminoids, indicating that these two plant functional groups, forbs and graminoids, had complementary allocation strategies under warmer conditions with adequate soil water resource. Under persistent water stress, we found that graminoid species were best able to maintain reproductive and vegetative performance, while forbs and legumes showed a decrease in investment into reproductive organs, a decrease in ANPP, or they even went locally extinct. However, there is a lack of generality regarding graminoid response to drought; graminoids reduce the number of reproductive shoots relative to forbs and legumes in some systems (Zeiter et al. 2016), while they may recover better from drought in terms of biomass production in others (Grant et al. 2014, Stampfli et al. 2018, Mackie et al. 2019). In temperate grasslands, graminoid species typically develop shallower and more flexible rooting systems compared to forbs or legumes, thus increasing the graminoid's drought sensitivity but also response flexibility (Bardgett et al. 2014, Kübert et al. 2019). Yet, graminoids were shown to react quickly after rewetting events due to their dense mat of roots in upper soil layers (Michalet et al. 2016, Rosbakh et al. 2017) and also respond fast to warming in high latitude grasslands (Klanderud et al. 2015). Capturing small amounts of precipitation after drought periods could lead to the observed positive performance of graminoids with respect to both flower abundance and ANPP.

Declines in species richness

Local declines in species richness likely reflect competitive interactions under decreasing resource levels, finally leading to species loss due to environmental stress, as indicated by decreases in community biomass and green cover. However, this is likely exacerbated by the fact that we observed less investment into reproductive organs under climate change. Moreover, the downslope translocated monoliths were not in their native matrix vegetation, meaning there is less potential for recovery of native species from surrounding seed rain (Stein et al. 2008). This is especially important in alpine and montane plant communities, since they have been shown to lack competitive traits to resist novel species colonization from warmer climate vegetation (Alexander and Levine 2019, Meineri et al. 2020). Investigating actual seed rain in target sites of translocation experiments combined with germination trials of collected seeds is a valuable future avenue of research.

Implications for plant community composition

Almost all species of the translocated plant communities were able to track warmer climate by advancing their flowering onset. Our study highlights the vulnerability of species-rich montane grasslands to future climate changes, mainly due to the inability to withstand drought events under warmer temperatures. Montane plant communities exposed to warmer and drier environments suffered under drought as evidenced by early senescence and decreased plant investments into both reproductive organs and vegetative growth. Decreased number of flowers across many species translates into a decrease in potential seed rain and reproductive success (Liu et al. 2012). This is particularly important since high elevation communities have been shown to be highly susceptible to colonization by either non-native or more competitive graminoid species due to the lack of competitive traits, such as a fast and opportunistic resource acquisition and growth form (Meineri et al. 2020). Furthermore, this study contributes to a growing body of literature (i.e., Klanderud et al. 2015, Rosbakh et al. 2017, Wellstein et al. 2017, Berauer et al. 2019) observing shifts toward graminoid dominated, forb-depressed states in both subalpine and montane semi-natural grassland communities under changing climate. Future plant community dynamics, ecosystem services such as fodder quality (i.e., loss or extirpation of legumes), and biodiversity conservation efforts are highly dependent on species being able to maintain reproductive output under increasingly uncertain temperature and precipitation dynamics.

ACKNOWLEDGMENTS

We are grateful to the German Ministry for Education and Research (BMBF) for funding this research (SUSALPS; grant number: FKZ 031B0516C). We thank the project partners of SUSALPS, in particular the Karlsruher Institute of Technology (IMK-IFU) for strong support during the field campaign, Michael Bahn for providing climatic data, and Sarah Fütterer, Toni, and our international interns for assisting in fieldwork. This study is also part of AJ's research project MindTheGap! financed by the Upper Franconian Trust (Oberfrankenstiftung; grant number: OFS FP00237).

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DATA AVAILABILITY

Data are available from Zenodo: https://doi.org/10.5281/zenodo.4772698.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3661/full

Ecosphere

Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming

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Appendix S1

Figure S1. Green cover of translocated plant communities along the elevational gradient modelled as GAM (solid green line) with 95 confidence interval (green ribbon). Green cover showed different speed in greening up once growing season conditions, indicated by soil temperature at 5cm (red line), were met. Soil temperature threshold of 5°C is shown as a dashed grey line.

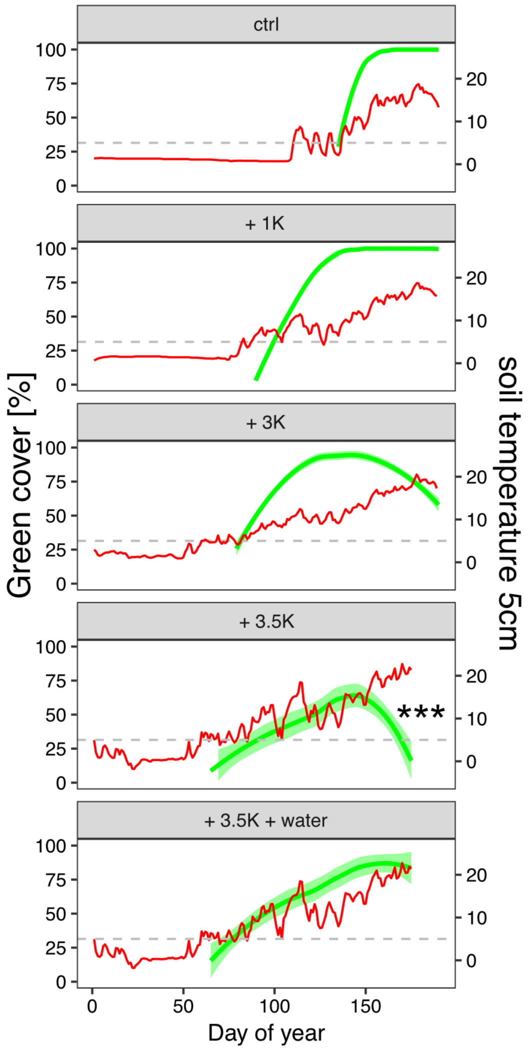

Table S1 Changes in aboveground net primary production of recipient sites compared to climatic control (contrast), split by functional groups (FunGroup).

		All Species		**Graminoids**		**Forbs**		**Legumes**	
Model output	F value	24.06 on 4		12.47 on 4		11.29 on 4		1.761 on 3	
	p value	**<0.001**		**<0.001**		**<0.001**		0.204	
	Adj. R^2	0.68		0.51		0.48		0.099	
	DF	40		40		40		13	
	contrast	**t value**	**p.value**	**t value**	**p.value**	**t value**	**p.value**	**t value**	**p.value**
Post-hoc comparison	ctrl vs + 1K	2.328	**0.025**	3.887	**<0.001**	-3.745	**<0.001**	2.189	0.047
	ctrl vs + 3K	-1.928	0.061	2.006	0.051	-5.943	**<0.001**	0.052	0.959
	ctrl vs + 3.5K	-6.334	**<0.001**	-2.368	**0.023**	5.398	**<0.001**	NA	NA
	ctrl vs + 3.5K + water	-4.578	**<0.001**	-1.155	0.255	-4.89	**<0.001**	0.437	0.669

Table S2 Changes in species richness of recipient sites compared to climatic control (contrast), split by functional group.

		Graminoids		**Forbs**		**Legumes**	
Model output	F value	9.67 on 4		41.69 on 4		1.7 on 3	
	p value	**<0.001**		**<0.001**		0.207	
	Adj. R^2	$R^2 = 0.44$		0.79		0.099	
	DF	40		40		16	
	contrast	**t value**	**p.value**	**t value**	**p.value**	**t value**	**p.value**
Post-hoc comparison	ctrl vs + 1K	0.247	0.806	-1.122	0.269	6.000	0.176
	ctrl vs + 3K	-0.371	0.713	-9.309	**<0.001**	1.414	0.514
	ctrl vs + 3.5K	-4.325	**<0.001**	-7.290	**<0.001**	NA	NA
	ctrl vs + 3.5K + water	-3.707	**<0.001**	-9.533	**<0.001**	-1.044	0.312

Table S3 Species present per site (X) split by early and late flowering species.

Species	FunGroup	ctrl	+1K	+3K	+3.5K	+3.5K + water
early flowering species						
Ajuga reptans	forb	X	X			
Alchemilla vulgaris	forb	X	X	X		X
Anthoxanthum odoratum	graminoid	X		X		X
Bellis perennis	forb	X				
Cerastium holosteoides	forb	X	X			X
Chaerophyllum temulum	forb	X				
Crocus albiflorus	forb		X			
Dactylis glomerata	graminoid		X	X		
Festuca rubra	graminoid	X	X	X	X	X
Galium album	forb		X			
Geum urbanum	forb	X	X	X		X
Glechoma hederacea	forb		X	X		
Helictotrichon pubescens	graminoid	X	X	X		
Lolium perenne	graminoid		X	X	X	X
Pilosella piloselloides	forb				X	
Plantago lanceolata	forb				X	X
Poa pratensis	graminoid	X	X	X	X	X
Primula elatior	forb	X				
Ranunculus aconitifolius	forb	X				
Ranunculus acris	forb	X	X			
Ranunculus ficaria	forb		X			
Rhinanthus minor	forb	X				
Rhinanthus angustifolius	forb	X				
Rumex acetosa	forb	X	X			
Senecio vulgare	forb					X
Silene flos-cuculi	forb	X				
Stellaria media	forb		X			
Taraxacum sect. Ruderalia	forb		X	X	X	X
Trifolium dubium	legume	X	X			
Trifolium repens	legume		X			
Trisetum flavescens	graminoid	X	X	X		X
Veronica chamaedrys	forb	X	X		X	
Veronica filiformis	forb		X			
Veronica hederifolia	forb				X	
Veronica persica	forb				X	
Vicia sepium	legume	X	X	X		X
late flowering species						
Achillea millefolium	forb				X	
Agrostis capillaris	graminoid	X	X	X	X	X
Agrostis stolonifera	graminoid		X			
Arrhenatherum elatius	graminoid	X				X
Cynosurus cristatus	graminoid	X		X		
Elymus repens	graminoid	X	X	X		X
Festuca pratensis	graminoid	X	X	X		X
Holcus lanatus	graminoid		X		X	
Lathyrus pratensis	legume		X			X
Leontodon helveticus	forb	X	X		X	
Leucanthemum ircutianum	forb					X
Myosotis alpestris	forb	X	X			
Phleum pratensis	graminoid	X				
Poa trivialis	graminoid	X				
Trifolium pratense	legume	X	X			
	total species present	**31**	**32**	**16**	**13**	**18**

Manuscript 2

Drought erodes mountain plant community resistance to novel species under a warming climate

(2022, *10.1111/oik.09922 10.1111/oik.09922* ; doi: 10.1080/15230430.2023.2174282)

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Experimental site in Graswang, 2019, © M. Schuchardt

ARCTIC, ANTARCTIC, AND ALPINE RESEARCH
2023, VOL. 55, NO. 1, 2174282
https://doi.org/10.1080/15230430.2023.2174282

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Drought erodes mountain plant community resistance to novel species under a warming climate

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ABSTRACT

Warming in mountain regions is projected to occur three times faster than the global average. Recently, a small number of observational studies have reported species loss in mountain plant communities and have explored mechanisms facilitating the colonization by novel species. We monitored translocated mountain plant communities and their novel competitor interactions following five years of exposure to downslope climates. We found increasing species turnover under two future climate scenarios with time. Local loss of native species was followed by the colonization by novel species after a severe drought year in the third year after translocation. Here, the assumed mechanism facilitating novel species colonization in mountain communities is direct environmental filtering. We find a time lag between the local loss of native species and the colonization by novel species, which can be explained by interacting climate stressors—that is, warming and drought—pushing communities across a threshold of resistance to colonization. Interestingly, despite significant changes in species identity and strong colonization by novel species, the proportional contribution of plant functional groups to aboveground biomass stayed stable across both sites of origin and over time. Our study provides experimental evidence of local species loss in mountain plant communities prone to severe climatic change, revealing abrupt threshold dynamics.

ARTICLE HISTORY
Received 28 February 2022
Revised 11 August 2022
Accepted 24 January 2023

KEYWORDS
European Alps; invasion; species turnover; extinction debt; translocation experiment

Introduction

The climate of mountain regions is projected to warm three times faster than the global average, particularly in winter (Pepin et al. 2015; Körner 2021). Climate warming is driving shifts in species' distributions, with native species tracking their optimal climate to higher latitudes (Pauchard et al. 2016), in the special case of mountain regions to higher elevations (M. J. Steinbauer et al. 2018) or nearby refugial microhabitats (Scherrer and Körner 2011; Körner and Hiltbrunner 2021). Few studies have reported species replacement in real-world mountain plant communities by novel species from lower elevations (Kudo et al. 2011; Rixen and Wipf 2017). In addition to the increase in species richness in mountain plant communities (M. J. Steinbauer et al. 2018), the thermophilization of species (Lamprecht et al. 2018; K. Steinbauer et al. 2020) and a reduction in range size and abundance of cold-adapted species (Rumpf et al. 2018) were found in observational studies. These observations are an early warning signal and raise the question: Why have mountain plant communities experienced such a high inertia so far? Or, in other words, why are mountain plant communities creating a so-called extinction debt? Extinction debt is defined as extinctions that are expected to occur as consequence of climate change that have not yet occurred (see Tilman et al. 1994; Figueiredo et al. 2019). Current theories explaining low extinction rates in mountain regions include (1) extinction debt driven by the long life span of mountain species (demographic inertia; Dullinger et al. 2012), (2) time lags between warming and novel biotic interactions (Alexander et al. 2018; Nomoto and Alexander 2021), and (3) missing novel competitors due to topography-driven isolation (M. J. Steinbauer et al.

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/15230430.2023.2174282.

2016). We theorize an additional mechanism: though communities have some resistance to warming per se, warming reduces resilience to subsequent abiotic stressors. Events such as drought can launch the “payment” of the extinction debt and create windows of opportunity (Diez et al. 2012) that lead to colonization by novel species. Translocation experiments, like the one presented in this study, offer a great opportunity to simulate future climate scenarios in combination with removal of dispersal barriers for novel lowland species.

In addition to temperature (see Körner and Hiltbrunner 2018), growing season precipitation and, more important, the precipitation regime (temporal distribution of precipitation) are benchmarks for studying mountain plant communities’ vulnerability to climate change (Müller and Bahn 2022). Though extreme weather events such as heat waves and droughts are rarely observed in alpine ecosystems, they will likely become more frequent at mid-elevations, the montane belt, and the subalpine belt (Spinoni et al. 2018; Intergovernmental Panel on Climate Change 2021). Not only are these elevational belts the most vulnerable from a climate change perspective (Stephan et al. 2021) but they are simultaneously the trailing range edges of many alpine plant species (Rixen et al. 2022). The impact of climatic warming interacting with drought on plant communities is likely to elicit nonadditive and nonlinear responses that are difficult to predict (Scheffer and Carpenter 2003; Buma 2015; Turner et al. 2020), especially in mountain environments that are underrepresented in the literature (but see Berauer et al. 2019). In a translocation experiment of mountain plant communities, De Boeck et al. (2016) found that heat waves in combination with drought had a strong effect on aboveground productivity, whereas heat waves alone had no significant impact. Their follow-up study exploring legacy and recovery effects (De Boeck et al. 2018) demonstrated that the combined effect of warming and drought led to a forb-depressed state dominated by graminoid species (see also Rosbakh et al. 2017; Collins et al. 2022). Exploring such nonadditive processes is particularly important on a plant community level because species track climatic changes at different rates (Gibson-Reinemer, Sheldon, and Rahel 2015; Mamantov et al. 2021; Rixen et al. 2022), leading to species turnover due to the interactions with novel species or changing outcomes of interactions among existing species over time (Alexander, Diez, and Levine 2015).

Therefore, investigating the variation in number, identity, and abundance of species through time plays a key role for community dynamics, which is often analyzed in light of community stability (Hector and Bagchi 2007; Allan et al. 2011; Valencia et al. 2020). We use two simple metrics to define turnover: species gains and losses and changes in relative abundances of single species. From a species turnover perspective, three important aspect should be considered. First, though species turnover may remain at high rates only explaining that a particular plant community is changing, the two underlying drivers (species gains and losses) may be opposing and reflect a different ecological story: colonization and local species loss (Thompson and Gonzalez 2017). Detecting specific time points when species appear versus when species disappear from a community reveals mechanisms underlying community reassembly and the trajectory of community structure. Second, relative abundances between species and plant functional groups (PFGs) can determine community functioning. Some studies have shown that particular PFGs tend to draw more benefits from climate change than others, consequently changing proportional PFG contributions to aboveground biomass (AGB) upon warming and drought (J. S. Hallett et al. 2014; Hoover, Knapp, and Smith 2014; Stampfli et al. 2018; Wilfahrt et al. 2021). In particular, legumes have been identified to be vulnerable to drought (Grant et al. 2014) likely due to their tight soil biodiversity interaction (Prudent et al. 2020). Ma et al. (2017) found that less abundant species had little effect on community biomass stability and concluded that species diversity was an unimportant driver of community biomass stability. Yet, this conclusion ignores that changed community structure affects plant–plant interactions (Ploughe et al. 2019) and is likely controlling ecosystem functioning and related ecosystem services, such as water retention, including feedback loops to plant available water, feed value, slope stability, or plant–pollinator mutualisms (Schmidt et al. 2016; Box et al. 2019). More important, key measures such as aboveground primary production may remain stable under climate warming in species-rich plant communities due to compensatory effects as a result of functional redundancy (Isbell et al. 2015; Valencia et al. 2020) where species identity and abundance are crucial. Compensatory shifts in PFGs in proportion to AGB after disturbances remain underexplored (McLaren and Turkington 2010; Jentsch and White 2019). Also, knowing whether colonizing species are native or novel to a particular plant community is fundamental for biological diversity and its conservation (Alexander, Diez, and Levine 2015; Vetter et al. 2018). Thus, understanding the mechanisms behind community assembly and its implication for the stability of plant communities as well as single PFGs and a species resident status (native vs novel) is crucial to understanding the effects of climate change and its consequences for future ecosystem functioning.

There is a growing body of literature acknowledging the importance of both native species persistence and resistance to novel species under climate warming to protect ecosystem resilience and functioning (Crepaz et al. 2021; Usinowicz and Levine 2021). It has been shown that reproductive output of mountain plant species is decreasing under warmer and drier conditions (Bektaş et al. 2021; Schuchardt et al. 2021), thus changing population demography (Körner 2021). Moreover, seedling emergence and, even more important, seedling establishment of mountain plant species are likely to be diminished under warmer and drier conditions (Meineri et al. 2020; Stampfli and Zeiter 2020; Margreiter, Walde, and Erschbamer 2021), especially if highly competitive novel species are present to colonize open space (Alexander and Levine 2019; Vetter et al. 2019). The lack of competitive traits in mountain plant species against novel biotic interactions is likely increasing mountain plant communities' vulnerability at the trailing edge under climate change.

Here, we experimentally translocated intact mountain plant–soil communities from a semi-natural subalpine grassland and a natural alpine pasture within the European Alps downslope to a warmer and drier environment. Furthermore, the downslope translocation removed topography-driven isolation of the respective mountain plant communities and thus dispersal barriers for novel lowland species. We passively simulated warming for two different sites of origin and monitored species-specific losses of mountain species, species-specific gains of species from the local lowland communities, as well as biomass responses over five consecutive years. By pairing an extreme climatic gradient (+3.3 K and +4.4 K average growing season air temperature; see Table 1) with a natural drought event that took place in central Europe in 2018 (year 3 of experimental exposure; Bastos et al. 2020), we pushed mountain plant communities beyond their typical climatic envelopes. We hypothesized that (1) relative to reference dynamics in control communities, rates of species turnover over time increase under experimental warming and drier conditions; (2) species turnover in warmed communities is initially driven by species loss, followed by the colonization by novel species in subsequent years; and (3) the relative contributions of PFGs to community aboveground biomass change post-colonization (novel species belong to different PFGs as lost natives).

Material and methods

Experimental setup

In the spring of 2016, thirty-six intact plant–soil mesocosms (hereafter: communities) were extracted from two experimental sites. Communities from high-elevation site Furka (2,440 m.a.s.l; Switzerland) represent alpine pasture vegetation (Hefel and Stöcklin 2010), whereas communities from the mid-elevation site Stubai (1850 m.a.s.l.; Austria) belong to an lightly managed, semi-natural subalpine grassland (Bahn et al. 2009; Ingrisch et al. 2018). The translocated alpine pasture communities were classified as *Caricetum curvulae* and the subalpine grassland communities as *Trisetetum flavescentis*; for detailed information on dominant and characteristic species, see Berauer et al. (2019).

At the high- and mid-elevation sites, one set of communities (n = 9) was reburied as climatic control, and another set of communities (n = 9) was translocated downslope to Bayreuth (350 m.a.s.l.; Germany). The plant–soil communities were 30 cm in diameter and 25 cm in depth, representing an area shown to be sufficient to study community responses and interactions in small-statured grasslands (Milbau et al. 2007) while maintaining belowground processes. In this study, we tracked

Table 1. Geographic and climatic characteristics of study sites from low to high elevation.

			Experimental site (country)		
			Bayreuth (Germany)	Stubai (Austria)	Furka (Switzerland)
Geography	Elevational belt		Colline	Subalpine	Alpine
	Coordinates		49°55′16″N 11°34′55″E	47°07′44″N 11°18′19″E	46°34′36″N 08°25′17″E
	Elevation (m.a.s.l.)		350	1,850	2,440
Climate	Long-term mean	MAT (°C)	8.2	3.0	−0.5
		MAP (mm)	724	1,097	1,600
	Ø growing degree days (heat sum)	Total	2,155	1,344	403
		Growing season	885	623	210
	Ø MAT (°C) exposure	Total	9.58	6.94	0.35
		Growing season	13.2	9.87	8.8
	Ø MAP (mm) exposure	Total	608	1,031	1,096
		Growing season	166	397	181

Total values were calculated during the period of experimental exposure (2016–2020). Growing season start was defined as the fifth day of five consecutive days with a mean daily air temperature at 2 m ≥ 5°C and the end of the growing season as the day of biomass harvest. Data shown were calculated from on-site weather station data.

mountain plant community dynamics annually between 2016 and 2020 (five years of novel climate exposure).

Climatic parameters

In spring 2017, a sensor for soil temperature and moisture (EcH2O 5-TM) was installed horizontally at 5-cm depth together with data loggers (EcH2O Em50) in one mesocosm at each site used in this study. The translocation gradient represents differences in many climatic parameters, including mean annual temperature (MAT), mean annual precipitation (MAP), growing season mean air temperature, growing season precipitation, and growing degree days, which were measured at 2 m using on-site climate stations.

Both warming treatments presented here are calculated as the deviation in growing season temperature between the respective climatic control site of origin and the recipient lowland site. Plant communities translocated from Furka to Bayreuth were exposed to a warming treatment of Furka +4.4 K and plant communities translocated from Stubai to Bayreuth were exposed to a warming treatment of Stubai +3.3 K (Table 1). Five-year mean (2016–2020) growing season precipitation was 166 mm at Bayreuth, 397 mm at Stubai, and 181 mm at Furka. Growing degree days during the growing season increased by a factor of 4.2 at Furka +4.4 K and by a factor 1.4 at Stubai +3.3 K.

The start of growing season was defined by the fifth day of five consecutive days with a mean daily air temperature at 2 m higher than 5.0°C. This early season temperature threshold has been shown to primarily drive the green-up of grassland species (Scherrer and Körner 2010; Guo et al. 2018). End of growing season was defined by the day of biomass harvest at peak biomass, thereby generating a clear metric for cross-site comparisons where different growing season lengths are inevitable.

Environmental parameters

AGB was harvested annually at 3 cm aboveground at site-specific peak biomass (between mid-June and beginning of August) mimicking, for example, high elevation sheep or cattle grazing. AGB was sorted to species, dried at 60°C to constant weight (minimum 48 hours), and weighed (Berauer et al. 2019). Each species was assigned a treatment-level resident status ("native" or "novel") based on whether the species occurred within any experimental community of the same origin in the year of experimental setup (2016). In three cases (*Geranium sylvaticum* L., *Gentiana punctata* L., and *Sibbaldia procumbens* L.) where community native species were assigned as "novel," we decided upon local expert knowledge and adjusted the species status (e.g., perennial species first seen in second year of experiment due to disturbance of translocation itself). All species names were checked according to the Global Biodiversity Information Facility (2021). One woody species (*Vaccinium uliginosum* L.) originating from the alpine Furka site was excluded from analysis because it occurred in only one replicate.

Data analyses

Community-specific species turnover, colonization, and species loss rate between yearly time steps were calculated using the "codyn" package v2.0.5 (L. Hallett et al. 2018) as

$$\frac{\text{species gained} + \text{species lost}}{\text{total species in both timepoints}}.$$

To compare turnover rates (i.e., total turnover, species loss, and colonization) across time, we conducted generalized least square models with year-to-year species turnover as a response variable and year interacting with treatment (control versus warmed) as an explanatory variable. To cope with the nonindependence of repeated sampling of mesocosms, which introduces a temporal autocorrelation, we included variance structure in the model with mesocosm nested in year. This model was performed separately for the two sites of origin (Furka, Stubai) because they consisted of two (ecological and botanical) different mountain plant communities (alpine versus subalpine). If significant, we conducted separate post hoc Tukey's honestly significant difference tests to compare, first, between years within one treatment (temporal change of turnover for a given treatment) and, second, within each single year between treatments (effect of climatic difference between treatments). This approach was repeated for species colonization and species loss.

We calculated PFG-specific and resident status-specific species richness and proportional AGB (levels: forb native, forb novel, graminoid native, graminoid novel, legume native, legume novel) for each community for each time step. This approach allowed us to compare relative success of PFGs while excluding the effect of community-level productivity responses. To identify relationships in PFG replacement, we first calculated mean PFG-specific AGB proportions for each community and time step. Second, we used a linear regression model for each site of origin with proportional AGB as a response variable and year and treatment as explanatory variables. Third, we conducted a post hoc Tukey's honestly significant difference test for pairwise comparisons per PFG separately for each treatment (control versus warmed) and site of origin (Furka, Stubai).

All data analysis was performed within the R programming environment (v4.1.0, R Core Team 2021). All assumptions of parametric modeling were verified.

Results

Species turnover

Species turnover rate was influenced by year (p_{Stubai} = .002; p_{Furka} < .001), treatment (p_{Stubai} < .001; p_{Furka} < .001), and their interaction (p_{Stubai} = .01; p_{Furka} < .001) for communities from both sites of origin (degrees of freedom = 64 for both sites of origin). Species turnover rate at both climate control treatments did not significantly change over time, indicating community stability in the absence of experimental manipulation (Figure 1). Species turnover rate only changed significantly at Furka control between 2017 and 2018 (p < .001), which can be explained by elevated species turnover from 2016 to 2017 as a result of the translocation process itself (e.g., cutting of roots) and a later decrease in species turnover to natural fluctuation rates. In contrast, species turnover in warmed plant communities increased significantly with time (p_{Stubai} < .001; p_{Furka} < .001). Furthermore, species turnover of warmed mountain plant communities differed significantly from their climatic control for every year except for the alpine plant community in 2017. Averaged across four years (excluding the year of setup), annual species loss was −2.9 ± 2.7 species out of 9.4 ± 4.2 species under the Stubai +3.3 K treatment and −2.4 ± 1.6 species out of 6.3 ± 3.1 species under the Furka +4.4 K treatment, and annual species gain was 0.4 ± 2.6 and 0.7 ± 1.8 respectively. Here, high values of standard deviation highlight strong interannual differences in local species loss and colonization. Linking the average annual losses and gains of species to the average species number present in single communities across time facilitates understanding species turnover rates above 50 percent in both warming treatments (Figure 1).

Local species loss and colonization

Species loss rates were influenced by year (p_{Stubai} = .001; p_{Furka} = ns), treatment (p_{Stubai} < .001; p_{Furka} < .001), and their interaction (p_{Stubai} = .003; p_{Furka} = .024) for communities from both sites of origin. Colonization rates were influenced by year (p_{Stubai} = .001; p_{Furka} < .001), treatment (p_{Stubai} < .001; p_{Furka} = .017), and their interaction (p_{Stubai} = .001; p_{Furka} < .001) for communities from both sites of origin (degrees of freedom = 64 for

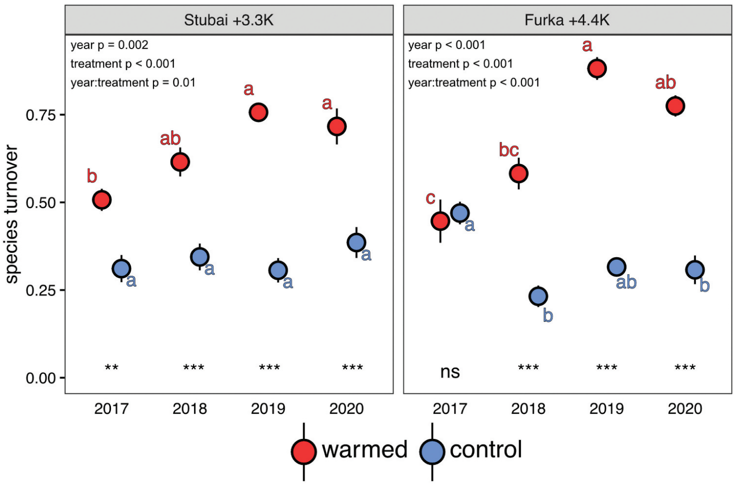

Figure 1. Species turnover of mountain plant communities originating from Stubai (Austria) and Furka (Switzerland) across years in two warming and drought treatments. Warming and drought caused a significant increase in species turnover in plant communities compared to climatic control sites. Species turnover increased over time in warmed communities compared to their climatic control, where species turnover remained low. Shown are mean and standard error of turnover rates. Asterisks indicate differences between warming and control per year; letters indicate differences across years per treatment and site of origin (n = 9; p < .05 for both notations).

both sites of origin). Both warmed mountain plant communities rapidly showed high rates of local species loss (Table S1) between 2016 and 2018, followed by the increased colonization of species in 2019 ($p_{\text{Stubai+3.3K}} < .001$ and $p_{\text{Furka+4.4K}} < .001$; Figure 2). Local species loss rates decreased from 2018 to 2019 in the Stubai +3.3K treatment ($p_{\text{Stubai+3.3K}} < .001$), followed by another increase from 2019 to 2020 ($p_{\text{Stubai+3.3K}} < .001$), whereas species loss rates remained high in the Furka +4.4K treatment throughout the entire experimental exposure. Species colonization rates decreased significantly in 2020 compared to 2019 in both treatments ($p_{\text{Stubai+3.3K}} < .001$ and $p_{\text{Furka+4.4K}} = .013$) and leveled off at initial colonization rates.

Averaged across years, species loss rates in warming treatments were higher by a factor of 2.28 compared to Stubai control and 3.07 compared to Furka control ($\bar{X}_{\text{Stubai+3.3K}} = 0.41 \pm 0.18$; $\bar{X}_{\text{Stubaictrl}} = 0.18 \pm 0.10$; $\bar{X}_{\text{Furka+4.4K}} = 0.43 \pm 0.19$; $\bar{X}_{\text{Furkactrl}} = 0.14 \pm 0.10$). Colonization rates in warming treatments were higher by a factor of 1.50 compared to Stubai control and 1.26 compared to Furka control ($\bar{X}_{\text{Stubai+3.3K}} = 0.24 \pm 0.21$; $\bar{X}_{\text{Stubaictrl}} = 0.16 \pm 0.10$; $\bar{X}_{\text{Furka+4.4K}} = 0.24 \pm 0.24$; $\bar{X}_{\text{Furkactrl}} = 0.19 \pm 0.10$; Figure S1; note

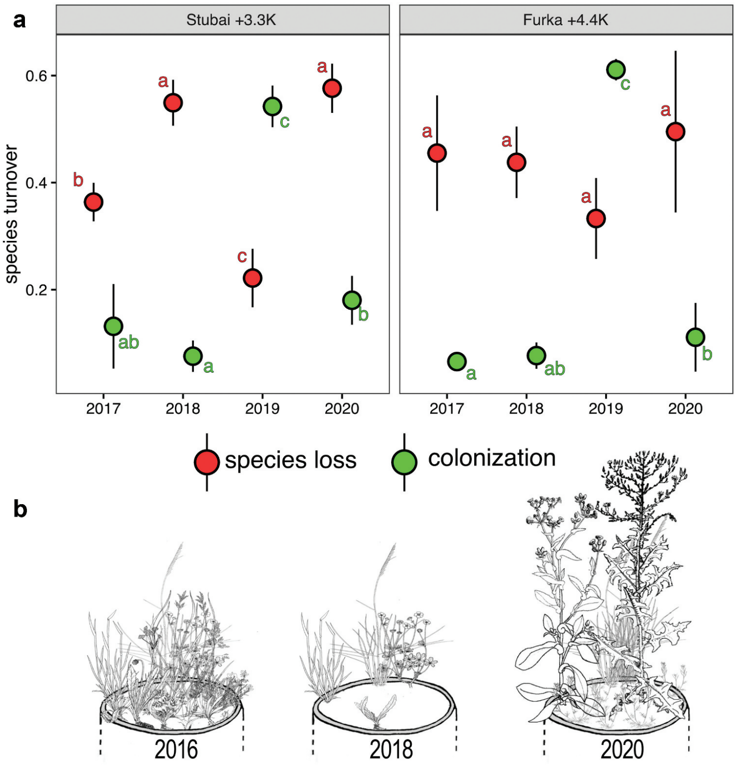

Figure 2. (a) Yearly rates of species loss and gain in two warmed mountain plant communities. Warming combined with drought led to destabilized communities gradually losing native species, creating a window of opportunity for the colonization of novel species after the severe drought in 2018. For in situ control communities, see Figure S1. Shown are mean local rates of species loss and gain (*n* = 9) and standard errors (*p* < .05). Letters indicate differences across years per treatment. (b) Schematic of turnover of species composition at three time steps under warmed conditions: initially and after two and four years of climatic exposure. Here, the typically dense and low-statured mountain plant community from Furka (Switzerland) was disrupted by interacting stressors in 2018, creating windows of opportunity for novel species to colonize. Note that only one native species (*Nardus stricta*) was able to persist over a four-year warming period, and tall-statured, highly competitive novel species started to dominate the translocated communities from 2019 on, in both proportions of aboveground biomass (AGB) species richness. Sketches adapted from Jäger and Rothmaler (2017).

strong interannual differences as indicated by the high standard deviation, especially for colonization under warming).

Proportions of native vs. novel species in AGB across years

In both climatic controls at Furka and Stubai, mountain plant communities showed low colonization rates of novel species (Figure S3A and Table S1). By the end of the experiment, novel species accounted for 2.00 ± 0.04 percent and 1.00 ± 0.03 percent of mean community AGB at the control mesocosms installed in situ at Stubai and Furka, respectively (Figure S3B). In contrast, after translocation to warmer and drier conditions, mountain plant communities showed high susceptibility to the colonization by novel species particularly after the severe drought year 2018 (Figure 3a). In 2019, fourteen out of thirty-three and twenty-four out of twenty-six species present across all replicates were novel species in the Stubai +3.3K and Furka +4.4K treatments, respectively (Table S1). Novel species such as *Lolium perenne* L., *Holcus lanatus* L., *Taraxacum* sect. *Ruderalia* Weber, *Lactuca serriola* L., *Sonchus asper* L. Hill, and *Cerastium holosteoides* Fr. dominated mountain plant communities from both origins in 2019, accounting for 56 ± 1.1 percent and 63 ± 0.37 percent of mean community AGB under the Stubai +3.3K and Furka +4.4K treatments,

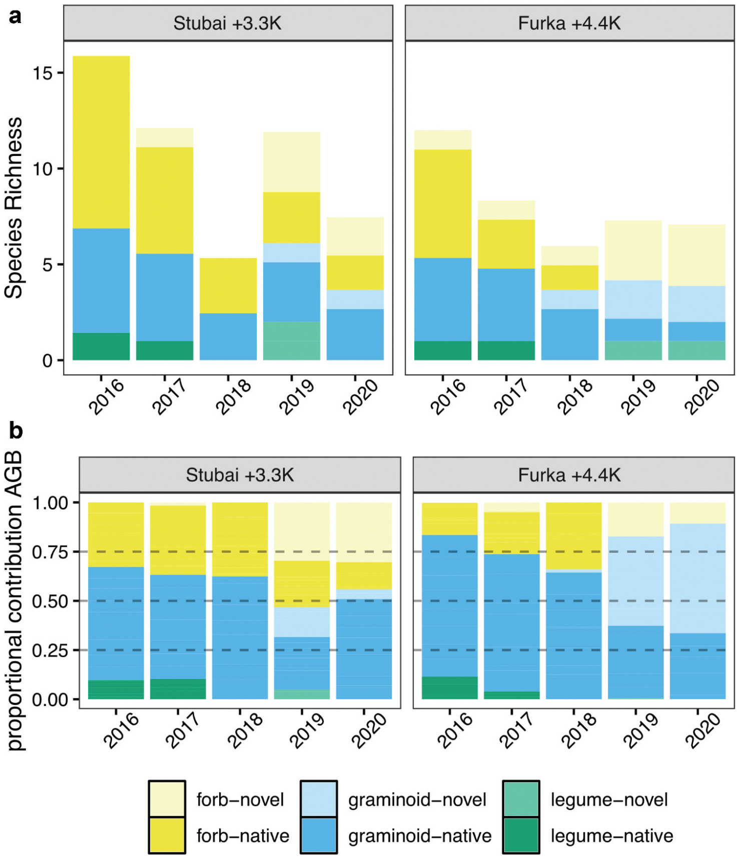

Figure 3. (a) Mean species richness of warmed mountain plant communities split by plant functional groups (PFG) and resident status. In both warming treatments the presence of native species is declining with time and novel species began dominating plant communities after the 2018 drought. (b) Proportional contribution of aboveground biomass (AGB) split by PFG and resident status in warmed plant communities. Relative contributions of PFGs to community productivity remain stable across years even though proportions of native and invading species have changed significantly (see also Figure S2).

respectively (Figure 3b). Whereas novel species proportion decreased in the Stubai +3.3K treatment to 39 ± 0.26 percent in 2020, it increased to 74 ± 0.31 percent in the Furka +4.4K treatment.

At Stubai control, the relative contribution of PFGs to community aboveground biomass remained stable (Figure S2). At Furka control only graminoids decreased their relative contribution to community AGB from 2016 to 2020 (p = .024). Forbs and one legume (*Trifolium alpinum* L.) showed no significant changes in relative contribution to community AGB across years at Furka control. Despite strong changes in species identity and colonization by novel species under warmed conditions, we found no significant difference in PFG proportions to AGB across years irrespective of site of origin, indicating within-PFG replacement. Though year-to-year fluctuations in PFG proportions remained insignificant, we found a tendency of increased forb proportions at cost of graminoid proportions one year after the drought in the Stubai +3.3K treatment and during the year of the drought in the Furka +4.4K treatment (Figure 3b and Figure S2). Further, we found an increase in legume proportions to AGB from 2016 to 2017 (p = .017) in the Stubai +3.3K treatment (Figure S2), which is likely biased by low replicate number (n_{2016} = 10; n_{2017} = 5). Notably, there was no legume present in the year of the severe drought (2018) in the Stubai +3.3K warming treatment, whereas two novel legumes (*Vicia hirsuta* Fisch., *Vicia tetrasperma* Moris.) were found post drought in 2019.

Discussion

Our study provides critical insights regarding the dynamics of mountain plant community turnover when exposed to abrupt climate warming followed by an extreme drought, a combination of stressors with increasing likelihood in the near future (Turner et al. 2020; Intergovernmental Panel on Climate Change 2021; Stephan et al. 2021). We found increasing species turnover in mountain plant communities and thus local species loss under climate warming and observed local native species losses already after the first year of abrupt warming in 2017. We provide evidence that interacting climate change drivers, such as sudden warming processes interacting with a severe drought event, drive a threshold response of the studied plant communities. Specifically, we illustrate that climatic extremes may result in gradually thinned-out and less colonization-resistant communities (Kreyling, Jentsch, and Beierkuhnlein 2011), with native species first disappearing, thereby providing windows of opportunity for novel species to appear.

Native species responses

Most native species in warmed mountain communities experienced tremendous diebacks. In particular, forbs such as *Campanula scheuchzeri* Vill., *Leontodon hispidus* L., and *Geum montanum* L. did not persist post drought. Interestingly, the few native species, such as *Nardus stricta* L. persisting under Furka +4.4K, *Alchemilla vulgaris* L., *Veronica chamaeadrys* L., or *Plantago lanceolata* L. persisting until the end of the experiment under Stubai +3.3K, were species common in semi-natural grasslands in central Europe with distributional and elevational ranges that encompass the warmed treatment conditions or were found in only a few replicates, indicating individual-specific persistence. Further, only two native alpine graminoid species (*Anthoxanthum alpinum* Schur and *Nardus stricta* L.) persisted post drought (2019) in the Furka +4.4K treatment. Though the role of graminoids under climate change is controversial (Bardgett, Mommer, and De Vries 2014; Klanderud, Vandvik, and Goldberg 2015; Olsen et al. 2016; Rosbakh et al. 2017; Stampfli et al. 2018), here we found a high persistence of two species to drought, potentially due to their clonal, long-lived life cycle, representing the inertia of some mountain species and making it difficult to study long-term effects in warming experiments. However, interannual fluctuations in productivity and low presence rates of these native species in the replicates leave the exact mechanism of persistence unresolved in this study. Moreover, results may have been overestimated by our experiment, because it is likely that limited rooting space (Körner, Hoflacher, and Wiser 1978) in our experimental setup affected soil hydrological processes, making a direct comparison to natural mountain plant communities difficult. Further, this experimental constraint may have been extrapolated due to a general soil water depletion in the lowland study region (Landesamt für Umwelt 2020) after the extreme drought year (2018) followed by another extraordinarily dry year in 2019 (see Figure S4 for in situ measured soil moisture in warmed mesocosms).

In a previous study within the same experimental setup, Berauer et al. (2019) did not find significantly increased productivity of plant communities under warmed conditions, most likely due to the severe drought in the experimental treatment compared to climatic controls (see Figure S4). This aligns with previous studies that found negative drought effects nullifying benefits from warming (De Boeck et al. 2016; Lamprecht et al. 2018; Tomiolo, Bilton, and Tielbörger 2020; Schuchardt et al. 2021). Yet, our observed decreases in native species' AGB proportions and local diebacks of native species align with findings from other experimental studies (e.g., Rumpf et al. 2018; Oldfather and Ackerly 2019), critically discussed simulations (Dullinger et al. 2012; Cotto et al. 2017), and permanently installed plots at the long-term GLORIA site in Schrankogel, Austria (K. Steinbauer et al. 2020). In the latter study, the cover of most mountain species declined, and the local loss of native species became more frequent over time. Moreover, the same study concluded that gaps arising from native species diebacks were not immediately filled by native or novel species. This indicates that the mechanism facilitating novel species colonization in mountain communities is most likely not competitive pressure. Instead, increasing climatic unsuitability for native species (occasionally combined with local mechanical disturbance) leads to an initial loss of native species, resulting in potential windows of opportunity for novel species, given that such species have colonization opportunities.

Sensitivity of mountain plant communities to compound climatic change

Meineri et al. (2020) found that mountain plant communities have low invasion resistance after disturbance because mountain species typically lack competitive traits such as tall stature, large leaves, heavy seed rain, or fast and opportunistic growth. Moreover, seedling establishment of mountain species is poor outside their maternal environment and community (Meineri, Spindelböck, and Vandvik 2013; Basto et al. 2018; Haynes et al. 2021), increasing the risk of unsuccessful sexual reproduction under climate warming. Further, Vázquez-Ramírez and Venn (2021) concluded that warming alone had no significant impact on seed germination and establishment in most studies, whereas reduced precipitation had a strong negative impact. The high rates of local species loss between 2016 and 2018 in our study are likely the direct result of abiotic conditions, particularly interactions between warming and drought.

Another crucial and often ignored factor that may explain our observed local native species loss is the phenological cues of single species. Mountain specialists are adapted to or can at least tolerate well short growing seasons (Körner 2021). The extension of growing seasons in temperature-limited mountain ecosystems under climate warming may play an essential role in generating windows of opportunity for novel species from lowland: whereas mountain species senesce early in the season, novel species continue to grow and reproduce (Alexander and Levine 2019; K. Steinbauer et al. 2020). Berauer et al. (2019) showed that warmed plant communities suffered severely from the persistent European-wide drought in 2018 (indicated by an early overall senescence). This can be interpreted as low resistance toward persistent drought effects, subsequently providing opportunities for colonization by novel species. Here, we report a significant increase in species colonization for mountain plant communities subjected to strong warming in the year after the severe drought relative to all other years.

This indicates that the nonadditive effect of abrupt warming and drought has gradually destabilized communities and created an ideal window of opportunity for novel, highly competitive species that occur locally at the recipient lowland site, such as *Lolium perenne* L., *Holcus lanatus* L., *Taraxacum* sect. *Ruderalia* Weber, *Lactuca serriola* L., *Sonchus asper* L. Hill, and *Cerastium holosteoides* Fr., irrespective of site of origin. Further, our findings suggest that once a canopy opening has formed (either through the progression of the warming treatment itself or by an additional extreme event like the drought in 2018) and potentially invading species are present in the matrix (see Lembrechts et al. 2018), community structural changes can happen quickly and may result in the dominance of novel species. Interestingly, our observed patterns under warming and drought did not differ between the site of a plant community's origin (subalpine Stubai 1,850 m.a.s.l. and alpine Furka 2,440 m.a.s.l) even though community structure and phenological cues, and thus single species life cycles, differed tremendously, with only five shared native species (*Campanula scheuchzeri* Vill., *Leontodon hispidus* L., *Rhinanthus glacialis* Personnat, *Rumex alpestris* Jacq., and *Scorzoneroides helvetica* (Mérat) Holub) in the climatic control communities. Thus, a new research frontier is emerging in understanding system response to future climatic regimes that push plant communities across ecotones. Despite the feasibility constraints when translocating plant–soil mesocosms from pristine mountain ecosystems, our study highlights the importance of investigating climate change drivers—that is, increased warming and decreased precipitation—separately, to enhance mechanistic understanding of the relative importance of each of the climatic drivers to community stability and turnover. In our study, the effect of persistent warming, drying, and the extreme drought of 2018 could not be disentangled because our experimental setup explored the general net effect of future climate scenarios.

The documented time lag between loss of native species and colonization by novel species supports our hypothesis that canopy openings in mountain plant communities will not be filled immediately but gradually when disturbance interactions yield critical threshold conditions (e.g., due to nonadditive climate extremes or anthropogenic disturbances) suitable for novel species to appear. This is in line with K. Steinbauer et al. (2020), who found that open space in high-elevation mountain communities was not filled immediately. This demonstrates that abiotic factors, namely, climatic unsuitability, were dominant over novel biotic competition. Such threshold dynamics potentially play a crucial role for the high inertia of mountain ecosystems, creating the so-called extinction debt. In our experimental translocation study, we found strong native species loss, because unlike previous studies exploring the extinction debt under natural conditions, we manipulated both climate (warmer and drier conditions) and novel competitor seed rain (from available matrix species pool at low elevation), with the latter factor actively removing the dispersal barriers that are still present in natural mountain ecosystems. It is likely that in previous studies investigating extinction debt, experimental treatments were not severe enough or focused on warming alone. Such a tendency was supported by Nomoto and Alexander (2021), who found the strongest impacts of novel species on population growth under the highest warming scenario, and Lembrechts et al. (2016, 2018), who found that anthropogenic disturbances create gaps, thereby enhancing the establishment success of novel species. This highlights that mountain plant communities show some resistance to warming per se; however, warming reduces resilience to subsequent stressors. Continuing warming (longer experimental exposure) or single events such as drought can launch the loss of native species and create windows of opportunity (Diez et al. 2012) that lead to colonization by novel species.

Extreme events may facilitate novel species establishment in semi-natural grassland communities, and the positive and stabilizing effect of species diversity on native species recovery of AGB was nullified under novel species presence (Vetter et al. 2020). In line with suppressed species recovery potential (see also De Boeck et al. 2018), our results show that disturbed mountain communities that are dominated by novel species likely remain unstable; for example, local species loss rates for mountain plant communities subjected to strong climate warming remained high during the postdrought recovery phase. A potential explanation for the second highest species turnover rates in the last year of our experiment is the dominance of annual ruderal species that took advantage of free space and resources in the year after the drought but did not persist longer than one growing season, irrespective of site of origin. An important factor that likely influenced our findings is the limited recovery potential of native species due to (1) a lack of native species seed rain from the matrix and (2) limited reproduction from native species within the mesocosm due to the applied land use regime (the annual harvest of AGB in mid-June to the beginning of August). The latter point is important for late-flowering species originating from the Furka site with no historical harvest adaptation except extensive sheep grazing. However, we consider the harvest influence minor due to the fast and early annual phenological cycle of alpine species.

Given the limited recovery potential of native species in our experimental setup, it is likely that communities shift toward an alternative stable state dominated by novel perennial species in the future. In natural mountain ecosystems, postdisturbance recovery will highly depend on the return interval of interacting climate stressors and propagule dispersal of both novel and native species.

Plant functional group replacement

Overall, we found strong changes in community structure as evidenced by local loss of native species, colonization by novel species, and shifts toward community productivity being dominated by novel species under warming. In previous studies, native species recovery was found to be suppressed under novel species presence in experimentally planted communities (Vetter et al. 2020) or after disturbances favoring growth of novel species over natives (Pinto and Ortega 2016). Here we found that two native graminoid species (*Poa pratensis* L. and *Lolium perenne* L.) as well as one native forb (*Plantago lanceolata* L.) were able to increase their postdrought dominance in 2020 in the Stubai +3.3K treatment, whereas none of the native species regained their predisturbance dominance in the Furka +4.4K treatment. The only legume native to Furka +4.4K (*Trifolium alpinum* L.) was lost during the severe drought in 2018. *Trifoilim repens* L. and *Trifolium pratense* L., common species in the Stubai +3.3K treatment during the first years of the experiment, were lost in the year of the severe drought (2018). One native (*Vicia hirsuta* Fisch.) and one novel (*Vicia tetrasperma* Moris.) legume were found post drought in 2019, indicating both species-specific recovery potentials and limitations (Isbell et al. 2015; Wilfahrt et al. 2021). Further, the loss of legumes after the severe drought may be partially attributed to the loss of mycorrhizal soil mutualists suppressing legumes post drought recovery (Prudent et al. 2020; Yang et al. 2021), though we lack the data to test this. A potential reason for the high colonization by novel species after drought might be the lack of a mountain species seed pool in the surrounding matrix (no native species seed rain). Yet, it is likely that lowland species, which are known to be highly competitive, would have outcompeted mountain species. Nevertheless, this mechanism was excluded by the experimental design.

Interestingly, relative contributions of graminoids versus forbs to community productivity did not change significantly over time and irrespective of site of origin (subalpine Stubai 1,850 m.a.s.l. and alpine Furka 2,440 m.a.s.l) due to self-replacement of species within the same PFG. Others have found functional dissimilarity of traits between native and novel species to be crucial to allow novel species colonization in warmed but undisturbed mountain communities (Catford, Jansson, and Nilsson 2009; Alexander, Diez, and Levine 2015“”). This highlights that under less severe climate scenarios, novel invading species might be forced into competitive niche carving. The observed PFG self-replacement irrespective of site of origin is likely the result of disturbance-induced windows of opportunity that promote novel species similar to natives for replacement. Further, our findings emphasize the need to focus on underlying functional traits and stronger—threshold- and biome-crossed—experimental gradients in future studies to detect mechanisms that may become critical in the future.

Conclusion

The diverse alpine and subalpine plant communities of mountain regions are vulnerable to nonadditive effects of interacting stressors such as warming and drought, especially once single species are close to their respective trailing edge. We report clear threshold responses in community dynamics, namely, abrupt increases in the dominance of novel species, when prone to sudden and compound climatic change. We suggest that competitive pressure from novel species on the native community is not the sole mechanism by which such abrupt changes occur. Instead, we show that climatic extreme events destabilized mountain plant community structure and provided windows of opportunity for novel species to establish. Notably, lost native species were replaced by novel species of the same plant functional group, with legumes being most adversely affected by warming and drought. Interacting climatic stressors are likely to increase the vulnerability of mountain plant communities in the near future.

Acknowledgments

We thank Erika Hiltbrunner and Christian Körner for climate data and valuable feedback on an earlier version of the article, as well as Peter Wilfahrt and Franklin Alongi for fruitful discussions.

Author contributions

AJ developed and designed the research project, developed and framed the research question and contributed to data collection and the writing of the article. MAS developed and framed the research question and contributed to data collection and data analysis and the writing of the article. JG developed and framed the research question and contributed to data collection and data analysis and the writing of the article. BJB developed and framed the research question and contributed to data collection and data analysis and the writing of the article. MB developed and framed the research question and contributed to data collection and the writing of the article. AvH contributed to data collection and the writing of the article. NY contributed to data analysis and the writing of the article.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

We are grateful to the Federal Ministry of Education and Research (BMBF) for funding this research (SusAlps; grant numbers 031B0027C, 031B0516C, 031B1067C). This study is also part of AJ’s research project MindTheGap! financed by the Upper Franconian Trust (Oberfrankenstiftung; Grant No. OFS FP00237). Additionally funded by the German Research Foundation grant number 491183248. Funded by the Open Access Publishing Fund of the University of Bayreuth.

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Drought erodes mountain plant community resistance to novel species under a warming climate

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Fig. S1 Low rates of species disappearance and appearance at climatic control treatments reflecting stable and inert mountain plant communities (Stubai = 1850 m a.s.l, Furka = 2440 m a.s.l). Note that y axis is scaled as in Fig. 2 for warmed plant communities to facilitate comparisons. Shown are mean disappearance and appearance rates (n=9) and standard error (*p*<0.05).

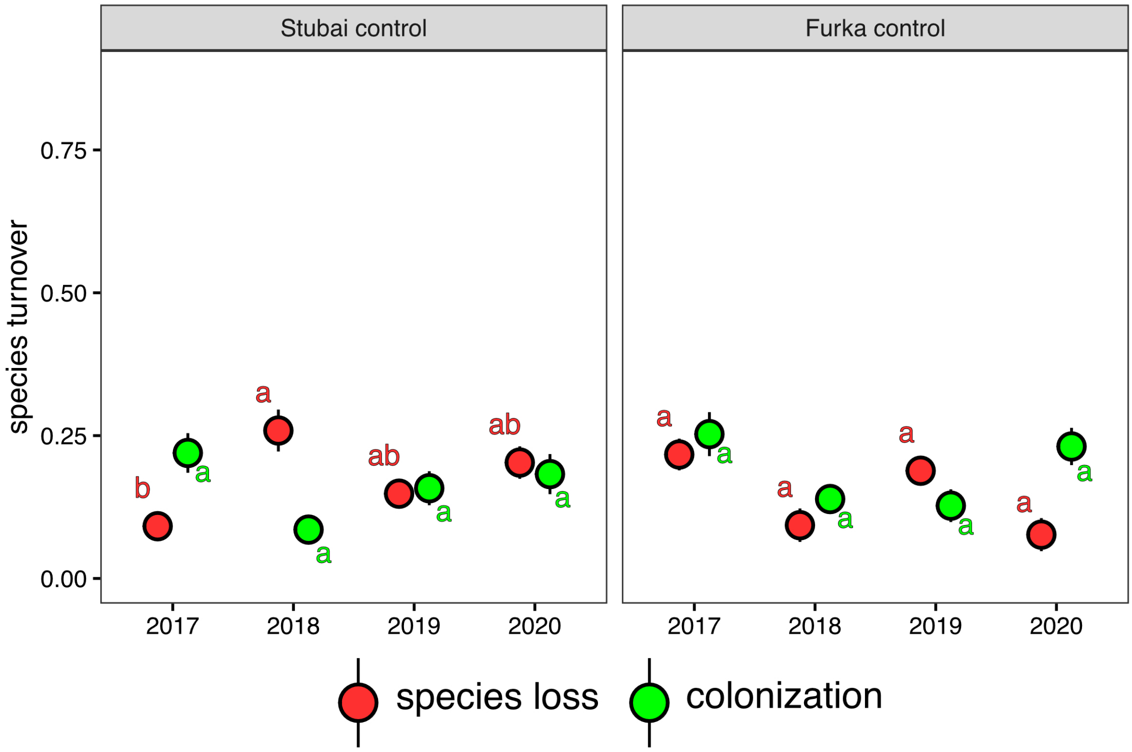

Fig. S2 Shown are mean proportional contributions to above ground biomass AGB (n=9) per PFG and standard error (*p*<0.05). In both warmed mountain plant communities proportions of PFGs to AGB stayed stable across years as indicated by Tukey's year wise comparison of each PFG. Only legumes at Stubai +3.3K increased their proportional contribution to AGB from 2016 to 2017. While proportions to AGB stayed stable for all PFGs at the Stubai control site (1850m a.s.l), we found a significant increase in forb proportions on the cost of graminoids at the Furka control site (2440m a.s.l).

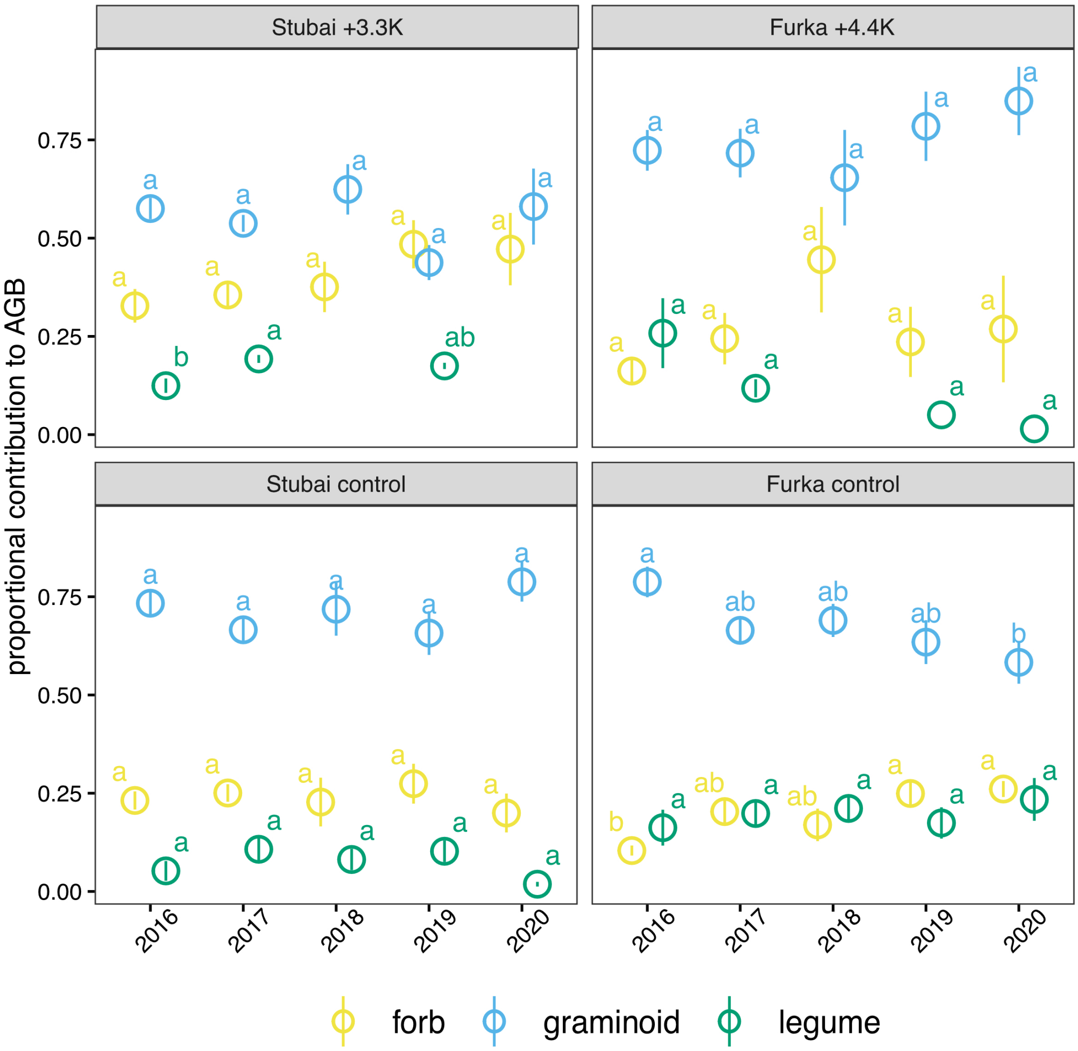

Fig. S3 **A** Mean species richness of control plant communities split by PFG and resident status. In both control treatments the presence of native species stays stable over time while only one novel forb species is invading into plant communities after the drought in 2018. PFG proportions to species richness show little fluctuations through time. **B** Proportional contribution of above ground biomass (AGB) split by PFG and resident status in warmed plant communities. Relative contributions of PFGs to community productivity remains at pre-warming equilibrium. Note that in contrast to warmed communities (Fig. 2 B) novel species did not significantly contribute to AGB of any PFG.

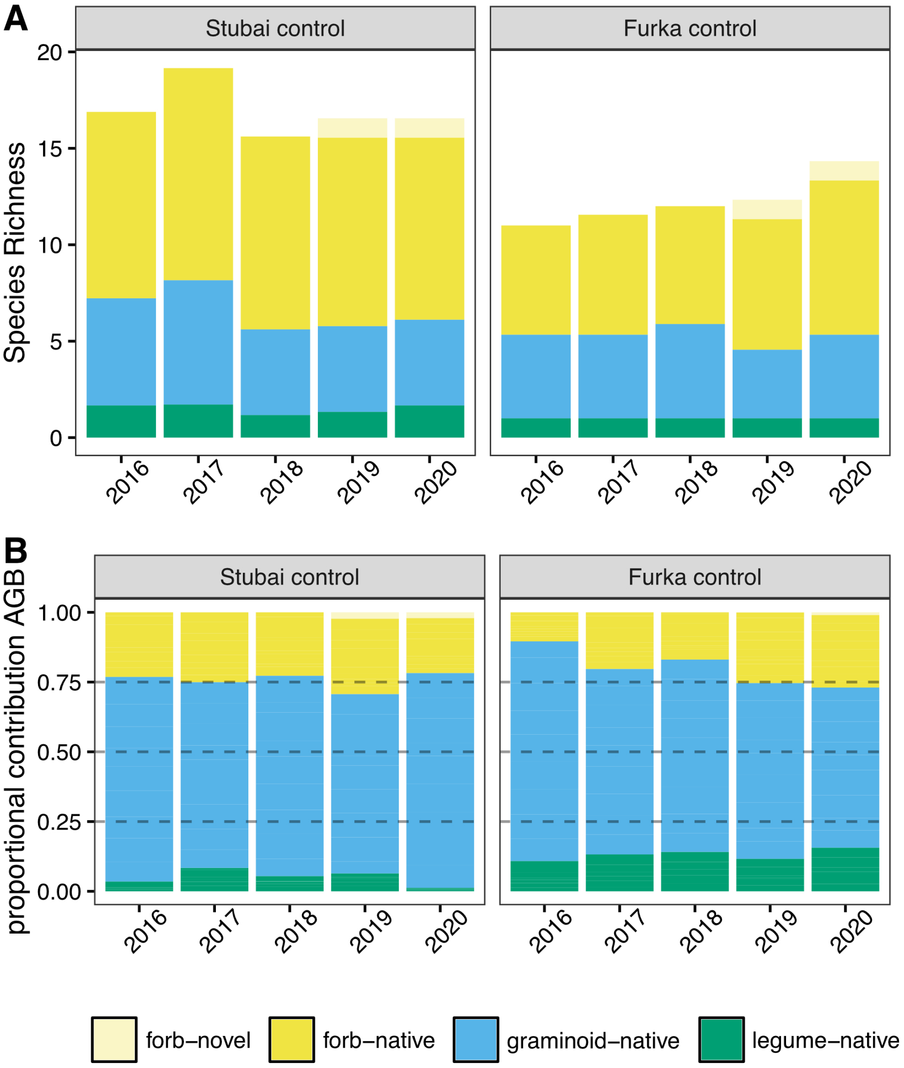

Fig. S4 Mean daily soil moisture at -5cm for the experimental exposure time at the recipient site Bayreuth. Green shaded areas indicate time between growing season start and day of biomass harvest. Dashed line indicates a soil moisture threshold of 15 vol % to facilitate comparisons between years and treatments. Grey bars represent daily precipitation. Note the different water holding capacities of the three different soil types and that soil moisture never fully recovered after the 2018 drought (as in winter 2017 across all three soil types).

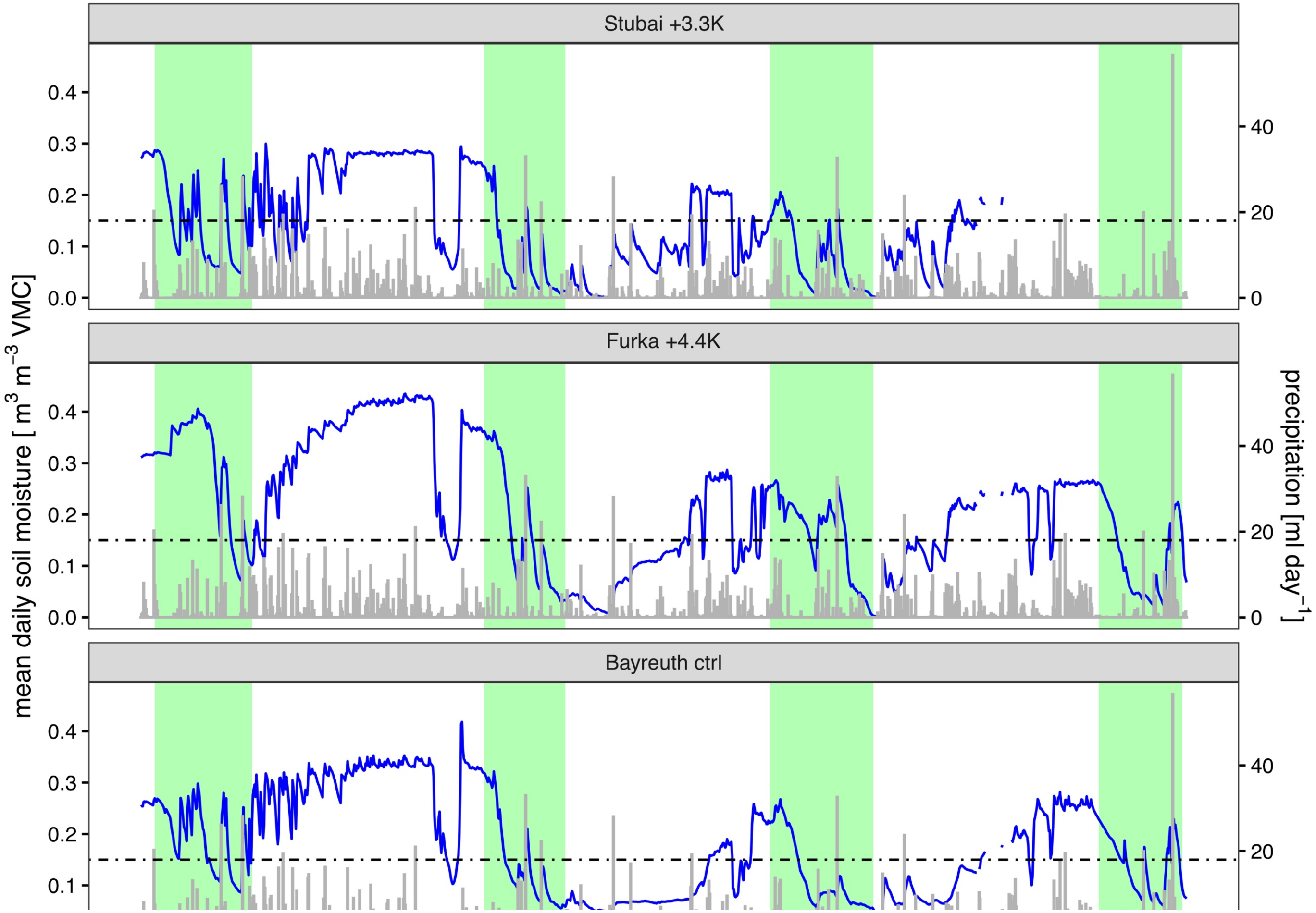

Table S1 Species presence in two warming treatments. Shown are species' last present year and number of replicates of that particular species in that particular year. Species native to a particular treatment are marked bolt. Note that the majority of species present in the last year of the experiment (2020) are novel species in warming treatments while native species are present in only few replicates or disappeared in previous years. In contrast, only one novel species per site appeared at control treatments.

Species Name	*Stubai Control*	*+3.3K*	*Furka Control*	*+4.4K*
Achillea millefolium L.	**2020 ; 6**	**2020 ; 1**	-	2020 ; 1
Agrostis capillaris L.	**2020 ; 9**	**2020 ; 5**	-	2020 ; 2
Alchemilla vulgaris L.	**2020 ; 7**	**2019 ; 4**	-	-
Alopecurus pratensis L.	-	-	-	2019 ; 1
Anthoxanthum alpinum Schur	-	-	**2020 ; 9**	**2019 ; 2**
Anthoxanthum odoratum L.	**2020 ; 3**	**2017 ; 1**	-	-
Arrhenatherum elatius L.	-	-	-	2020 ; 1
Bartsia alpina L.	-	-	**2019 ; 1**	-
Bellis perennis L.	**2016 ; 1**	-	-	-
Bistorta officinalis Delarbre	**2019 ; 1**	**2019 ; 1**	-	-
Campanula barbata L.	-	-	**2020 ; 4**	**2018 ; 1**
Campanula scheuchzeri Vill.	**2020 ; 3**	-	**2020 ; 3**	**2017 ; 1**
Cardamine hirsuta L.	-	2020 ; 3	-	2020 ; 1
Carduus crispus L.	-	2017 ; 1	-	-
Carex curvula All.	-	-	**2020 ; 7**	**2018 ; 4**
Carex pallescens L.	**2019 ; 1**	**2017 ; 1**	-	-
Carum carvi L.	**2020 ; 2**	**2017 ; 1**	-	**2016 ; 6**
Centaurea jacea L.	-	2020 ; 1	-	2020 ; 1
Centaurea nigra L.	-	-	-	2019 ; 1
Cerastium holosteoides Fr.	**2020 ; 3**	**2020 ; 2**	-	2020 ; 3
Chaerophyllum hirsutum L.	**2020 ; 5**	**2016 ; 4**	-	2019 ; 1
Chenopodium album L.	-	2019 ; 1	-	-
Cirsium oleraceum L.	**2018 ; 1**	-	-	-
Collomia grandiflora Lindl.	-	2020 ; 3	-	2020 ; 3
Convolvulus arvensis L.	-	2019 ; 1	-	2020 ; 1
Crepis conyzifolia A. Kern	-	-	**2016 ; 4**	**2017 ; 3**
Crocus vernus Mill.	**2020 ; 2**	-	-	-
Dactylis glomerata L.	**2020 ; 9**	**2020 ; 2**	-	2020 ; 1
Deschampsia flexuosa L.	-	2017 ; 3	-	-
Epilobium obscurum Schreb.	-	2019 ; 2	-	-
Euphrasia minima Jacq.	-	-	**2020 ; 3**	**2016 ; 3**
Festuca pratensis Huds.	**2019 ; 5**	**2017 ; 7**	-	2020 ; 1
Festuca rubra L.	**2020 ; 9**	**2020 ; 7**	-	2020 ; 2
Gentiana punctata L.	-	-	**2020 ; 3**	-

Geranium pratense L.	-	**2018 ; 2**	-	-
Geranium sylvaticum L.	2020 ; 2	-	-	-
Geum montanum Gouan L.	-	-	**2020 ; 5**	**2017 ; 1**
Geum rivale L.	**2020 ; 1**	**2016 ; 1**	-	-
Gnaphalium supinum L.	-	-	**2020 ; 2**	-
Helictotrichon pubescens Huds.	-	2016 ; 1	-	-
Helictotrichon versicolor Vill. Pilg.	-	-	**2020 ; 1**	**2018 ; 2**
Heracleum sphondylium L.	-	2019 ; 1	-	-
Hieracium alpinum L.	-	-	**2020 ; 1**	-
Holcus lanatus L.	-	2020 ; 3	-	2020 ; 2
Homogyne alpina L. Cass.	-	-	**2020 ; 9**	**2017 ; 3**
Lactuca serriola L.	-	2020 ; 1	-	2020 ; 1
Lapsana communis L.	-	2020 ; 1	-	2020 ; 1
Leontodon autumnalis L.	**2016 ; 1**	-	-	-
Leontodon hispidus L.	**2020 ; 6**	**2018 ; 1**	**2020 ; 8**	**2017 ; 2**
Leucanthemopsis alpina L.	-	-	**2020 ; 2**	**2016 ; 2**
Leucanthemum ircutianum DC.	**2020 ; 4**	**2020 ; 1**	2020 ; 1	2020 ; 1
Lolium perenne L.	**2020 ; 4**	**2020 ; 7**	-	2020 ; 4
Luzula alpina Hoppe	-	-	-	**2018 ; 1**
Luzula lutea (All.) DC.	-	-	**2020 ; 7**	-
Lysimachia nemorum L.	**2017 ; 1**	-	-	-
Mutellina adonidifolia (J.Gay) Gutermann	-	-	**2020 ; 9**	**2018 ; 1**
Myosotis alpestris F.W.Schmidt	**2019 ; 2**	-	-	-
Nardus stricta L.	-	-	**2020 ; 7**	**2020 ; 6**
Papaver rhoeas L.	-	2019 ; 4	-	2019 ; 1
Phleum pratense L.	**2020 ; 2**	**2017 ; 2**	-	-
Pilosella piloselloides (Vill.) Soják	-	2020 ; 2	-	-
Pimpinella major Wallr. ex Steud.	**2020 ; 1**	**2018 ; 1**	-	-
Plantago lanceolata L.	**2020 ; 6**	**2020 ; 2**	-	**2019 ; 3**
Poa alpina L.	-	-	**2020 ; 8**	**2018 ; 5**
Poa pratensis L.	**2020 ; 2**	**2020 ; 3**	-	2020 ; 2
Potentilla aurea L.	-	-	**2020 ; 9**	**2018 ; 7**
Primula veris L.	**2020 ; 1**	**2016 ; 2**	-	-
Prunella vulgaris L.	**2020 ; 2**	**2016 ; 3**	-	-
Ranunculus aconitifolius L.	-	-	**2020 ; 1**	**2017 ; 1**
Ranunculus acris L.	**2020 ; 9**	**2017 ; 1**	-	-
Ranunculus alpestris L.	**2017 ; 2**	-	-	-
Ranunculus montanus Willd.	**2017 ; 1**	**2017 ; 5**	-	-
Rhinanthus glacialis Personnat	**2020 ; 2**	-	**2016 ; 1**	-
Rumex acetosa L.	**2020 ; 9**	**2019 ; 1**	-	2019 ; 1

Rumex alpestris Jacq.	**2016 ; 2**	**2017 ; 3**	**2020 ; 1**	-
Scorzoneroides helvetica (Mérat) Holub	**2020 ; 6**	**2019 ; 2**	**2020 ; 7**	**2017 ; 4**
Senecio vulgaris L.	-	2020 ; 1	-	2020 ; 1
Sibbaldia procumbens L.	-	-	**2020 ; 5**	-
Silene latifolia Poir.	**2019 ; 1**	**2020 ; 1**	-	-
Soldanella alpina L.	-	**2016 ; 1**	-	-
Sonchus asper L. Hill	-	2020 ; 1	-	2019 ; 1
Stellaria graminea L.	-	2019 ; 1	-	-
Taraxacum sect. Ruderalia Weber	**2020 ; 1**	**2020 ; 4**	-	2020 ; 2
Trifolium alpinum L.	-	-	**2020 ; 6**	**2017 ; 3**
Trifolium pratense L.	**2020 ; 4**	**2017 ; 4**	-	-
Trifolium repens L.	**2020 ; 5**	**2017 ; 1**	-	-
Trisetum flavescens L. P. Beauv.	**2020 ; 2**	**2019 ; 1**	-	-
Veronica chamaedrys L.	**2020 ; 9**	**2019 ; 3**	-	2019 ; 2
Veronica filiformis Sm.	**2017 ; 1**	-	-	-
Veronica hederifolia L.	-	2019 ; 1	-	2019 ; 2
Veronica montana L.	-	**2017 ; 2**	-	-
Veronica persica Poir.	-	-	-	2019 ; 1
Vicia hirsuta Fisch.	-	2019 ; 1	-	2020 ; 1
Vicia tetrasperma Moris	-	2019 ; 3	-	2019 ; 1
Vicia villosa Roth	**2020 ; 1**	-	-	-
Viola biflora L.	-	2017 ; 1	-	-

Manuscript 3

Increases in functional diversity of mountain plant communities under warming is mainly driven by species turnover under warming (2023; *OIKOS*; doi: 10.1111/oik.09922)

Max A. Schuchardt, Bernd J. Berauer, Anh Le Duc, Johannes Ingrisch, Yujie Niu, Michael Bahn, Anke Jentsch

PFT measurements in Stubai valley (above) and Furka Pass (below) in summer 2020, © M. Schuchardt

OIKOS

Research article

Increases in functional diversity of mountain plant communities is mainly driven by species turnover under climate change

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Oikos
2023: e09922
doi: 10.1111/oik.09922
Subject Editor: Bente J. Graae
Editor-in-Chief: Pedro Peres-Neto
Accepted 27 June 2023

Warming in mountain regions is projected to be three times faster than the global average. Pronounced climate change will likely lead to species reshuffling in mountain plant communities and consequently change ecosystem resilience and functioning. Yet, little is known about the role of inter- versus intraspecific changes of plant traits and their consequences for functional richness and evenness of mountain plant communities under climate change. We performed a downslope translocation experiment of intact plant-soil mesocosms from an alpine pasture and a subalpine grassland in the Swiss and Austrian Alps to simulate an abrupt shift in climate and removal of dispersal barriers. Translocated plant communities experienced warmer and dryer climatic conditions. We found a considerable shift from resource conservative to resource acquisitive leaf-economy in the two climate change scenarios. However, shifts in leaf-economy were mainly attributable to species turnover, namely colonization by novel lowland species with trait expressions for a wider range of resource use. We also found an increase in vegetative height of the warmed and drought-affected alpine plant community, while trait plasticity to warming and drought was limited to few graminoid species of the subalpine plant community. Our results highlight the contrast between the strong competitive potential of novel lowland species in quickly occupying available niche space and native species' lack of both the intraspecific trait variability and the plant functional trait expressions needed to increase functional richness under warming and drought. This is particularly important for the trailing range of many mountain species (i.e. subalpine zone) where upward moving lowland species are becoming more abundant and abiotic climate stressors are likely to become more frequent in the near future. Our study emphasizes mountain plant communities' vulnerability to novel climates and biotic interactions under climate change and highlights graminoid species as potential winners of a warmer and dryer future.

Keywords: alpine grassland, functional diversity, invasion, species turnover, traitspace, translocation

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Introduction

Mountain regions are known to warm three times faster than global average temperatures (Pepin et al. 2015, IPCC 2021). The highest deviations from global average occur during the winter and lead to an elongation of the growing season (Körner 2021). There is general agreement that mountain plant species 1) adapt to novel climates through intraspecific plasticity (Rixen et al. 2022), 2) track their optimal climatic niche to higher elevations (Steinbauer et al. 2018) or nearby 'escape-refugia' (Scherrer and Körner 2011, Körner and Hiltbrunner 2021) or 3) lag behind climatic changes due to a high rate of inertia and thus likely blur local extinction patterns (Dullinger et al. 2012, Alexander et al. 2018, Nomoto and Alexander 2021).

Observational studies in mountain regions have so far reported a lack of native species replacement by novel lowland species. Still, some observational studies in mountain plant communities have found a thermophilisation of species (Lamprecht et al. 2018, Steinbauer et al. 2020) or a reduction in range size and abundance of cold-adapted species (Rumpf et al. 2018, Steinbauer et al. 2022). In contrast, many experimental studies (Alexander et al. 2015, Meineri et al. 2020, Vandvik et al. 2020, Margreiter et al. 2021) suggest that competitive pressure on native mountain species is likely increasing under climate change due to novel plant-to-plant interactions affecting the biotic niche (Eltonian dimension (Elton 1926)). Increasing competition by novel lowland species in combination with native species loss will likely affect ecosystem structure and functioning. Moreover, plant growth in cold biomes is traditionally known to be restricted by temperature and growing season length, which results in low nitrogen (N) mineralization rates (Grogan and Chapin 2000, Huber et al. 2007) and N availability (Mayor et al. 2017). Such a narrow abiotic niche (Grinnellian dimension (Grinnell 1917)) mostly favors species with a rather resource conservative growth strategy (Körner 2021). However, mineralization rates are expected to increase under climate warming (Wang et al. 2016, Salazar et al. 2020). Warming in combination with the climate change-induced elongation of the growing season is likely increasing the abiotic niche of mountain ecosystems – when not restricted by water availability. Climate models predict that precipitation patterns in the European Alps will change along with climate warming (Mastrotheodoros et al. 2020, Böhnisch et al. 2021), especially in its seasonal distribution with an elevated risk of summer drought for many subalpine areas (Spinoni et al. 2018, IPCC 2021, Stephan et al. 2021). The likely increased drought risk for mountain regions is especially important as the effects of warming and drought have been found to be opposing (De Boeck et al. 2016, Volk et al. 2021). While warming alone generally releases mountain plant communities from abiotic limitations, drier conditions increase abiotic stress. Various studies have shown contradictory results from the interactive effect of warming and drought compared to warming alone. As an example, De Boeck et al. (2016), Berauer et al. (2019), Schuchardt et al. (2021) and Niu et al. (2023) found large die-backs of native species resulting from the synergistic impacts of warming and drought. In particular, De Boeck et al. (2016) found that heat spells combined with drought had strong effects on the aboveground productivity of alpine plant communities, while heat spells alone had no significant impact. A follow up study in the same experiment (De Boeck et al. 2018) found strong legacy effects of combined warming and drought in mountain grassland communities shifting community structure post-drought (Klanderud et al. 2015, Rosbakh et al. 2017, Collins et al. 2022a, Müller and Bahn 2022). Environmental filters, such as the drought imposed in the De Boeck et al. (2018) study, select individuals based on their responses and thus help shape community structures which have specific functional trait compositions (Keddy 1992, Lavorel and Garnier 2002).

Functional trait expressions are descriptive indicators of growth and resource use strategy of single plant species and the communities they assemble. The range of trait expressions, from acquisitive to conservative, observed within a plant community can thus be used as a description of niche space available to the species within it. Niche space will be affected by climate change mainly through the modification of resource availability and the arising shifts in competitive outcomes between species. Functional diversity is a valuable measure to quantify resource use complementarity and niche dynamics (Dehling and Stouffer 2018, Ceulemans et al. 2019). The impact of climate change on plant communities' functional diversity and the resulting changes in plant resource-use strategies remains poorly explored (Díaz et al. 2016, Carmona et al. 2021). This is especially true for cold biomes and mountain ecosystems (de Bello et al. 2013, Bjorkman et al. 2018, Thomas et al. 2020, Asplund et al. 2022, Rixen et al. 2022). Mountain plant communities' functional diversity may be low because of large-scale environmental filtering due to limited resource availability (e.g. short growing seasons) which leads to high functional evenness and trait convergence sensu de Bello et al. (2013). Such limited resource availability results in a conservative growth strategy (dominated by species with low specific leaf area (SLA), high leaf dry matter content (LDMC), and a small stature (Körner 2021)) with plant-to-plant interactions being more facilitative than competitive (Callaway et al. 2002, Körner 2021). On the other hand, climate warming may relieve mountain plant communities from limited resource availability, thus expanding available abiotic niche space (Rumpf et al. 2018, Hagedorn et al. 2019). An abiotic niche space expansion will likely cause niche filling through 1) intraspecific plasticity of native species (single species niche divergence) as a consequence of limitation-relief (Bolnick et al. 2011, Rixen et al. 2022) or 2) novel lowland species filling up unoccupied niche space bringing novel trait expressions (Alexander et al. 2015, Munson and Sher 2015, Nomoto and Alexander 2021) – both processes increase functional diversity (Zanzottera et al. 2020).

High functional diversity – that is, greater variation in resource use than species diversity (Craven et al. 2016) – has been shown to enhance ecosystem functions such as productivity (Tilman et al. 1997, Díaz and Cabido 2001, Hooper et al. 2005, Chanteloup and Bonis 2013, Brun et al. 2019) and the stability of productivity through time (Polley et al. 2013, Craven et al. 2016). Furthermore, increased functional diversity was found to enhance resilience to disturbances like droughts (Hallett et al. 2017, Craven et al. 2018) or resilience to colonization by novel species (Dukes 2001, Cavieres 2021). The three key measures to assess functional diversity are: 1) functional richness – the spread of trait values across species within a plant community (occupied trait space); 2) functional evenness – the degree to which species biomass is distributed in the niche space and 3) functional divergence – the abundance-weighted, species-specific distance from the center of gravity (the mean of all species) in the functional space indicating the degree of resource use differentiation across species (Villéger et al. 2008, Mouillot et al. 2013). So far, little is known about how climate change in mountain regions will alter these measures of functional diversity and their underlying ecological processes. As an example, intraspecific trait variation (ITV) was found greater in species with large range sizes and lower median elevations (Rixen et al. 2022). High ITV likely leads to an increased capability to respond to climate warming (Jónsdóttir et al. 2022). In contrast, small ranged species are expected to suffer from climatic changes as their ability to track climate change is limited through low ITV. The general uncertainty how single species perform in future communities is complicated by the upslope shift of novel lowland species, which bring novel functional trait expressions into mountain communities and may render any trait plasticity of the native species negligible, as well as the interacting, sometimes antagonistic, effects of the expected changes in temperature, water availability, and length of growing season with climate change.

Mountain plant communities with low functional richness, high functional evenness, and low functional divergence are likely more vulnerable to climate change, as buffering of extremes (through trait complementarity) is limited and unoccupied trait space may be available for competing colonizers (Dukes 2001, Vetter et al. 2018, Haider et al. 2022). In a study across 117 vegetation surveys, Bjorkman et al. (2018) found that temperature-driven changes in plant trait expressions were generally strong across the tundra and alpine biome with soil moisture being direction-decisive. Further, this study found a biome-wide increase in vegetative height, decreases in LDMC, and increases in leaf nitrogen and SLA, mainly because of species turnover due to colonization of available niche space by novel species. These shifts from rather resource conservative towards more resource acquisitive trait expressions under climate change are supported by leaf economic theory (Wright et al. 2004, Reich 2014) and by findings from Read et al. (2014), van Zuijlen et al. (2021) and Stanisci et al. (2020), with the latter two additionally highlighting the importance of local soil moisture.

To test the interactive effect of warming and drought on shifts in mountain species trait expressions, the role of novel species in filling unoccupied trait niches, and their implications on functional diversity, we have translocated plant-soil mesocosms from the European Alps downslope to a warmer and drier climate. The translocation of plant communities outside their maternal environments creates an experimentally abrupt shift in climate conditions, simultaneously manipulating temperature and precipitation, and removes dispersal barriers. This approach combines future abiotic stressors and novel biotic interactions for many mountain species at the trailing edges of their range where both climate change and novel competitive outcomes are expected to be the most severe. After five years of exposure to the novel climate, we measured the traits of 1551 leaves of all present species to elucidate dynamics in resource-use strategy via functional richness, evenness, and divergence. In situ measured traits are a valuable asset to account for intraspecific trait variation, which is often ignored when using data-base derived trait means across various study sites and habitats with different life histories (Albert et al. 2011, Bolnick et al. 2011). Our study addresses three questions: 1) how will community biomass and species-specific trait expressions respond to the net effect of interacting warming and drought? 2) to what degree are observed shifts in trait expressions driven by intraspecific trait variation of native species and by turnover and the arrival of novel lowland species? 3) how will functional richness, functional evenness and functional divergence respond to the net effect of interacting warming and drought?

Material and methods

Experimental setup

In the spring of 2016, 36 intact plant-soil mesocosms were extracted from two experimental sites for downslope translocation (for detailed methods see Berauer et al. 2019). Plant communities from the high elevation site Furka (2440 m a.s.l.; Switzerland) represent alpine pasture vegetation (*Caricetum curvulae*; dominated by perennial species) (Hefel and Stöcklin 2010), while communities from the subalpine site Stubai (1850 m a.s.l.; Austria) belong to an extensively managed, semi natural subalpine grassland (*Trisetum flavescentis*; dominated by perennial species) (Bahn et al. 2009, Ingrisch et al. 2018). At the high and mid elevation site, one set of mesocosms (n = 9) was reburied as a climatic control, while another set of mesocosms (n = 9) was translocated downslope to Bayreuth (350 m a.s.l.; Germany), a typical lowland semi-natural grassland community *Arrhenatheretum elatioris* which provides the novel matrix community for warmed plant communities (Fig. 1). Plant-soil communities were 30 cm in diameter and 25 cm in depth, representing a volume shown to be sufficient to study community responses and interactions in small statured grasslands (Milbau et al. 2007) while maintaining belowground processes. Each experimental site was fenced to avoid grazing. Aboveground biomass (AGB) was harvested yearly at peak biomass.

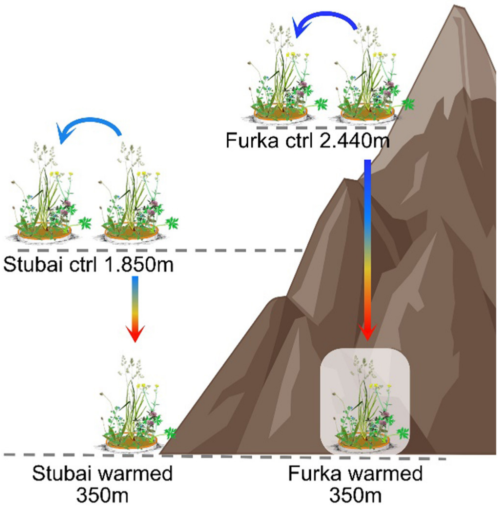


Figure 1. Experimental setup. Two mountain plant communities originating from different elevations (alpine Furka and subalpine Stubai) were reburied at site of origin as climatic control (blue arrows) and translocated downslope to Bayreuth (350 m) to simulate climate change (red arrows). Each translocation direction was replicated nine times.

Climatic parameters

The translocation scenarios represent changes of various climatic parameters such as mean annual temperature (MAT), mean annual precipitation (MAP), growing season air temperature, growing season precipitation, and growing degree days (GDD). All parameters were derived from on-site climate stations at 2 m as these represent the longest continuous time series of available climatic data but note the atmospheric decoupling described in Körner and Hiltbrunner (2018). Soil moisture was derived from horizontally installed soil moisture sensors (EcH2O 5-TM, Decagon Devices Inc., USA; EcH2O Em50, Decagon Devices Inc., USA) at −5 cm in one mesocosms at each respective experimental site (Supporting information).

Both climate change scenarios presented here are quantified as the deviation of growing season temperature at the climatic control site of origin and the recipient lowland site. Plant communities translocated from Furka to Bayreuth (Furka$_{\text{warm}}$) were exposed to a warming treatment of + 4.4°C and communities translocated from Stubai to Bayreuth (Stubai$_{\text{warm}}$) to a warming of + 3.3°C (Table 1). Five-year mean growing season precipitation was 181 mm at Furka, 397 mm at Stubai, and 166 mm at Bayreuth (note that growing season length is shorter at Furka and Stubai compared to Bayreuth; Supporting information). The number of growing degree days during the growing season increased by a factor of 4.2 for Furka$_{\text{warm}}$ and by a factor 1.4 for Stubai$_{\text{warm}}$. The start of the growing season was defined as the fifth day of five consecutive days with a mean daily air temperature higher than 5.0°C. This early season temperature threshold has been shown to primarily drive the green-up of grassland species (Scherrer and Körner 2010, Guo et al. 2018). In this study, the end of growing season was defined by the day of biomass harvest varying across sites.

Aboveground biomass

AGB of individual mesocosms was harvested in 2020, 3 cm above ground, at site-specific peak biomass (from low to high elevation sites: 29 June, 20 July, and 1 August) directly after trait measurements. AGB was sorted to species, dried at 60°C to constant weight (> 48 h) and weighed (Berauer et al. 2019, Halbritter et al. 2020). Each species was assigned a treatment level resident status ('native' or 'novel') based on whether the species occurred within any experimental mesocosm of the same origin in the year of experimental setup (2016). We defined all species present in 2016 across the 18 mesocosms per site of origin as 'native' to the respective

Table 1. Geographic and climatic characteristics of study sites from low to high elevation. Total values are calculated for the period of experimental exposure (2016–2020). Growing season start defined as the fifth day of five consecutive days with a mean daily air temperature at 2 m ≥ 5°C and end of growing season as the day of biomass harvest. Data shown was calculated from on-site weather station data. For details on the annual precipitation regime and soil moisture in mesocosms see the Supporting information.

			Experimental site (country)		
			Bayreuth (D)	Stubai (A)	Furka (CH)
Geography	Elevational belt		Colline	Subalpine	Alpine
	Coordinates		49°55′16″N 11°34′55″E	47°07′44″N 11°18′19″E	46°34′36″N 08°25′17″E
	Elevation (m a.s.l.)		350	1850	2440
Climate	Long-term mean	MAT (°C)	8.2	3.0	-0.5
		MAP (mm)	724	1097	1600
	x̄ Growing degree days (heat sum)	Total	2155	1344	403
		Growing season	885	623	210
	x̄ Temperature (°C) exposure	MAT	9.58	6.94	0.35
		Growing season	13.2	9.87	8.8
	x̄ Precipitation (mm) exposure	MAP	608	1031	1096
		Growing season	166	397	181

community. In three cases (*Geranium sylvaticum*, *Gentiana punctata* and *Sibbaldia procumbens*) community native species were assigned as 'novel'. We made these decisions using local expert knowledge and adjusted the species status accordingly (e.g. perennial species first seen in the second year of experiment due to low AGB in the year of setup as a result of the disturbance by the translocation itself). All species names were checked according to the Global Biodiversity Information Facility (GBIF 2021). We excluded biomass that we could not assign to a species (e.g. a single senesced leaf) but these cases were extremely rare and AGB amounts negligible (< 0.001 g).

Plant functional trait measurements

Following the handbook of Pérez-Harguindeguy et al. (2013), we sampled 3–5 leaves from 1–3 individuals (limited by the amount of available individuals per replicate) per species for each mesocosm (replicate) in summer 2020, for a total of 1551 leaf-samples across two climatic control communities and two warmed and drought-affected communities with each treatment replicated nine times. Fresh leaves were scanned (Portable Area Meter LI-3000C), stored in moist and cooled conditions until processing, and weighed within 48 h of sampling. We collected dry weight of single leaves after a minimum of 48 h at 60°C in the drying oven. Additionally, vegetative height (not lifted, excluding inflorescence) was measured for each individual where leaf-samples were taken.

Data analyses

Single traits across treatments

To calculate shifts in SLA and LDMC between climatic control and climate change scenarios, we collected a total of 1551 leaf-samples at an individual level (up to three individuals per species and mesocosm). Additionally, we measured vegetative height at an individual level. To test overall trait expression shifts across all species between treatments, we used linear mixed effect models with the respective trait value as response variable, treatment as fixed effect, and mesocosm-ID, individual, and species as random effects. In a separate model, we split the fixed effect 'treatment' into the three levels, 'native ctrl', 'native warmed' and 'novel warmed', to test the effect of 'resident status' on plant communities in the climate change scenarios. Next, we conducted a post hoc Tukey HSD to compare respective trait values of plants in the climate change scenario (levels: 'native warmed' and 'novel warmed') to trait values of the native community (level: 'native control') at site of origin.

We did not measure individual specific AGB but sorted biomass on a species level per mesocosm. To meet lme-model assumptions, we transformed AGB values of both sites of origin using 'Tukey's Ladder of Powers' in the *transformTukey()* function (Mangiafico 2022). For AGB we used the same lme-model structure and Tukey HSD post hoc test as for the other traits but used only mesocosm-ID and species as random effects.

To explore species-specific shifts in trait values (ITV) of native species in the climate change scenarios compared to native species remaining at the respective climatic control site, we used the same linear mixed effect model structure as above but ran single models for selected species. In all models, we analyzed both sites of origin separately as they consisted of two (ecological and botanical) different mountain plant communities (alpine versus subalpine).

Functional diversity analysis

To examine the functional diversity of mountain plant communities, we averaged the following three traits: vegetative height as well as LDMC and SLA. First, we averaged the respective trait values to the level of an individual (mean out of 2–5 leaves). Second, we averaged trait values to the level of a mesocosm (mean out of up to three individuals) and third to a treatment level (mean out of nine mesocosms for each respective experimental treatment). We did not measure specific AGB for individuals, but sorted biomass on a species level per mesocosm. Thus, we used averaged species-specific AGB out of nine mesocosms in each experimental treatment.

To examine if individual plant species shifted their functional diversity, measured by their growth form (stature and leaf-economics), upon translocation, we used the 'mFD' package (Magneville et al. 2022) to both calculate and evaluate functional spaces of single experimental treatments. We used Euclidean distances to calculate trait-based distances between single species. In this step, all four traits were equally weighted. We found the minimum mean absolute deviation (mad = 0.015) between the trait-based distances and the space-based distance in a three-dimensional space (Supporting information) with no negative eigenvalues (Maire et al. 2015). Thus, presented indices are computed in a 3D space. Next, we correlated the PCoA (Principal coordinates analysis) axis with underlying traits using linear regression models of the *mFD::traits.faxes.cor()* function (Supporting information). Further, we calculated the three fundamental functional diversity indices: functional richness, functional divergence and functional evenness (Mason et al. 2005, Villéger et al. 2008) using the *mFD::alpha.fd.multidim()* function. Here, functional richness was defined as the volume of the convex hull shaped by the species of single treatments (i.e. the filled functional space). Thus, functional richness increases as a function of a community's trait value variability values as a result of species' trait expression. Functional evenness was defined as the regularity of species abundance distribution in the functional space using the minimum spanning tree (MST) method linking all species present in a treatment. Thus, functional evenness decreases if vertex species (species with extreme trait values) are widely spread throughout functional space, indicating a wide range of resource use strategies. Functional divergence was defined as the abundance-weighted species-specific distance from the center of gravity (mean of all species) in the functional space (Villéger et al. 2008). For instance, if the most abundant species are vertex species (with extreme trait values), functional divergence and consequently niche differentiation is high.

All data analyses were performed within the R programming environment (ver. 4.2.1, www.r-project.org).

Results

Community trait responses and native species loss

Compared to their climatic control sites, we found no effect for AGB but increases in vegetative height ($p < 0.001$), decreases in LDMC ($p = 0.02$), and increases in SLA ($p < 0.001$) across all warmed and drought-affected species and replicates in the alpine plant community originating from Furka. The observed shifts in vegetative height, LDMC and SLA for the warmed and drought-affected alpine plant community were mainly driven by novel species (species not present in the initial plant community). We found increases in native and novel species' vegetative height ($p_{native} < 0.001$; $p_{novel} < 0.001$), decreases in novel species LDMC ($p_{native} = ns$; $p_{novel} < 0.01$) and increases in novel species SLA ($p_{native} = ns$; $p_{novel} < 0.001$) for the warmed and drought-affected alpine plant community compared to native species at the climatic control site (Fig. 2A).

Compared to their climatic control site, we found no effect of warming and drought on community AGB, vegetative height, LDMC, or SLA across all species and replicates in the subalpine plant community originating from Stubai (note some different species-specific responses in Fig. 4). Nevertheless, we detected leaf-trait expression differences between the group of novel species growing under the

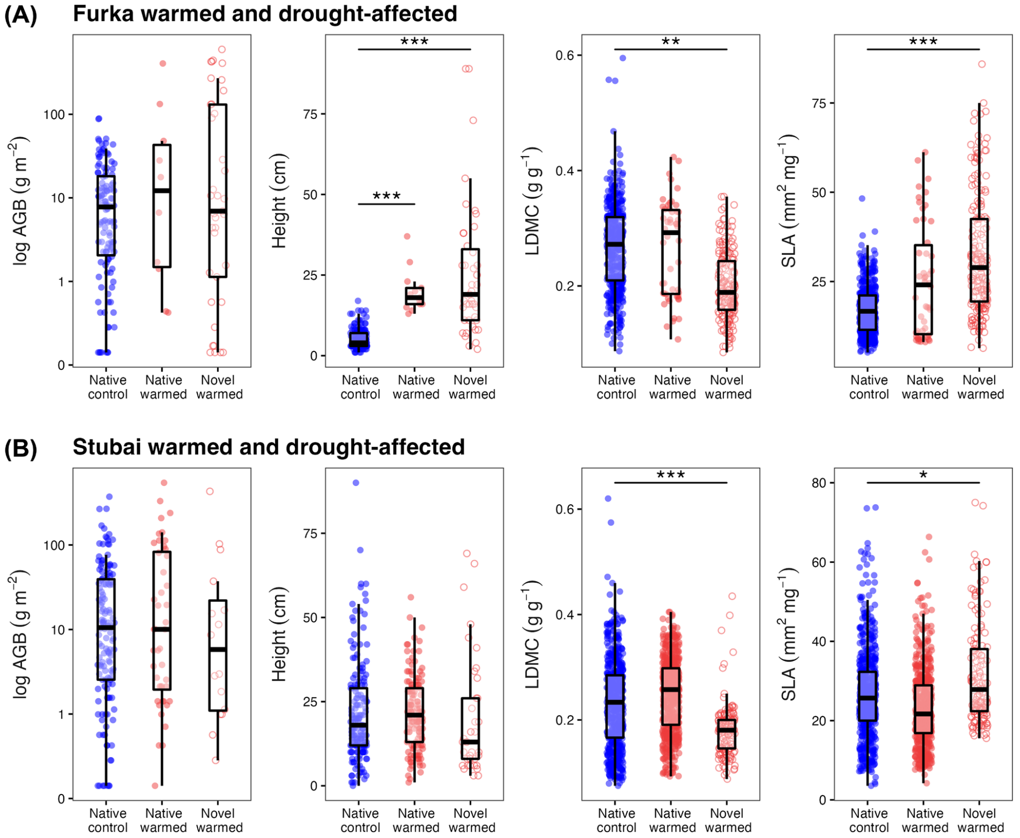
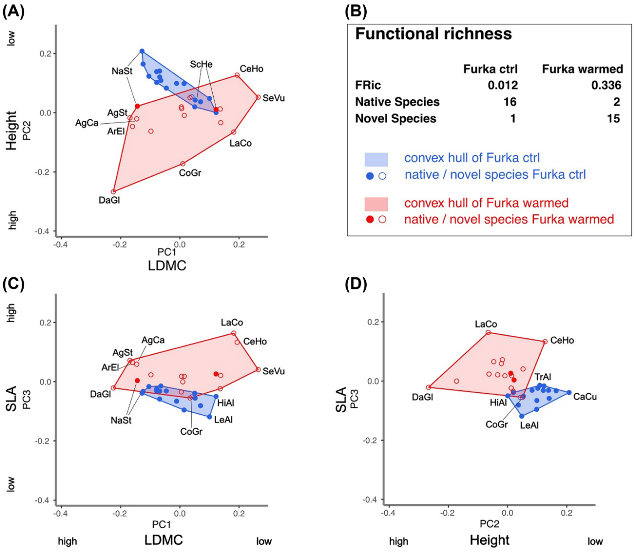


Figure 2. Plant functional trait responses between two climate change scenarios and their respective climatic control site. Shown are individual specific trait values across nine mesocosms per climatic treatment (1150 individual leaves in total). (A) Trait responses of the alpine plant community originating from Furka experiencing a + 4.4°C growing season temperature increase and (B) trait responses of the subalpine plant community originating from Stubai experiencing a + 3.3°C growing season temperature increase. Asterisks indicate significant trait shifts compared to native species at control site ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***). Note different axis scales across panels.



Functional richness

	Furka ctrl	Furka warmed
FRic	0.012	0.336
Native Species	16	2
Novel Species	1	15

Figure 3. Effect of warming and drought on the functional richness (FRic) of the alpine plant community. FRic (defined as the convex hull volume) in the climatic ctrl (blue) and in the climate change scenario (red). Compared to the climatic control site, functional richness increased as species present in the warmed plant community showed a higher variability in vegetative height, aboveground biomass, LDMC and SLA (wide range from minimum to maximum expanding the volume of the occupied trait space). Indices were computed in a three-dimensional space. Filled dots and circles indicate if a species was native or novel to the initial plant community. Species abbreviation only of selected species (Supporting information).

climate change scenario and the native species growing at the subalpine control site. For novel species in the warmed and drought-affected subalpine plant community, we found significant decreases in LDMC ($p_{native} = ns$; $p_{novel} < 0.001$) and increases in SLA ($p_{native} = ns$; $p_{novel} = 0.03$) compared to native species growing at the site of origin (Fig. 2B).

Across all replicates originating from the alpine community Furka, we found strong species turnover (loss of native species and colonization of novel species) with 16 native and one novel species at $Furka_{ctrl}$ and two native and 15 novel species at $Furka_{warm}$ (Fig. 3B). For the subalpine community from Stubai, we found 20 native species at $Stubai_{ctrl}$ and 10 native and eight novel species at $Stubai_{warm}$ (Fig. 4B).

Functional richness

For both climate change scenarios of the two mountain plant communities, we found an increase in functional richness compared to their respective climatic control site. Occupied trait space (i.e. functional richness) expanded under warming as previously unoccupied niche space was colonized by mainly novel vertex species (note symbol shape depending on resident status in Fig. 3, 4).

Furka warmed and drought-affected

Functional richness increased by 28-fold (Fig 3B) in $Furka_{warm}$ compared to $Furka_{ctrl}$, indicating the use of unoccupied niche space in the climate change scenario. Compared to $Furka_{ctrl}$, functional richness increased as species present in the translocated plant community showed a higher variability in vegetative height, aboveground biomass, LDMC, and SLA (a wide range from minimum to maximum expands the volume of the occupied trait space).

This is supported by strong species turnover and replacement of native species by novel species ($n_{native} = 2$ in 2020; *Nardus stricta* and *Scorzoneroides helvetica* while $n_{novel} = 15$). Functional richness increased mainly through the expansion of occupied trait space due to the increase in the community's vegetative height and AGB (mainly explained by PC 2; Supporting information) driven by novel vertex species (Fig. 2A, 3A). Novel fast-growing species like *Senecio vulgaris*, *Cerastium holosteoides* and *Lapsana communis* occupied the trait space of low LDMC (mainly explained by PC1; Supporting information) while novel graminoid species like *Agrostis stolonifera*, *Agrostis capillaris*, *Arrhenatherum elatius* and *Dactylis glomerata* occupied the trait space of high LDMC, indicating rather resource conservative growth (Fig. 3C). Both native species persisting until the end of the experiment, *Nardus stricta* and *Scorzoneroides helvetica*, increased their vegetative heights ($p_{NarStr} = 0.002$; $p_{ScoHel} < 0.001$) showing trait plasticity under warming and drought. SLA of *Scorzoneroides helvetica* increased ($p = 0.04$) while *Nardus stricta* remained

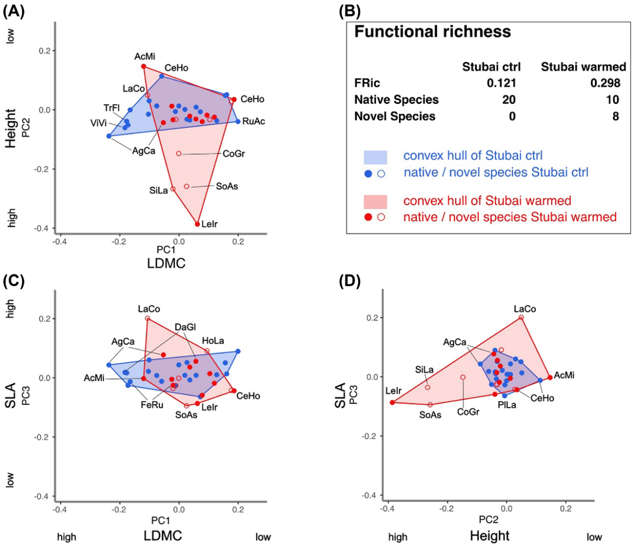


Figure 4. Effect of warming and drought on the functional richness (FRic) of the subalpine plant community. FRic (defined as the convex hull volume) in the climatic ctrl (blue) and in the climate change scenario (red). FRic increased as species present in the warmed plant community mainly showed a higher variability in vegetative height and aboveground biomass (indicated by PC2) compared to the plant community remaining at the climatic control site. Indices were computed in a three-dimensional space. Filled dots and circles indicate if a species was native or novel to the initial plant community. Species abbreviation only of selected species (Supporting information).

resource conservative, with high LDMC and low SLA level in Furka$_{warm}$.

Stubai warmed and drought-affected

We found a 2.5-fold increase in functional richness in the Stubai$_{warm}$ treatment with eight out of 18 species being novel species (Fig 4B). Functional richness mainly increased due to the vegetative height of the two novel species, *Sonchus asper* and *Silene latifolia*, and the native species *Leucanthemum ircutianum* (three minimum vertices of PC2) and *Achillea millefolium* (the maximum vertex of PC2; Fig. 4A). The increase in functional richness can be explained by two novel species (*Sonchus asper* and *Lapsana communis*) occupying the opposite extremes of PC3 (mainly displaying SLA Fig. 4C). These species increase the convex hull volume of Stubai$_{warm}$, but not the mean community SLA across all warmed and drought-affected species, rather driving the significant increase in SLA between the groups 'native control' and 'novel warmed' (Fig. 2B). We found a strong decrease in LDMC for the traditionally resource conservative graminoids surviving through the end of the experiment (*Agrostis capillaris* $p < 0.001$; *Dactylis glomerata*, $p < 0.01$; *Festuca rubra*, $p < 0.001$) in Stubai$_{warm}$ compared to Stubai$_{ctrl}$. This indicates niche divergence towards a more opportunistic, resource acquisitive, and thus rapid growth in the climate change scenario through trait plasticity of these three species. Importantly, the two other species originally occupying the resource conservative space of high LDMC at Stubai$_{ctrl}$ (*Vicia villosa* and *Trisetum flavescens*) were no longer present in Stubai$_{warm}$ at the end of the experiment.

Functional evenness

Both mountain plant communities experiencing climate change decreased their functional evenness compared to their respective climatic control site. Minimum spanning tree (mst) values increased in both climate change scenarios, with increased numbers indicating complementary resource use strategies across species (Furka$_{warm}$ versus Furka$_{ctrl}$ = 0.55-fold increase; Stubai$_{warm}$ versus Stubai$_{ctrl}$ = 0.74-fold increase; Table 2, Supporting information). Branch length of the 'minimum spanning tree' in the Furka$_{warm}$ treatment was mainly elongated, indicating a decrease in functional evenness, by one native species *Cerastium holosteoides* and the novel

Table 2. Functional diversity measures and species numbers of climatic control and respective climate change scenarios. Calculated values are based on mesocosm average trait values and are shown in Supporting information in more detail.

	Stubai ctrl	Stubai warmed	Furka ctrl	Furka warmed
Functional evenness	0.603	0.444	0.711	0.393
Functional divergence	0.881	0.767	0.774	0.916
Native species number	20	10	16	2
Novel species number	0	8	1	15

vertex species *Senecio vulgaris*, *Lapsana communis*, *Collomia grandiflora* and *Dactylis glomerata* (Supporting information). Branch length of the 'minimum spanning tree' in the Stubai$_{warm}$ treatment was mainly elongated by the native forb *Leucanthemum ircutianum* and the two novel, tall growing vertex species *Sonchus asper* and *Silene latifolia* in addition to *Lapsana communis* as a novel small statured vertex species of PC2 (Supporting information).

Functional divergence

Plant communities at both the climatic control sites and climate change scenarios showed high values of functional divergence (Table 2, Supporting information) indicating a high degree of niche differentiation and thus low resource competition. This is likely because both frequent and rare species (size of points indicates abundance) are found to be vertex species in the trait space. We found small but contrasting differences in functional divergence between the two mountain plant communities under climate change and their climatic control. Functional divergence increased slightly by a 1.18-fold in Furka$_{warm}$ and decreased slightly by a 0.87-fold in Stubai$_{warm}$. In Furka$_{warm}$, functional divergence tended to increase as vertex species with high abundance were found further away from the center of gravity (mean of all species), indicating a higher degree of niche differentiation with climate change. In Stubai$_{warm}$, functional divergence tended to decrease as species with high abundance were located closer to the center of gravity compared to Stubai$_{ctrl}$, indicating a tendency of niche convergence with climate change.

Discussion

Species adaptation to novel climates and novel species colonization are key components affecting plant community functional diversity, and thus functioning, under climate change. In a translocation experiment, we found consistent leaf-trait responses across two climate change scenarios using two different grassland types (alpine and subalpine). Leaf-trait expressions shifted from more resource conservative to resource acquisitive growth for both the alpine and the subalpine plant community. This was mainly driven by the appearance of novel species in the climate change scenarios and was rarely attributable to a plastic shift in resource use of native species. The assumed underlying mechanism, the experimentally induced extreme shift in climate conditions, favored the colonization of novel lowland species since native species seemed to lack trait expressions (e.g. big fast-growing leaves or high stature) suitable for quickly occupying niche space freed by the climate change scenarios. Novel species colonization drove patterns of three main functional diversity measures. After extreme climate change, we observed 1) a strong increase in functional richness – likely due to the (temporary) co-existence of community native and novel lowland species expanding occupied trait space, 2) a decrease in functional evenness – due to increased interspecific resource use complementarity and 3) varying responses of functional divergence depending on the degree of niche differentiation among species.

Native species loss and trait responses

In contrast to findings by Cui et al. (2018), Volk et al. (2021) and Haider et al. (2022), we did not find shifts in aboveground biomass following climate change. The previously mentioned studies found that increases in aboveground productivity were correlated with increases in temperature and peaked at sites with medium temperature increases and no water limitation. These insights highlight the adaptation of mountain species to high daytime canopy temperatures and the often-ignored atmospheric decoupling of air and tissue temperature (sensu Körner and Hiltbrunner 2018). While most mountain species can translate higher temperatures into increased AGB, our study reveals that the net-effect of warming and drought did not lead to changes in AGB. This finding is circumstantial – only fifth year AGB data consisting of surviving native and novel species is presented. We assume that previously lost native species experienced a decrease in abundance over time, highlighting the vulnerability of many mountain species to severe climate change. This pattern is supported by Steinbauer et al. (2020) that found decreases in cold adapted species cover and richness on mountain tops. The strong species turnover and native species loss found in our experiment align to the tendency of strong changes in abiotic conditions, namely the interaction of warming and drought, to drive species loss (De Boeck et al. 2016). Previous studies in our experimental setup have found very large diebacks of community native species (Berauer et al. 2019) and strong colonization by novel species with replacements becoming stronger with increasing climatic distance to the site of origin and time (Schuchardt et al. 2023a). In a common garden experiment, Haider et al. (2022) found that survival and flowering probability of the invasive forb *Senecio inaequidens* decreased with increasing climatic distance to the source population. Their finding is similar to Cui et al. (2018) who report mortality rates of 90–100% of the study species *Viola biflora* upon translocation outside the present species range. Consistent with the extensive literature highlighting native species loss following climate change, the severe climatic changes in our study led to the gradual loss of native species through time with novel lowland species propagule presence in the matrix accelerating the colonization by novel species. This is especially important as novel species dominated the shift in leaf-trait expressions towards a more resource acquisitive trait expression in the year of trait measurements (the end of the experiment).

Leaf-trait expressions shifted from rather resource conservative at control sites towards resource acquisitive in the two climate change scenarios. While this pattern was significant for all species present in the warmed and drought-affected alpine plant community (including the two native species), these shifts were only significant for novel species colonizing the warmed and drought-affected subalpine plant community as the surviving native species (n = 10) did not show a plastic response. The increases in SLA and decreases in LDMC we observed under warmed and drought-affected climate conditions are consistent with findings from various studies focusing on warming alone. As an example leaf economic theory (Wright et al. 2004, Reich 2014) suggests that leaf-economy shifts towards a more resource acquisitive growth under warming. This pattern has been observed in a cold-biome wide meta studies (Bjorkman et al. 2018), various field studies (Stanisci et al. 2020, Rixen et al. 2022) and experiments (Meineri et al. 2020, van Zuijlen et al. 2021). Our findings, combined with the consistency of previous studies in finding strong shifts in trait expressions due to species turnover under warming, highlight three important insights: 1) the lack in many mountain plant species of trait expressions that would increase colonization resistance under climate change (i.e. big and fast growing leaves or high seed output to occupy free niche space), 2) novel species bring along novel trait expressions which offer competitive advantages over native trait expressions (e.g. bigger and faster growing leaves) and 3) for many mountain species, intraspecific trait variation to adapt to novel climates is limited or overshadowed when novel species are present. Our observed shifts in intraspecific trait values were limited to a few graminoid species in the subalpine plant community and the two surviving native species in the alpine plant community (*Nardus stricta* and *Scorzoneroides helvetica*) with all trait expressions converging towards the novel matrix community (i.e. growing more resource acquisitive).

Furthermore, we found no significant increase in vegetative height for plant communities originating from the subalpine grassland Stubai when translocated downslope. Here, the lack of shifts in vegetative height for native and novel species was likely due to the absence of a dense plant community matrix at the warming and drought-affected site, reducing the need to grow vertically when AGB could spread horizontally. Contrary to the pattern in the subalpine plant communities, we found an increase in vegetative height for both native and novel species in the alpine communities. While the latter is not surprising, the increase in vegetative height of the two surviving species may point towards intraspecific trait variation as an underlying mechanism for survival under climate change (Henn et al. 2018, Rixen et al. 2022).

Functional diversity responses upon abrupt climate change

Theory (stress-gradient hypothesis sensu Bertness and Callaway (1994) and Maestre et al. (2009) and) states that interspecific competition decreases with elevation and plant-to-plant interactions become facilitative rather than competitive in alpine plant communities (Callaway et al. 2002). Thus, we expected low functional richness at both climatic control sites (as most community members share similar trait expressions) and an increase in functional richness with climate change (Harpole and Tilman 2007). We found a strong increase in functional richness in both climate change scenarios with the stronger effect for the translocated alpine plant community indicating that mainly warming and species turnover was driving the pattern as the effect of drought would have selected species with rather resource conservative trait expressions (Reich 2014). The underlying mechanism of the observed shift towards more resource acquisitive trait expression under warming and drought was mainly attributable to the (temporary) co-existence of species from different environments (the alpine or subalpine in addition to lowland), which used an overall wider range of resources (i.e. expressed as functional richness or niche space). Mountain communities are known to be more susceptible to colonization under changed climatic conditions, especially after soil disturbances (Haider et al. 2022), as they lack the competitive trait expressions to fill available niche space post-disturbance (Meineri et al. 2020). It has been shown that gaps in such communities can be quickly exploited by novel species (Dukes 2001, Milbau et al. 2013, Haider et al. 2022, Schuchardt et al. 2023a). Given the consistency of studies finding high colonization rates after soil disturbance and abrupt shifts in climate conditions, it is not surprising that we found a strong increase in functional richness due to trait space expansion in our experiment. In our study, severe climatic change led to community disturbance effects comparable to those of soil disturbances in other studies (i.e. a significant removal of native species). Consequently, this indicates two contrasting processes affecting community structure and functioning of future mountain plant communities. First, high colonization susceptibility (openness, weak biotic filter) of resident mountain plant communities will likely favor fast growing, opportunistic novel species over native species, increasing the systems' vulnerability to climate change and disturbances (Lembrechts et al. 2016, 2018, Nomoto and Alexander 2021). This is especially important at a species' trailing edge (where climatic change and novel biotic interactions are the most severe) or disturbed habitats, such as the sides of roads or trails where novel species' seeds are either already present in the matrix or vectored by humans or cattle. Second, the weak biotic filter of mountain plant communities may also facilitate native species migration to higher elevations (Lembrechts et al. 2018, Steinbauer et al. 2018) or nearby escape habitats (Körner and Hiltbrunner 2021) likely contributing to the system's high inertia (Tilman et al. 1994, Alexander et al. 2018, Figueiredo et al. 2019).

In our study, only few species showed the ability to adapt to novel climates and make use of available resources by growing more resource acquisitive e.g. *Scorzoneroides helvetica* in Furka$_{\text{warm}}$ and *Agrostis capillaris*, *Dactylis glomerata* and *Festuca rubra* in Stubai$_{\text{warm}}$. The ability to shift towards more resource acquisitive trait expression among these species indicates intraspecific plasticity allowing species to track experimentally induced changes in climatic conditions, highlighting plasticity as an important mechanism to persist within plant communities (Henn et al. 2018). Even though only a few surviving species were able to shift their trait values, these trends align with Rixen et al. (2022) who show that species with larger range sizes were found to have greater intraspecific trait variation, which likely increases survival under climate change. Conversely, two other resource conservative species (*Vicia villosa* and *Trisetum flavescens*) and two small statured species (*Prunella vulgaris* and *Trifolium repens*) present at the subalpine control site died over the course of the experiment at Stubai$_{\text{warm}}$ (data not shown but see Schuchardt et al. 2023a). This pattern likely indicates that species in the climate change scenarios had to adapt by growing taller in stature with more resource acquisitive leaves (increasing SLA and decreasing LDMC) or were outcompeted by novel species with a locally adapted resource acquisitive growth. For species originating from the alpine pasture Furka, the abrupt climate change combined with the 2018 central Europe-wide drought (Bastos et al. 2020) was likely too severe for survival (see the Supporting information for soil moisture depletion in mesocosms over the duration of the experiment), especially as these highly specialized species lack fast enough plastic responses to quickly fill available niche space. This assumption is supported by another study in the same experiment (Schuchardt et al. 2023a) showing that the loss of native species was gradual and that novel species colonization only began in 2019 after the central Europe-wide drought of 2018. Since the study presented here lacks the temporal resolution and consists of a single trait measurement at the end of the experiment, we cannot prove whether lost species showed intraspecific responses to warming and drought before going locally extinct.

We found contrasting patterns in functional divergence across the two warmed mountain plant communities. While species resource use strategies diverged for the alpine plant community in the climate change scenario, functional divergence decreased for the subalpine plant community (i.e. resource use became more even across species). These two contrasting signals are likely due to a high degree of niche differentiation of novel annual species colonizing the alpine plant communities (bringing along a higher variance in trait expressions in addition to higher proportional AGB contributions) while species contributing to major parts of the subalpine communities' productivity shared similar resource use traits (low variation in LDMC and SLA; Supporting information). This is particularly interesting as graminoid species in both climate change scenarios shifted their resource use towards the center of gravity (the mean of all species) instead of remaining in a resource conservative unoccupied niche, indicating strong species-specific competition trade-offs and likely differences in resource uptake between graminoids and tall growing forbs. While forbs likely draw resources (e.g. nutrients and water) from deeper soil layers, graminoid species are known for an increased nutrient uptake flexibility through a shallow but dense rooting system (Rosbakh et al. 2017), likely enhancing graminoids' climate change resilience but making them vulnerable to shifts in precipitation regimes (Bardgett et al. 2014, Kübert et al. 2019, Mackie et al. 2019). This observation highlights that hidden (belowground) traits likely allow the co-existence of species occupying similar aboveground niches, a mechanism that to date remains poorly explored.

Implication for mountain plant communities

Our experimental approach was unique in that we created scenarios with a strong increase in temperature, a decrease in available moisture, and the presence of novel lowland species to explicitly push mountain plant communities beyond their climatic envelopes and introduce novel biotic interactions. Consequently, our results shed some light on how mountain plant communities could respond to the net effect of climate change. We were able to highlight that the often-overlooked interaction of warming and drought pushed both mountain plant communities beyond a threshold of resistance, creating a window of opportunity for novel lowland species to colonize. The interaction of warming, drought, and the presence of many novel species in the matrix is a realistic scenario for many species at their current trailing edge, where upward moving lowland species are already present as future competitors. Today, these lowland species may be present with low abundances (at their leading edge), but their competitive potential once climate change-induced gaps are created was found to be strong in this study. In nature, the co-existence of native and upward moving lowland species will likely lead to a transient state of increased functional richness which does not necessarily indicate an increase in ecosystem function or stability but rather a shift in the community use of available resources (increased functional richness) to avoid competition (high divergence). Additionally, our study shows that an abundance weighted measure like functional divergence may primarily indicate that dominating species avoid competition while it is ignoring species turnover of small statured or less abundant species (loss of native and colonization of lowland species) happening in the background. Thus, we highlight the need for more studies exploring *in situ* species turnover along a time series under severe climatic change. We conclude that mountain plant communities' vulnerability to climate change is higher than previously reported, especially once their threshold of resistance to drought is crossed.

Alternative viewpoints

So far, species turnover in mountain plant communities has rarely been reported under natural conditions. Translocation studies like Cui et al. (2018), have found strongest species turnover rates under the most severe climatic changes. By using a very steep translocation gradient in our study, we intentionally pushed mountain plant communities beyond their climatic envelopes. It is likely that the study design overestimates the ability of lowland species to track climate change to higher elevations by completely removing dispersal barriers and excluding native mountain species seed rain from the matrix, which should be addressed in future studies with addition of native species seeds. Our approach, mimicking a severe future scenario, provoked strong species turnover resulting in the collapse of the alpine community. Our observed collapse is currently lacking in most previous translocation studies as they use less severe, 'closer future' scenarios based on true elevational gradients with intermediate steps (De Boeck et al. 2018, Nomoto and Alexander 2021). But which approach mimics a 'realistic' future scenario? We need to understand the consequences of crossing thresholds of persistence, especially knowing that many ecological responses are non-linear and threshold triggered (Collins et al. 2022b). A compartmentalization of climatic stressors ignores the interactive impacts of climate change. Rather than attempting to disentangle the effects of warming, drought, and novel species presence our approach studies the 'net effect of climate change' which should be picked up in future studies.

Funding – We are grateful to the Federal Ministry of Education and Research (BMBF) for funding this research (SUSALPS; grant number: FKZ 031B0516C). This study is also part of AJ's research project MindTheGap! financed by the Upper Franconian Trust (Oberfrankenstiftung; grant number: OFS FP00237). YN is a Humboldt fellow funded by the Alexander von Humboldt-Foundation. Open Access funding enabled and organized by Projekt DEAL.

Author contributions

Max A. Schuchardt: Data curation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Bernd J. Berauer**: Data curation (supporting); Formal analysis (supporting); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anh Le Duc**: Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Johannes Ingrisch**: Data curation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Yujie Niu**: Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Michael Bahn**: Funding acquisition (supporting); Project administration (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anke Jentsch**: Conceptualization (lead); Data curation (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (lead); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.79cnp5j1m (Schuchardt et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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Supplementary Material to:

Increases in functional diversity of mountain plant communities is mainly driven by species turnover under warming

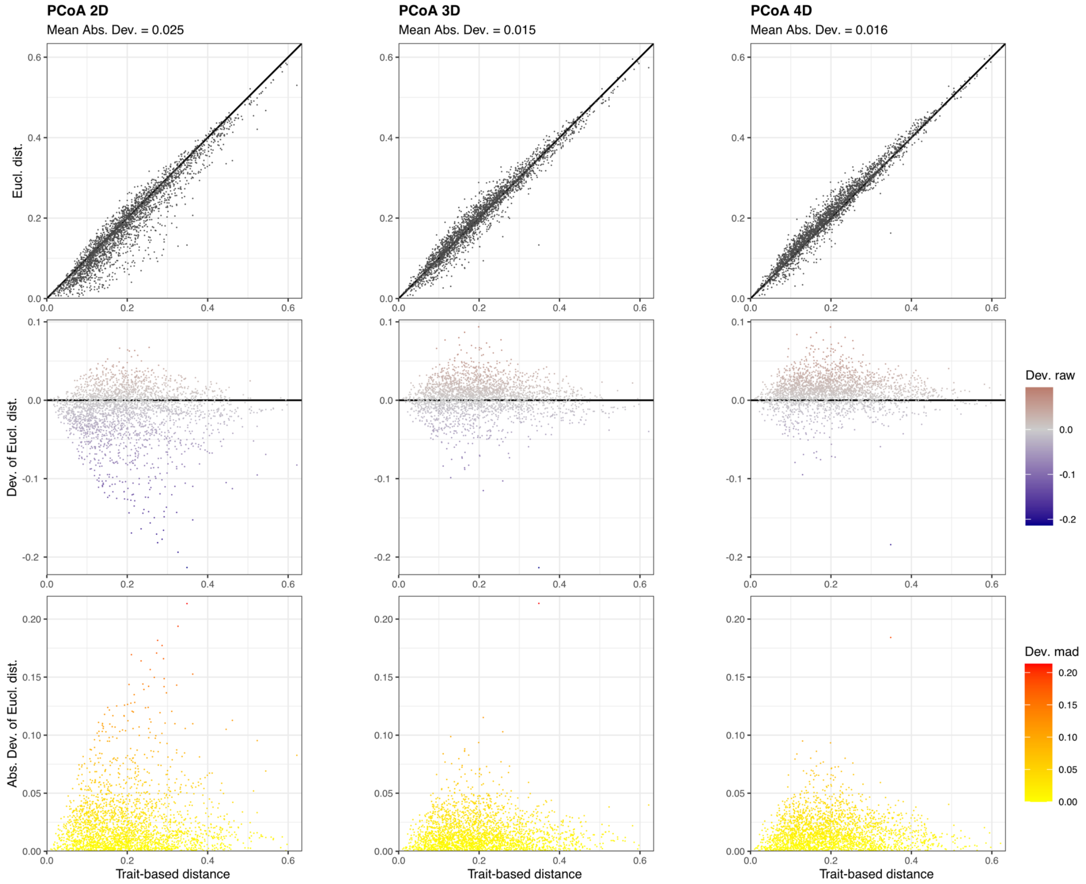


Fig. S1 Raw and absolute deviation of trait-based distance and Euclidean distance for 2, 3 and 4 dimensions.

Minimum mean absolute deviation was found for the 3D space (see scattering around 1:1 line and mad-values in top row) representing sufficient dimensions to accurately represent traits of two warmed and two climatic control plant communities in space (absolute deviation <0.1).

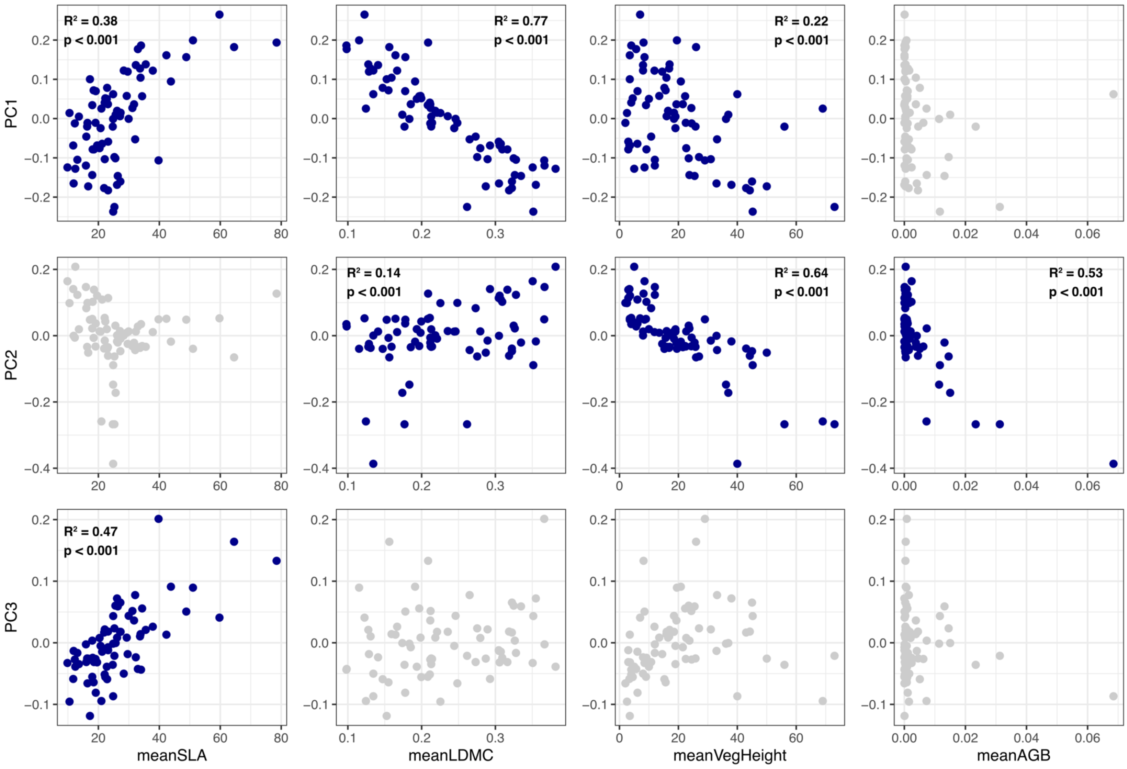
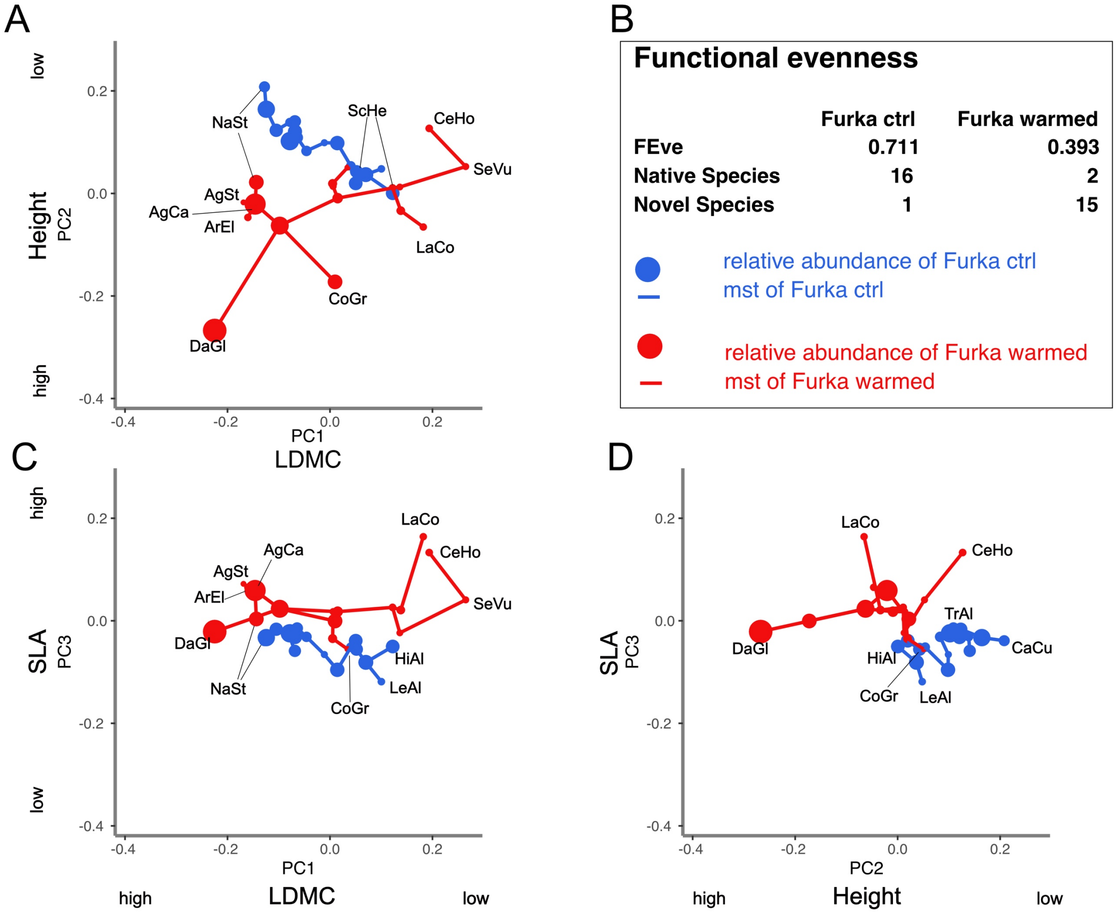


Fig. S2 Relation between traits and PCoA axis. PC1 was mainly driven by mean mesocosm LDMC, PC2 mainly by mean mesocosm vegetative height and mean mesocosm aboveground biomass, PC3 mainly by mean mesocoms SLA. Model evaluation (R^2) and significance testing derived from single linear regression.



Functional evenness

	Furka ctrl	Furka warmed
FEve	0.711	0.393
Native Species	16	2
Novel Species	1	15

● relative abundance of Furka ctrl
— mst of Furka ctrl

● relative abundance of Furka warmed
— mst of Furka warmed

Fig. S3 Functional evenness of the Furka plant community at the climatic ctrl (blue) and in the warming treatment (red). Functional evenness under warming mainly decreased as novel vertice species elongated minimum spanning tree (mst) branch length indicating an increase in effective utilization of a wider range of resource availability. Indices were computed in a 3-dimensional space. Species abbreviation only of selected species. Dot sizes correspond to relative abundance.

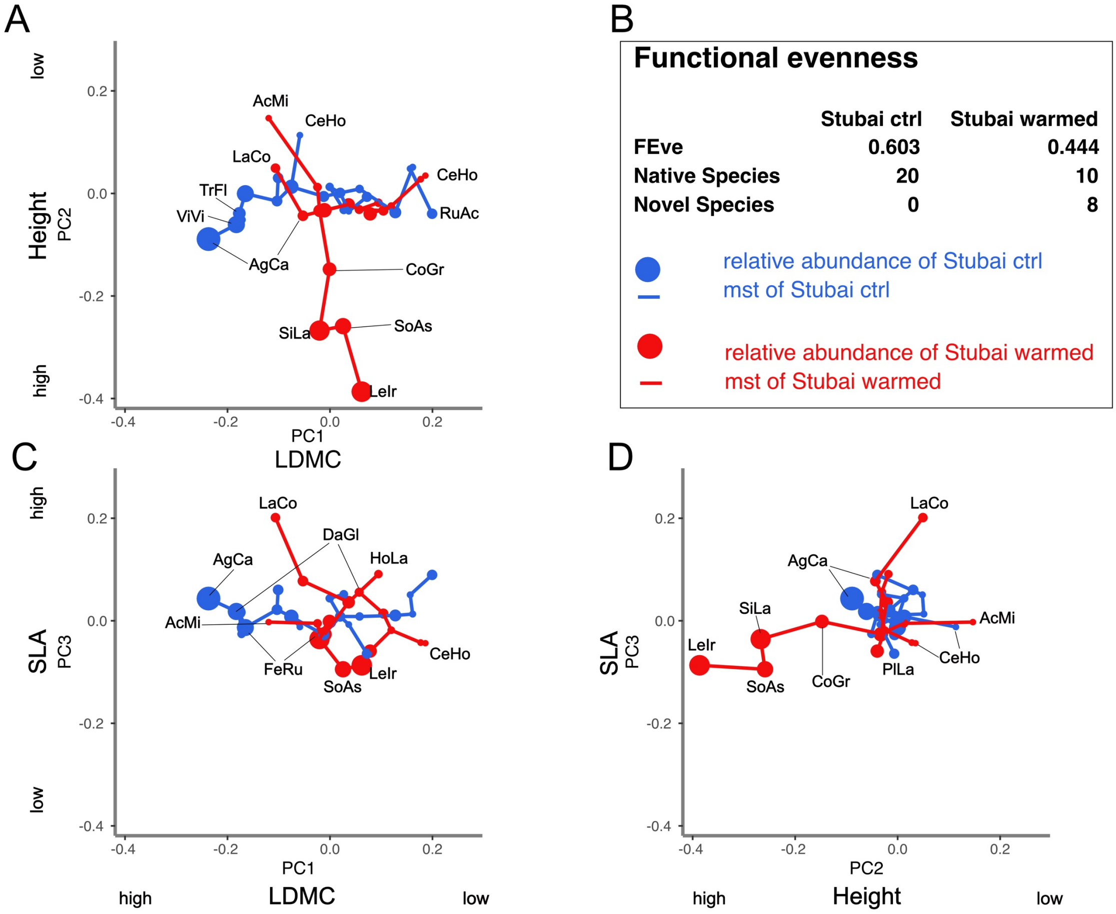
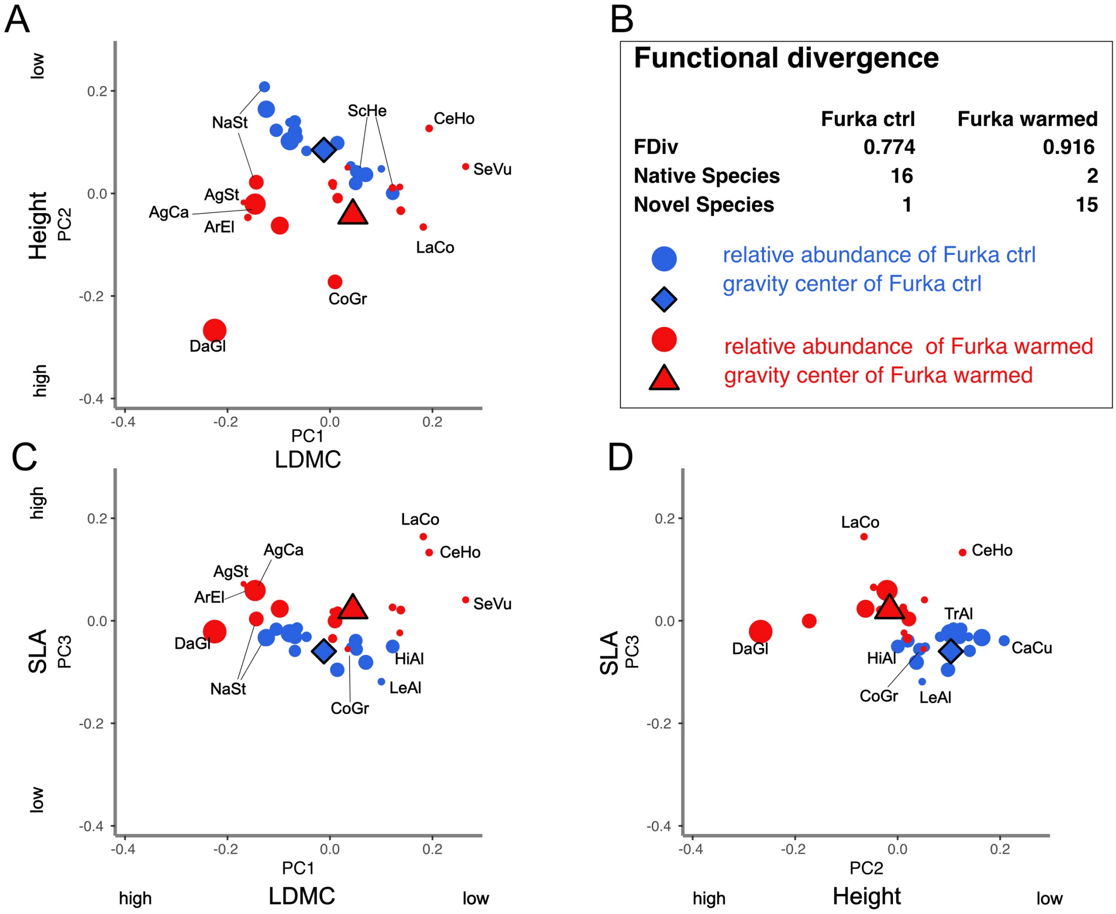
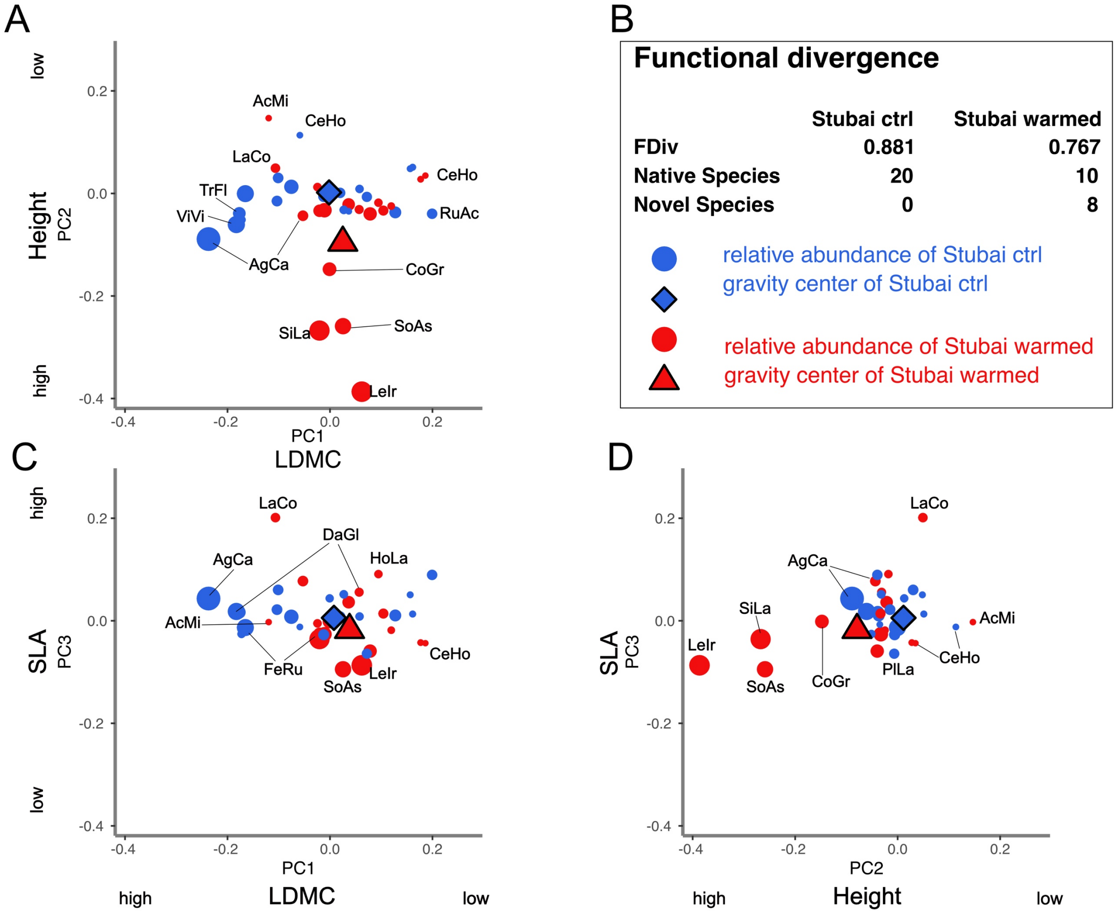


Fig. S4 Functional evenness of the Stubai plant community at the climatic ctrl (blue) and in the warming treatment (red). Functional evenness under warming mainly decreased as high statured vertice species (e.g. the native forb *Leucanthemum icutianum* and the two novel forbs *Sonchus asper* and *Silene latifolia*) elongated minimum spanning tree (mst) branch length. Indices were computed in a 3-dimensional space. Species abbreviation only of selected species. Dot sizes correspond to relative abundance.



	Furka ctrl	Furka warmed
FDiv	0.774	0.916
Native Species	16	2
Novel Species	1	15

Fig. S5 Functional divergence of the Furka plant community at the climatic ctrl (blue) and in the warming treatment (red). Functional divergence tended to increase under warming as species with high abundance were found to be vertice species further away from the center of gravity. Increased functional divergence is likely due to a high degree of niche differentiation under warming. Indices were computed in a 3-dimensional space. Species abbreviation only of selected species. Dot sizes correspond to relative abundance.



Functional divergence

	Stubai ctrl	Stubai warmed
FDiv	0.881	0.767
Native Species	20	10
Novel Species	0	8

Fig. S6 Functional divergence of the Stubai plant community at the climatic ctrl (blue) and in the warming treatment (red). Functional divergence tended to decrease under warming as species with high abundance were found closer to the center of gravity compared to Stubai ctrl. Species contributing to major parts in productivity shared similar resource use traits (low variation in LDMC and SLA in the multidimensional space). High values of functional divergence at Stubai ctrl indicate a higher degree of niche differentiation and thus less interspecific competition than at Stubai warmed. Indices were computed in a 3-dimensional space. Species abbreviation only of selected species. Dot sizes correspond to relative abundance.

Table S1 Species presence in two different mountain plant communities at climatic control and warmed sites. Shown are single species resident status per site for species where all four traits have been measured. Note the strong species turnover for the two warming treatments

Species name	Stubai ctrl	Stubai warmed	Furka ctrl	Furka warmed	Bayreuth ctrl
Achillea millefolium L.	native	native	-	invading	native
Agrostis capillaris L.	native	native	-	invading	native
Agrostis stolonifera L.	-	-	-	invading	-
Anthoxanthum alpinum Schur	-	-	native	-	-
Arrhenatherum elatius L.	-	-	-	invading	-
Campanula barbata L.	-	-	native	-	-
Campanula scheuchzeri Vill.	native	-	native	-	-
Cardamine hirsuta L.	-	invading	-		-
Carex curvula All.	-	-	native	-	-
Carum carvi L.	native	-	-	-	-
Centaurea jacea L.	-	invading	-	invading	native
Cerastium holosteoides Fr.	native	native	-	invading	native
Chaerophyllum hirsutum L.	native	-	-	-	-
Collomia grandiflora Lindl.	-	invading	-	invading	-
Convolvulus arvensis L.	-	-	-		invading
Crocus vernus Mill.		-	-	-	-
Dactylis glomerata L.	native	native	-	invading	-
Euphrasia minima Jacq.	-	-		-	-
Festuca rubra L.	native	native	-		native
Gentiana punctata L.	-	-	native	-	-
Geum montanum Gouan	-	-	native	-	-
Hieracium alpinum L.	-	-	native	-	-
Holcus lanatus L.	-	invading	-		native
Homogyne alpina L.	-	-	native	-	-
Lapsana communis L.	-	invading	-	invading	-
Leucanthemopsis alpina L.	-	-	native	-	-
Leucanthemum ircutianum Turcz.	native	native	invading	invading	-
Lolium perenne L.		native	-	invading	native
Luzula lutea All.	-	-	native	-	-
Phleum pratense L.	native	-	-	-	-
Hieracium piloselloides Vill.	-	invading	-	-	native
Pimpinella major Wallr. ex Steud.	native	-	-	-	-
Plantago lanceolata L.	native	native	-	invading	native
Poa alpina L.	-	-	native	-	-

Poa pratensis L.		native	-	invading	native
Potentilla aurea L.	-	-	native	-	-
Primula veris L.		-	-	-	-
Prunella vulgaris L.	native	-	-	-	-
Rhinanthus glacialis Personnat		-	-	-	-
Rumex acetosa L.	native	-	-	-	-
Rumex alpestris Jacq.	-	-	native	-	-
Scorzoneroides helvetica Mérat	native	native	native	native	-
Senecio vulgaris L.	-	-	-	invading	-
Sibbaldia procumbens L.	-	-	native	-	-
Silene latifolia Poir.	-	invading	-	-	-
Sonchus asper Garsault	-	invading	-	-	-
Trifolium alpinum L.	-	-	native	-	-
Trifolium pratense L.	native	-	-	-	native
Trifolium repens L.	native	-	-	-	-
Trisetum flavescens L.	native	-	-	-	-
Vicia hirsuta Fisch.	-	-	-	invading	native
Vicia villosa Roth	native	-	-	-	-

Manuscript 4

Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes (2019; *Arctic, Antarctic and Alpine Research* ; doi: 10.1080/15230430.2019.1618116)

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Fieldwork at Kaserstattalm, Stubai valley 2018 © M. Schuchardt

Esterberg Alm at the valley bottom in 2018 © M. Schuchardt

ARCTIC, ANTARCTIC, AND ALPINE RESEARCH
2019, VOL. 51, NO. 1, 215–231
https://doi.org/10.1080/15230430.2019.1618116

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Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes

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ABSTRACT

High-elevation ecosystems will experience increasing periods of above-average warmth and altered precipitation changes because of climate change. This causes uncertainties for community properties such as productivity and biodiversity. Increasing temperature may increase productivity by increasing growing season length and metabolic rate or decrease productivity by causing drought stress. Competitive outcomes between species may change with altered climatic conditions, causing shifts in community composition. This study investigates the resistance of aboveground biomass and plant community composition of montane and alpine grassland ecosystems to abruptly altered temperature and precipitation conditions. Intact plant-soil communities were translocated downslope spanning an elevational gradient of 2,090 m in the European Alps. We hypothesize that increasing temperature leads to (1) increased aboveground biomass in the absence of precipitation deficits, (2) decreased species richness, and (3) shifts in plant community composition. After one year of exposure to their new environment, aboveground biomass changes appeared to be dependent on precipitation regimes, whereas species richness declined consistently with changed climatic conditions. No deterministic shift in community composition was found. Abrupt changes in climatic conditions can lead to rapid responses of community properties, indicating that these high-elevation communities may have low initial resistance to future heat waves and droughts.

ARTICLE HISTORY
Received 10 January 2019
Revised 5 April 2019
Accepted 7 May 2019

KEYWORDS
Alpine; climate manipulation experiment; community ecology; elevational gradient; grasslands; resistance

Introduction

Temperature rise because of anthropogenic climate change is expected to be most extreme at high latitudes and elevations (Ceppi et al. 2012; Gobiet et al. 2014; Pepin et al. 2015). Temperature is a fundamental regulator of chemical and biological processes and is likely to both directly and indirectly affect plant community properties (Rustad et al. 2001). Properties such as biomass production and species diversity can be tightly linked (Fraser and Pither 2015; Hautier et al. 2015), and studying their joint responses to rapid environmental shifts can reveal additional properties of communities, such as resistance (Kreyling et al. 2017). Increased temperature within a single season can affect these properties in cold biomes by extending growing seasons for plants because of changes in snow regimes (Myneni et al. 1997; Inouye and Wielgolaski 2003; Laternser and Schneebeli 2003; Klein et al. 2016; Asam et al. 2017). In addition, higher metabolic rates at higher temperatures (Billings and Mooney 1968; Lucht et al. 2002; Larcher 2003) may increase the plant productivity of cold-adapted ecosystems. Despite these potential gains in productivity, plants may simultaneously suffer from even short-term increases in temperature. At more extreme temperatures, this may occur directly via the damage of tissue or overheated photosystems (Larcher 2003; Buchner et al. 2015). Although, well before such extremes, temperature can indirectly reduce productivity via reduced soil-water availability resulting from increased evapotranspiration and altered precipitation regimes (De Boeck et al. 2016). These conflicting drivers may explain why

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experimental warming studies of grasslands revealed contradicting results on productivity effects. Negative effects of increased temperature on productivity have been found in both in situ warming experiments (De Boeck et al. 2008) and translocation experiments (Egli et al. 2004); positive productivity effects have also been found in both in situ warming experiments (de Valpine and Harte 2001; Wan et al. 2005) and translocation experiments (Sebastià 2007). Additional studies have found no effect of warming on productivity (Dukes et al. 2005) or results that varied temporally or with soil moisture conditions (Harte and Shaw 1995; Cantarel, Bloor, and Soussana 2013). But to our knowledge it remains unclear which underlying mechanisms prevail and which environmental conditions cause a change in the importance of both conflicting drivers. The stability and resistance of community diversity to changing conditions may conserve ecosystem functions, such as productivity (Hodgson, McDonald, and Hosken 2015; Donohue et al. 2016). Given this lack of consensus in warming experiments and the risk of increased warm and dry periods in cold-biome ecosystems, continued research on the resistance of communities to abrupt environmental changes is needed.

Resource acquisition and allocation strategies determine species coexistence, as plants compete for limiting resources (Harpole et al. 2016). Temperature changes may alter plant-resource availability through multiple pathways, such as increased decomposition rate (Gavazov 2010; García-Palacios et al. 2013) or the depletion of soil moisture (Schär et al. 1999; Jung et al. 2010). Increased microbial activity may increase nitrogen availability (Rustad et al. 2001; Wang et al. 2016), potentially alleviating belowground competition and shifting it toward aboveground competition for light (Hautier, Niklaus, and Hector 2009; Borer et al. 2014). Such gains or reductions in plant-resource availability may shift competitive outcomes among species of an established community, leading to species loss or community-structure reorganization. An extended growing season may also shift the competition pattern and subsequently the community composition because cold-adapted species might be less adapted to leverage the extended growing season into higher growth and fertility (Wipf 2010). This can result because of the sensitivity of increased exposure to frost events as the insulating effect of snow is lost (Wipf, Rixen, and Mulder 2006), or by advantaging early emerging species that preempt resource uptake (Mwangi et al. 2007).

Thus, in montane and alpine grasslands future warm periods are likely to promote fast adapting, fast growing, high-statured species such as graminoids, which are able to benefit efficiently from the changed resource availability (Bret-Harte et al. 2004; Veen et al. 2015; Klanderud et al. 2017) and therefore outcompete others. Especially graminoids, with their taller stature, were shown to profit from increased temperature and nutrient availability and hence outcompete smaller-statured growth forms for light and space (Theurillat and Guisan 2001; Klanderud, Vandvik, and Goldberg 2015). In the absence of dispersal, this should lead to deterministic decreases in species richness by outcompeting species unable to adapt to the novel biotic and abiotic environment. These losses may be mitigated or even reversed, however, if novel plant species colonize into an existing community (Engler et al. 2009; Alexander, Diez, and Levine 2015; Rixen and Wipf 2017). Nonetheless, the life cycle and demographic properties of species will cause the processes underlying the colonization of new habitats to lag behind the speed of change (Alexander et al., 2017; Dullinger et al. 2012).

Here, we investigate community resistance by examining the initial, one-year responses of plant communities to simulated, abrupt changes in temperature and precipitation climatic conditions on montane and alpine grasslands using an experimental downslope translocation of intact plant-soil monoliths in the European Alps. We hypothesize that:

(1) Aboveground biomass increases with increasing temperature in the absence of severe precipitation differences.
(2) In the absence of colonization, increasing temperature leads to a loss of species because of shifts in interspecific competition reflected in shifting functional group dominance and light transmission.
(3) Community composition will shift with increasing temperature and both diverge compared to the original composition (between translocation sites) and show decreased variability relative to its original composition because of deterministic competitive exclusion (within translocation sites).

Materials and methods

Study sites

This study was conducted along an elevation gradient ranging from 350 m to 2,440 m a.s.l. across Germany (DE), Austria (AU), and Switzerland (CH) in the European Alps. Six representative grassland sites ranging from colline to alpine ecosystems were selected for downslope translocation of intact plant-soil monoliths. These six sites were Bayreuth (DE, 350 m a.s.l.), Fendt (DE, 550 m a.s.l.), Graswang

(DE, 900 m a.s.l.), Esterberg (DE, 1,300 m a.s.l.), Stubai (AU, 1,850 m a.s.l.), and Furka (CH, 2,440 m a.s.l.). All of the selected grasslands are seminatural, with the exception of alpine Furka, where natural grasslands occur above the tree line. For a description of the environmental site conditions see Table 1.

Experimental setup

In the summer of 2016, a total of 126 intact plant-soil monoliths were taken from native grasslands by inserting in PVC tubes with a diameter of 30 cm (similar method to Kreyling et al. 2017; Wu et al. 2012) using a modified jackhammer. This experimental unit size is sufficient to allow for studying the integrative responses to a multitude of community interactions in small statured grasslands (Milbau et al. 2007). The sampling depth was variable: At the four low- to mid-elevation sites (DE) monoliths were taken with a depth of 40 cm, but because of shallow soils and increasing stoniness, this depth was reduced to 25 cm for monoliths from Stubai (AU) and Furka (CH). The bottoms of the monolith units were left open to allow for water flow. The monoliths were taken with the turf 1–2 cm below the rim to minimize microclimatic effects while avoiding excess water runoff. The shallow soils of Furka (CH) prevented this, so the monoliths were instead filled from the bottom with local soil to achieve the desired distance between upper rim and turf. After excavation of the monoliths at their site of origin, they were translocated downslope to the recipient sites and dug into the extant vegetation with the rim of the monolith flush to its surrounding. Monoliths were installed in raised beds at the lowest (Bayreuth, DE) and highest (Furka, CH) location. This was done because of high groundwater tables at Bayreuth and to avoid excessive disturbance of the sensitive habitat at Furka. Monoliths of the four German sites, ranging from 1,350 m to 350 m a.s.l., were translocated to each site with a lower elevation than the monolith origin. Monoliths originating from Stubai (AU, 1,850 m a.s.l.) and Furka (CH, 2,440 m a.s.l.) were translocated only to Bayreuth to test the ecological limits of alpine and subalpine grasslands reacting to abrupt changes in environmental conditions. The high sensitivity of these grasslands to disturbance minimized the number of replicates that could be extracted, preventing translocation to intermediate elevations. At all study sites, additional sets of monoliths were translocated within the respective site as control monoliths (see Table 2 for an overview of replicates from origin and recipient sites, as well as Figure 1). The installation of site-specific control monoliths allowed us to control for unintended treatment effects resulting from the extraction and the PVC tubes themselves (e.g., isolation from surrounding soil, which might hamper or inhibit lateral subsurface flows, root damage, etc.).

Measured environmental and ecological parameters

Within the first ten days after snowmelt in spring 2017, sensors for soil moisture (EcH_2O 5-TM, Decagon Devices Inc., USA) were installed horizontal at 5 cm depth together with data loggers (EcH_2O Em50, Decagon Devices Inc., USA) using one monolith from each origin at each recipient site. Data were recorded at 15 min intervals to allow fine scale resolution, but were aggregated to daily means for this study. Additionally, on-site weather station data were used to determine precipitation amounts and growing degree days (GDD) as a proxy for thermal time available for plant growth. The GDD was calculated as the sum of the area beneath a sinusoidal curve that was fit to the minimum and maximum daily temperature, with a lower bound of 5°C (Baskerville and Emin 1969). This provides a site-specific estimate for the thermal energy available for plants, although it should be noted that with increasing elevation, the thermal microclimate of plants becomes increasingly decoupled from air temperature (Scherrer and Körner 2009). Here, we present data for the entire calendar year until the date of harvest as well as for the site-specific growing-season length of 2017. Growing season was defined as the number of days between the first five consecutive days with mean air temperature above 5°C (Zhang et al. 2011) and the date of harvest; both dates are site specific.

During the 2017 growing season, aboveground biomass of each monolith was harvested 3 cm above ground level at the time of peak biomass at each site. Aboveground biomass was sorted into single vascular plant species, inventoried to provide species richness per monolith, and then dried at 60°C for 48 h and weighed. In 2016, all monoliths were harvested after translocation at peak season to provide a baseline of aboveground production in subsequent years. Because of harvests in the previous year, litter had not accumulated. Dead or senesced tissue from the 2017 growing season was included in the species-specific biomass. This represented one full year of exposure to the climate of the recipient sites.

The percentage of green cover of each monolith was estimated weekly by a visual survey during the growing season in Bayreuth, always by the same observer (from March 16 to July 10, 2017). This was measured as a proxy of environmental stress, as senesced tissue

Table 1. Geographic, climatic, and plant sociologic characteristics of the study sites along the elevational gradient in the European Alps from low to high. All vegetation-period specific values are site specific. Data shown were calculated from on-site weather-station data. Long-term data for Esterberg are not available.

			Site (Country)					
			Bayreuth (DE)	Fendt (DE)	Graswang (DE)	Esterberg (DE)	Stubai (AU)	Furka (CH)
Geographic	Elevational belt		Colline	Montane	Montane	Montane	Subalpine	Alpine
	Coordinates		49°55′16″N	47°49′44″N	47°34′11″N	47°30′59″N	47°07′44″N	46°34′36″N
			11°34′55″E	11°03′58″E	11°01′51″E	11°09′28″E	11°18′19″E	08°25′17″E
	Elevation (m a.s.l.)		350	550	900	1,300	1,850	2,440
Climatic	MAT (°C)		8.2	8.6	6.6	NA	3	−0.5
	MAP (mm)		724	959	1,285	NA	1,097	1,600
	Growing degree days 2017 (heat sum)	Total amount	1,035	1,106	916	879	763	337
		Vegetation period	982	1,046	860	779	664	285
	Precipitation 2017 (mm)	Total amount	275	513	643	556	550	658
		Vegetation period	204	419	489	418	465	320
	Temperature 2017 (°C)	Total amount	8.1	7	6.3	5.3	5.9	0.5
		Vegetation period	13.1	11.7	11.2	10.5	9.9	8.7
Plant Sociology	Plant association		*Arrhenatheretum elatioris*	*Arrhenatheretum elatioris*	*Trisetetum flavescentis*	*Cynosuretum cristati*	*Trisetetum flavescentis*	*Caricetum curvulae*
	Dominant species		*Agrostis capillaris* *Anthoxanthum odoratum* *Festuca rubra* *Achillea millefolium* *Pilosella piloselloides* *Plantago lanceolata* *Rumex acetosa*	*Alopecurus pratensis* *Dactylis glomerata* *Elymus repens* *Lolium perenne* *Poa angustifolia* *Poa pratensis* *Taraxacum officinalis*	*Dactylis glomerata* *Festuca pratensis* *Festuca rubra* *Trisetum flavescens* *Pimpinella major* *Plantago lanceolata* *Trifolium pratense*	*Anthoxanthum odoratum* *Cynosurus cristatus* *Elymus repens* *Festuca pratensis* *Festuca rubra* *Lolium perenne* *Trifolium pratense*	*Agrostis capillaris* *Trisetum flavescens* *Dactylis glomerata* *Carum carvi* *Leontodon helveticus* *Leontodon hispidus* *Rumex acetosa*	*Carex curvula* *Helictotrichon versicolor* *Poa alpina* *Nardus stricta* *Luzula lutea* *Campanula barbata* *Homogyne alpina*

Table 2. Experimental setup. Number of monoliths translocated from origin (rows) to recipient sites (columns).

Recipient/Origin	Furka	Stubai	Esterberg	Graswang	Fendt	Bayreuth	Number Excavated
Furka	9	–	–	–	–	9	**18**
Stubai		9	–	–	–	9	**18**
Esterberg			9	9	9	9	**36**
Graswang				9	9	9	**27**
Fendt					9	9	**18**
Bayreuth						9	**9**
Number Translocated	**9**	**9**	**9**	**18**	**27**	**54**	**Σ *126***

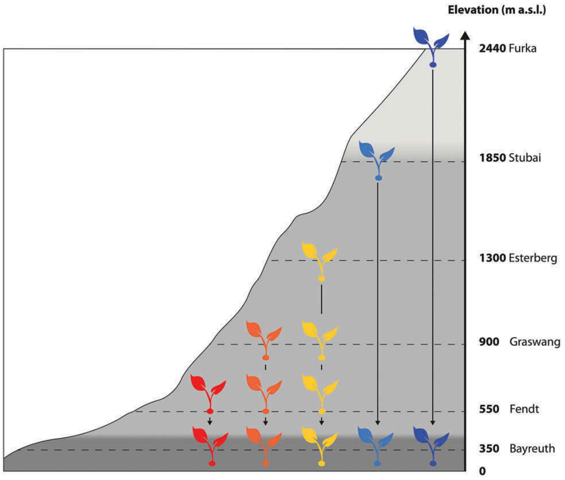

Figure 1. Scheme of experimental setup. Each colored plant represents nine plant-soil monoliths, either translocated as control at the respective origin or to a specific recipient site. Colors of plants represent the investigated temperature gradient, from cold (blue) to warm (red). The grey scale of the mountain represents ecological zones spanned along this elevational gradient, ranging from colline (low elevation) to montane to alpine (high elevation).

may indicate either drought stress or water limitation (De Boeck et al. 2016).

We quantified light transmission to ground level by measuring the photon flux density of photosynthetically active radiation (PAR) immediately before harvest for all monoliths. We measured PAR above vegetation and at ground level to build a ratio of intercepted light by vegetation structure aboveground. This integrated measure of light transmission was used as a proxy for aboveground competition and shifting resource limitation (from below- to aboveground) in relation to hypothesis 2. We conducted these measurements using a light-ceptometer (AccuPAR LP-80, Decagon Devices Inc., USA) with the calibration set to 30 cm gauge length to capture PAR along the full diameter of the monolith.

Statistical analyses

The treatment effects for all response parameters were calculated as relative changes compared to the control.

$$\text{Relative Change} = \left(\frac{Sample - \overline{X}Control}{\overline{X}Control} * 100 \right) \quad (1)$$

with *Sample* a single translocated monolith of a specific origin and $\overline{X}Control$ the mean of all excavated and reinserted control monoliths of the same specific origin.

Data were checked for normality and homoscedasticity. All analyses were done using R Statistics version 3.3.1 (R Core Team) and the packages "nlme" and "lsmeans." We tested the effects of translocation on aboveground biomass and species richness, using linear models with the origin of the monolith with either changes in elevation, GDD, or precipitation as predictors. Additionally, we tested for interactions between origin and each environmental variable. The effects of translocation on changes in relative proportion to community aboveground biomass of the plant functional groups graminoids, forbs, and legumes were tested in the same way to detect possible dominance shifts in communities' plant functional group composition in relation to hypothesis 3. Then, to compare recipient site-specific differences, we used linear mixed-effect models to test whether recipient sites had differing effects on the relative changes in aboveground biomass and total species richness with site of origin as a random factor. We then used a post hoc TukeyHSD to examine each pairwise comparison. To test if the change in aboveground biomass or species richness at a single recipient site was significantly different from zero we used similar linear mixed-effect models without intercept.

To demonstrate the robustness of our monolith approach, we report several additional components of our monolith communities in the supplementary material. First, mean species richness and mean maximum relative abundance (percentage of total aboveground biomass produced by the most abundant species within a monolith) of each origin's control and translocated monoliths demonstrates that our monoliths were of sufficient size for examining community dynamics. Second, we demonstrate that plant communities were initially indistinguishable following translocation and experimental setup in 2016. We examined the origin-specific effects of translocations on aboveground biomass and richness to different recipient sites from initial data collected in 2016 using ANOVA, followed by a TukeyHSD post hoc test for origins with multiple recipient sites. This comparison was unavailable for the Esterberg site because of recent mowing immediately before monolith extraction.

We tested for mechanisms underlying changes in species richness and aboveground biomass by correlating the relative changes of (1) biomass on light transmission and species richness, (2) light transmission on species richness, and (3) graminoid dominance (relative abundance of graminoids) on species richness, using linear mixed-effect models with a unique origin-recipient site ID nested within the site of origin as random effects.

Because of the observed non-linearity, we used generalized additive models (GAM) to model the observed green cover versus day of the year. GAM was implemented through the "mgcv" package in R using cubic regression splines and cross-validation to select the optimal amount of smoothers for estimating how green cover was predicted by day of the year interacting with monolith origin. Thus, model estimates are composed of six smoothing functions and an intercept value.

Differences in community composition were tested using the modified PERMANOVA approach proposed by Bacaro, Gioria, and Ricotta (2012). Bray-Curtis dissimilarity is an abundance-weighted beta diversity metric and was calculated for pairwise combinations of monoliths. For each combination of a translocation treatment (n = 9) and its control (n = 9) the following pairwise comparisons were made: Each monolith at the control site compared to all others at that site (labeled "within-control"), each monolith at the site of translocation compared to all others at that site (labeled "within-translocation"), and each monolith at the control site compared to each monolith at the translocation site (labeled "between"). To minimize the number of statistical comparisons made, we only tested for differences between the two "within" groups (e.g., does translocation to a given site cause monolith communities to become more or less alike one another than those at the site of origin?) and the "between" group to the "within-control" group (e.g., does translocation cause monolith communities to become more dissimilar than control monolith communities are to each other?). To avoid issues of inherent non-independence that arise as a result of each monolith being used for multiple comparisons, an F statistic was calculated for observed differences between each overall statistical comparison made, followed by 9999 Mantel randomizations of the observed values within the dissimilarity matrix and recomputation of the F statistic. A p value was calculated based on the percentage of randomized F statistics that were larger than the observed F statistic. Because of the multiple comparisons made, we adjusted the 0.05 level of significance using Bonferroni corrections for the number of comparisons made within each origin. This allowed us to be cautious in our interpretation of significant differences, while avoiding being overly conservative in these adjustments.

Results

Aboveground biomass

Downslope translocation led to increased thermal time (GDD) for all translocated monoliths, except for the translocation from Fendt (550 m a.s.l.) to Bayreuth (350 m a.s.l.). However, the increased thermal time of Fendt relative to Bayreuth is entirely the result of the five additional days until harvest in Fendt, as the sites were otherwise equivalent. All monoliths that were translocated to the lowest site (Bayreuth, 350 m a.s.l.) experienced a substantial decrease in precipitation (Table 1). After a full year of exposure to these new environments, changes in aboveground biomass of the montane and alpine grassland communities did not correlate with elevational distance or thermal time (GDD) changes because of translocation (effect of elevation: p = .17, R^2 = 0.05; effect of GDD: p = .7, R^2 = 0.04). However, aboveground biomass positively responded to changes in precipitation (effect of precipitation: $p < .001$, R^2 = 0.2; Figure 2a). Recipient sites of translocated plant communities had different influences on the relative change of aboveground biomass ($p < .001$; F = 18.51). Aboveground biomass increased for all communities that were translocated to the intermediate recipient sites Graswang (900 m a.s.l.) and Fendt (550 m a.s.l.) on average by 35 percent ($p < .01$) and 29 percent ($p < .01$), respectively, even where precipitation was slightly reduced (Figure 2a). However, the overall aboveground biomass decreased for communities that were translocated to the warmest, driest elevation site Bayreuth (350 m a.s.l.) by an average of 24 percent ($p < .05$; see Figure 3a). However, the aboveground biomass of communities originating from Fendt (decrease) and Furka (increase) showed no significant change after translocation to the warmest and driest site. Of note is the contrasting pattern of aboveground biomass between the two lowermost recipient sites, which both had reduced precipitation relative to higher sites but to different extents. This indicates a threshold of soil-water limitation. We found no significant effect of change in elevational distance, thermal

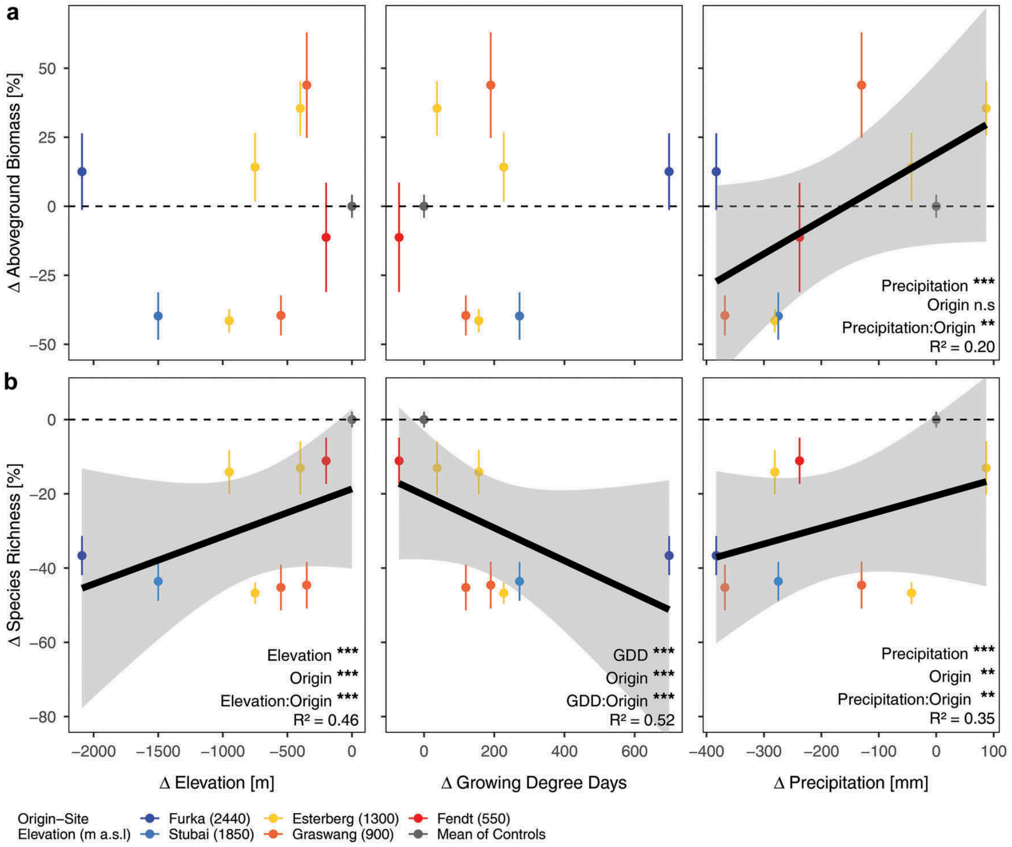

Figure 2. (a) Aboveground biomass and (b) Species richness change of plant communities in response to changes in elevation, growing degree days and precipitation resulting from downslope translocation. Significant influence of altered environmental conditions are shown as a black line with grey-shaded 95% confidence intervals. Significance of model factors indicated by asterisk (*** p < .001; ** p < .01; * p < .05; n.s non-significant) and overall model R^2 are displayed in the lower right corner of the respective panel. Mean and standard error are displayed in all graphs. For the control monoliths mean and standard error was calculated for all controls grouped. Color code of legend is valid for all panels.

time (GDD), or precipitation on the relative proportion of the plant functional groups graminoids, forbs, or legumes to community aboveground biomass (see Supplementary Table 1).

Species richness

The species richness of plant communities at all recipient sites consistently decreased with translocation. Thus, after the first year of exposure after downslope translocation, the species richness decline of montane and alpine grasslands was highly correlated with the change in elevation, thermal time, and precipitation (effect of elevation: $p < .001$, $R^2 = 0.46$; effect of GDD: $p < .001$, $R^2 = 0.52$; effect of precipitation: $p < .001$, $R^2 = 0.35$; Figure 2b). The recipient sites had a significant influence on the relative decrease of species richness ($F = 6.6$; $p < .01$). Species richness decreased in monoliths translocated to Graswang (900 m a.s.l.), Fendt (550 m a.s.l.), and Bayreuth (350 m a.s.l.) by a mean relative change of 13 percent ($p < .05$), 46 percent ($p < .001$), and 30 percent ($p < .001$), respectively (Figure 3b).

The mean species richness of the control monoliths ranges from 6.0 species to 20.4 species. While there is variation between origins, we see a significant loss of species in four of five origins at their respective transplanted sites (ranging from a mean species richness of 5.33 to 15.4; Supplementary Figure 1a). Further, the mean maximum relative abundance of control monoliths ranges from 29.1 percent to 48.5 percent, suggesting that single species (and thus individuals) are not dominating the monoliths. For translocated monoliths this generally increased (origin means ranging from 40.6 percent to

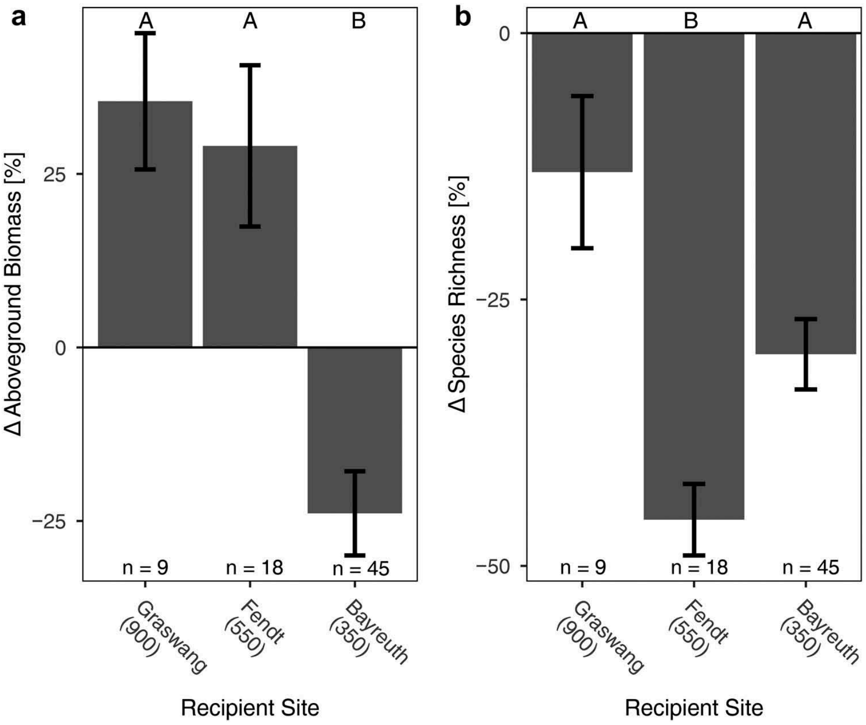

Figure 3. (a) Aboveground biomass and (b) species richness change in plant communities (monoliths) after one year of passive warming by translocation. Relative change for plant communities of all origins translocated downslope to the respective recipient site (m a.s.l. given) grouped together. Replicates at each recipient site given at the bottom of each panel. Mean and standard error are displayed in all graphs. Letters indicate significant differences between recipient sites as results of TukeyHSD post hoc tests conducted after ANOVA $p < .001$.

68.2 percent), showing a significant increase in two of the five origins (Supplementary Figure 1b).

Green cover

The amount of green cover in plant communities after a full year of exposure to warming at the lowest site (Bayreuth, 350 m a.s.l.) decreased during mid-summer in periods coinciding with low soil moisture measured in the monoliths (Figure 4). After translocation to the lowest elevation site, the rates of increase and amount of green cover of all plant communities from higher elevations—irrespective of elevational distance translocated—differ significantly from the local control communities of the lowest site ($p < .001$ for all origins, $R^2_{\mathrm{DOY\ x\ Origin}} = 0.77$). Plant communities from the lowest elevation site (Bayreuth) showed high resistance to dry periods regarding green cover. In contrast, green cover of plant communities originating from intermediate elevation decreased after an initial, less pronounced dry period of ten days in late May with only one 0.87 mm precipitation event. Notably, plant communities from the highest elevation alpine site (Furka) were generally slower to green up, maintained higher soil-moisture values during the initial dry period, and decreased in green cover only after a second dry period of 17 d without any precipitation in mid-June.

Light transmission and graminoid proportion within plant communities

Light transmission at the ground level of plant communities decreased significantly as aboveground biomass increased ($p < .001$, $R^2 = 0.15$; see Figure 5a). Yet, species richness was uncorrelated to both aboveground biomass ($p = .23$; see Figure 5b) and light transmission at ground level ($p = .35$; see Figure 5c). A significant but weak correlation of decreasing species richness with increasing relative proportion of graminoids to community aboveground biomass was found ($p < .01$, $R^2 = 0.12$; see Figure 5d).

Beta diversity

Bray-Curtis dissimilarity (abundance-weighted beta diversity) did not vary significantly between within-site of origin (control) and within-translocated

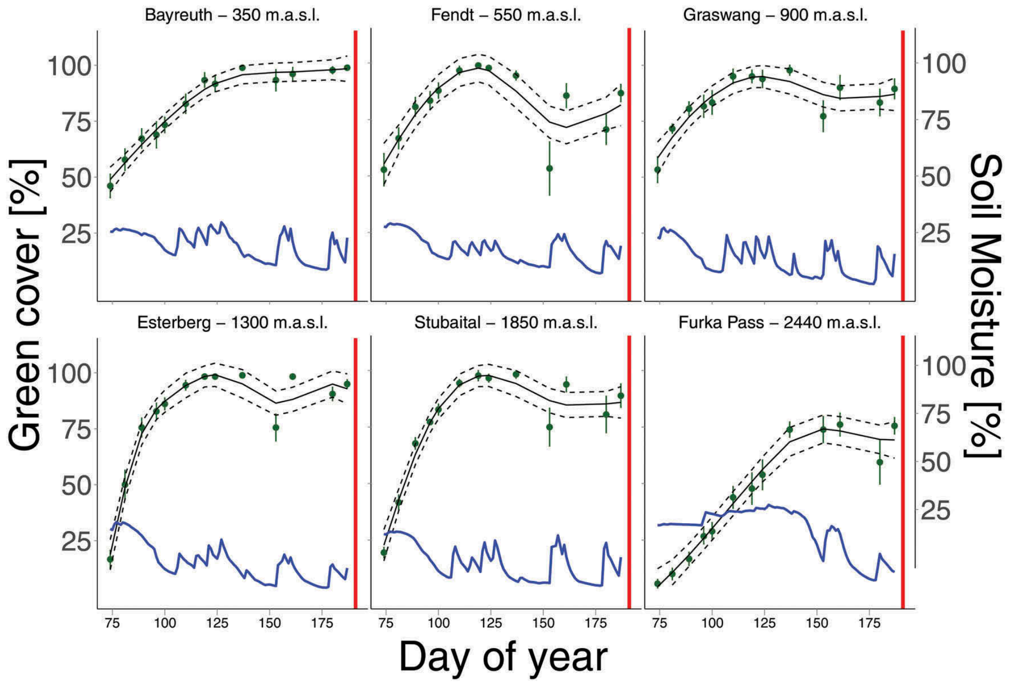

Figure 4. Green cover of translocated plant communities to the lowest elevation site (Bayreuth) showing different speed in greening up and different reaction to low soil-moisture availability. Green cover modeled as GAM shown as solid green line with 95 percent confidence intervals (dashed lines). Blue lines indicate soil moisture for the specific site of origin at the lowest elevation site (350 m a.s.l.). Red line shows harvest date at the recipient site (Bayreuth).

(warmed in respect of GDD) communities for any site. However, dissimilarity values between control and translocated communities did differ significantly for four of eight translocation combinations spanning a range between 200 m and 2,090 m of elevational distance. These significant differences in beta diversity were found for plant communities originating from the highest alpine site (Furka to Bayreuth, 2,090 m elevational distance, $p < .001$) and from intermediate montane sites (Esterberg to Bayreuth, 950 m elevational distance, $p < .01$; Graswang to Bayreuth, 550 m elevational distance; and Graswang to Fendt, 350 m elevational distance, both $p < .05$), with a fifth translocation (Esterberg to Fendt, 750 m elevational distance) showing a marginal significance after Bonferroni adjustments ($p = .08$). For a visual display of community dissimilarity results see Figure 6.

Initial state after experimental setup in 2016

In 2016, aboveground biomass increased in the monoliths originating from alpine Furka (2,440 m a.s.l.) and montane Graswang (900 m a.s.l.) after translocation to the lowest site, Bayreuth (350 m a.s.l.; $p < .05$), while all other translocations were nonsignificant (Supplementary Table 2). This suggests that the short-term residence in Bayreuth may have increased biomass shortly after translocation, but this influence was not evident in the 2017. Species richness in 2016 showed only one significant difference within origins, as Graswang (900 m a.s.l.) monoliths translocated to Fendt (550 m a.s.l.) had higher species richness than those in other sites ($p < .05$; Supplementary Table 2). This result did not persist in 2017, and was in fact inverted. Ultimately, the process of downslope translocation did not appear to negatively affect the monoliths, which may have been indicated by initial loss of species or aboveground biomass.

Discussion

Abrupt warming following downslope translocation of plant-soil monoliths from montane and alpine grasslands revealed rapid changes in productivity and diversity, indicating low resistance. Consistent with our hypothesis, aboveground biomass increased with temperature in mid-elevation sites where the precipitation regime was similar, but decreased at the lowest elevation site where warming was coupled with a strong reduction in precipitation. Downslope translocation consistently led to species loss, again consistent with our hypothesis.

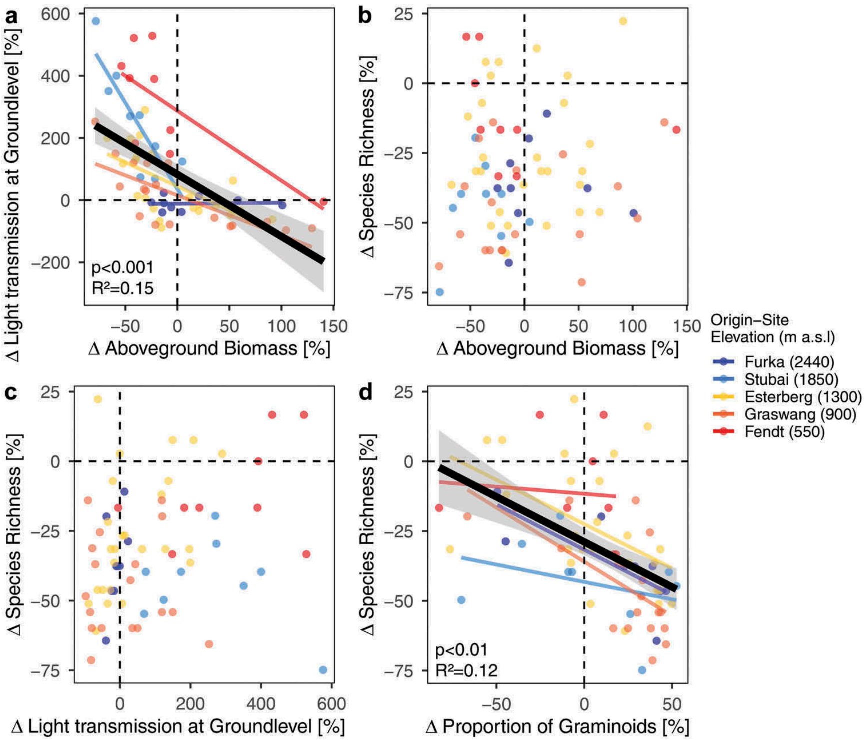

Figure 5. Changes in aboveground biomass and species richness showing relationship of relative change compared to the specific controls of (a) aboveground biomass versus light transmission, (b) aboveground biomass versus species richness, (c) light transmission versus species richness, and (d) proportion of graminoids versus species richness. Black lines with grey-shaded 95 percent confidence intervals are the overall model estimate; R^2 and p values are given if significant. Colored lines represent site-of-origin model estimates.

However, contrary to our expectations the detected loss of species richness was independent of variations in aboveground biomass and light transmission. This outcome suggests that increased aboveground competition did not drive species loss. Richness decline was significantly stronger with increasing graminoid abundance, although it was still observed at weaker levels in monoliths that showed reduced graminoid abundance. Together with the observed beta-diversity changes between translocation sites, but not *within* translocation sites, we conclude that community composition shifts were neither highly deterministic nor converging toward similar communities.

Initial aboveground biomass response to abrupt warming

The observed increases in aboveground biomass of grassland communities at intermediate translocation range is consistent with an increase in the length of the growing season because of an earlier snow melt (Inouye and Wielgolaski 2003; Laternser and Schneebeli 2003; Ernakovich et al. 2014; Gobiet et al. 2014) and faster metabolic processes (Lucht et al. 2002; Larcher 2003). The loss in aboveground biomass within plant communities that were translocated to the lowest site (350 m a.s.l.) may be the result of increasing water limitation (Schär et al. 1999, 2004; Kreyling et al. 2017), which is likely stressful for all the translocated plant communities that originated from regions of higher precipitation. The natural drought periods at the end of May (10 d) and in mid-June (17 d) at the lowest site (Bayreuth, 350 m a.s.l.), coupled with high summer temperatures, may have led to increased transpiration demand in the plants and a higher evaporation rate. This led to depleted soil moisture (Seneviratne et al. 2010; Quesada et al. 2012; Kreyling et al. 2016; Wolf et al. 2016) as shown by prolonged troughs in the soil-moisture trend lines in Bayreuth for monoliths of all origins. Low soil-moisture availability reduces stomatal conductivity, photosynthetic rate, and indirectly growth and carbon allocation (De Boeck et al. 2006, 2007; McDowell et al. 2008). Of note is the opposing

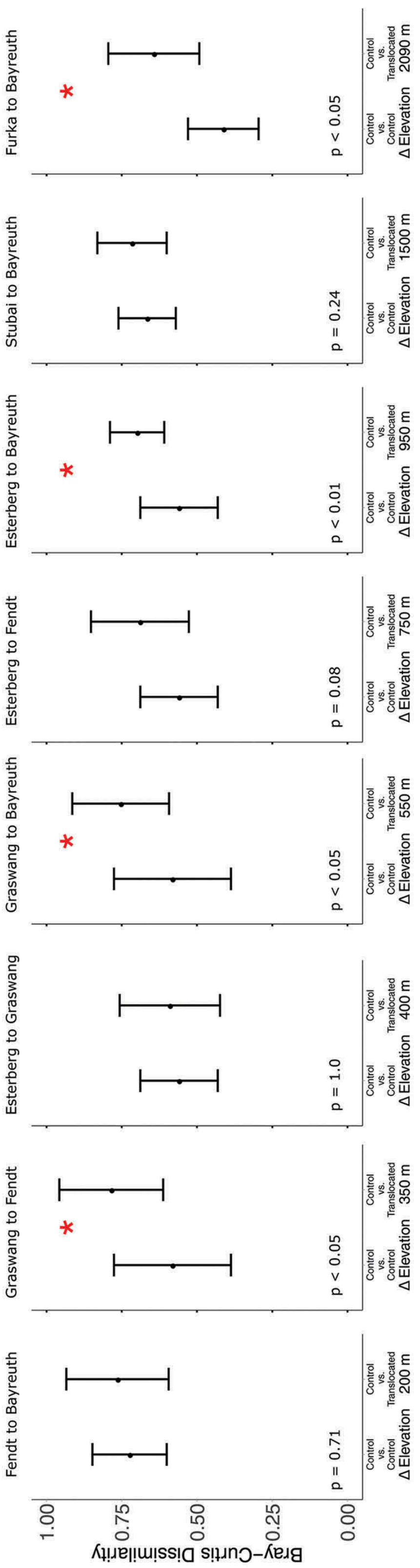

Figure 6. Dissimilarity in community composition among plant communities translocated along an elevational gradient from 2,440 m a.s.l. to 350 m a.s.l. Bray-Curtis dissimilarity values among indicated plant community (monolith) groupings for each monolith origin-translocated pairing. Panels are sorted according to elevational distance traveled by plant communities via translocation. Plotted values are means of all possible pairwise values in the indicated grouping with standard deviation error bars. PERMANOVA was used to test "within control dissimilarities" versus "between control/translocated" dissimilarities. Red asterisks indicate the significance between the translocated and control dissimilarities at $p < .05$ after adjusting for the multiple comparisons made within each origin group, additional p values are given in the lower left corner of each panel.

direction of aboveground biomass changes between monoliths translocated to the two lowest elevation sites (350 and 550 m a.s.l.). These sites had similar amounts of thermal time, but only half the amount of precipitation fell at the lowest site (Table 1). Together, this suggests that drought stress induced by high temperature and low precipitation at the lowest site drove the observed decrease in aboveground biomass at the lowest site. The slight reduction in precipitation experienced by communities that were translocated to the intermediate recipient site did not result in reduced aboveground biomass. We speculate that a critical threshold of reduced precipitation underlies the observed contrasting pattern of aboveground biomass between the two lowest recipient sites. This is in line with previous studies stating that aboveground biomass is more sensitive to soil water content than temperature under low precipitation regime (Fei et al. 2015; Winkler, Chapin, and Kueppers 2016). High-elevation plant communities have been shown to be prone to direct tissue damage by overheating after being translocated to lower elevation if transpirational cooling of the plant tissue is impeded because of limited soil-moisture availability (De Boeck et al. 2016). All of these drought effects together with the reduction of precipitation explain the observed reduction in aboveground biomass of plant communities from mid-elevations (550–1850 m a.s.l.) at our lowest and warmest site in Bayreuth at 350 m a.s.l. It underpins the importance of jointly considering both temperature and precipitation effects in experiments seeking the ecological impacts of either variable.

The occurrence of drought stress is supported by the rapid reduction in community green cover within plant communities originating from intermediate elevation (900–1,850 m a.s.l.) compared to the local control originating from the lowest elevation (350 m a.s.l.) during natural drought events. Interestingly, alpine plant communities from the highest elevation (2,440 m a.s.l.) show a delayed decrease in green cover starting only during the second natural drought event (mid-June) compared to the ones from mid-elevations (550 m–1850 m a.s.l.) starting during the first natural drought event (late May). Those high-elevation plant communities green up slower, which may be caused by photoperiod regulation of plant growth (Ernakovich et al. 2014). The measured soil moisture of the alpine plant communities remained higher than the measured soil moisture in plant communities from intermediate elevations throughout the year at the lowest elevation site. This may indicate that the edaphic properties of this system buffered the community response, although caution is warranted given the lack of replication in soil-moisture measurements.

Hence, our results suggest that montane grasslands may be less resistant to periods of water scarcity than grasslands of high, alpine elevation. Alternatively, as long-lived and clonal species inhabit plant communities of high, alpine elevation, they could be particularly slow in response to changing environments (Dullinger et al. 2012; Gritsch, Dirnböck, and Dullinger 2016).

Initial diversity response to abrupt warming

The consistent loss of plant species with downslope translocation is remarkable. In particular, mid- to high-elevation plant communities experienced significant species losses within one year at all recipient sites relative to the control mesocosms that were extracted and reinserted at their site of origin. However, as the loss of species richness was correlated with the degree of elevational distance, both temperature and precipitation change, our results suggest that the observed species loss is the result of complex interactions between multiple altered environmental drivers changed by translocation. Interestingly, species richness losses were highest at the second lowest site, where thermal time was similar to the lowest site and precipitation was similar to higher elevation sites. This could be an indication of water limitation restraining competitive exclusion at the lowest elevation site and merits further observation in future years. We note that because of the timing of translocations, monoliths are likely to experience limited colonization pressure from the matrix vegetation in this first year of sampling, meaning that future years could see a reversal in this species-loss pattern as the monoliths are colonized. Previous studies conducted at longer temporal scales did not detect a loss of plant species richness throughout time because of either natural global warming (Vittoz et al. 2009; Steinbauer et al. 2018) or experimental warming (Price and Waser 2000). Conversely, short-term experimental studies detect a loss of species richness after experimental warming (Debouk, de Bello, and Sebastià 2015; Sebastià, Kirwan, and Connolly 2008), which is aligned with the results presented here. This discrepancy between long- and short-term studies might be because of the time lag of colonization (Alexander et al., 2017; Dullinger et al. 2012). Additionally, observational studies can generally consider larger spatial scales than experimental studies, which inherently incorporates the role of habitat heterogeneity into maintaining diversity. Nonetheless, short-term studies reveal important aspects of community dynamics, such as the biotic conditions that promote resistance to abrupt changes (Kreyling et al. 2017). Our study shows a decrease in species richness that was stronger in communities with increased graminoid dominance. Evidence of alpine habitats suggests that shifts in plant-community composition can occur based on abundance shifts toward more thermophile species that outcompete more cold-adapted species (Gottfried et al. 2012). This has also been attributed to competitive interaction among various plant functional groups (Theurillat and Guisan 2001) and species resource acquisition and allocation strategies (Aerts 1999; Diaz et al. 2004). With shifting environmental conditions, the relative strengths of community assembly mechanisms and species interaction have been shown to shift as well (Gellesch et al. 2013; He, Bertness, and Altieri 2013), including temperature-limited ecosystems such as arctic (Klanderud, Vandvik, and Goldberg 2015), montane, and alpine habitats (Callaway et al. 2002). While in our study competition was not measured per se, the observed loss of species in relation to beta-diversity patterns, light availability shifts, and functional group shifts informs species interaction effects.

Despite the consistent species loss, observed beta-diversity shifts within one year after translocation were less consistent. Most notably, plant communities originating from subalpine Stubai (1,850 m a.s.l.) showed a significant loss of species, but no significant shift in community dissimilarity when comparing translocated communities with their high-elevation controls. Because our dissimilarity metrics are weighted abundances, this suggests a general loss of rare or low-abundance species with a maintenance of the dominant species in plant communities. The opposite was observed for plant communities originating from mid-elevation Esterberg (1,350 m a.s.l.), with no species loss because of translocation to the lowest elevation site, but a strong increase in abundance-weighted dissimilarity compared to the control communities remaining at the site of origin. This pattern is consistent with dominance shifts, where previously subordinate species are able to take advantage of their new environment at the expense of previously dominant species that are reduced in abundance but still persist as part of the population. Overall, this points to a high amount of local site specificity in predicting grassland changes.

While our observed loss of species is consistent with increasing interspecific competition from colder to warmer mountain habitats (Kikvidze et al. 2005), we found no evidence suggesting that aboveground competition induced this species loss, as we did not find any significant correlation of light transmission (a proxy for aboveground competition intensity, sensu DeMalach, Zaady, and Kadmon 2016) and the loss of species. Increased temperature has been observed to increase decomposition rates and thus increased nitrogen availability (Gavazov 2010; García-Palacios et al. 2013; Wang et al. 2016). An improved soil-nutrient status often leads to increased light competition (Hautier, Niklaus, and Hector 2009; Borer et al. 2014; DeMalach, Zaady, and

Kadmon 2016). Although we did not measure any soil parameters directly, we speculate that the lack of evidence of increased aboveground competition indicates a nonsignificance in changes of soil-nutrient competition in our monoliths. Potentially, any increased nitrogen availability with warming is masked by other temperature-regulated mechanisms, such as soil microbial activity or increasing asynchrony between nitrogen availability and plant growth (Ernakovich et al. 2014), causing a high level of belowground competition.

The observation of stronger species richness losses in plant communities with increased graminoid dominance is consistent with other studies that found graminoids to be most responsive to warming in cold-adapted habitats (Dormann and Woodin 2002; Brooker 2006; Winkler, Chapin, and Kueppers 2016). Nonetheless, the relative contribution of plant functional groups to aboveground biomass did not show a correlation with the degree of change of either temperature or precipitation. Furthermore, as species richness losses were also observed in plant communities with strong shifts toward forbs, our results of community composition suggest that non-deterministic processes such as priority effects prevail during initial phases of severe environmental change. If the variance of beta diversity within translocated communities converges with warming (i.e., increased similarity among translocated monoliths), this would support the idea of deterministic processes (Chase and Myers 2011; Kreyling, Jentsch, and Beierkuhnlein 2011; Segre et al. 2014). Overall, this suggests that translocated plant communities are not filtered in the initial stages according to a system-wide competitive hierarchy of resident species. Rather, within-monolith priority effects may allow previously subdominant species to take advantage of the more favorable temperature and to outcompete the now subordinate species (Suding et al. 2005), indicating a role of community asynchrony (Ma et al. 2017). Our results capture only the first-year initial dynamics of the translocated plant communities. As the monoliths continue to be exposed to their new environments, colonization pressure from the matrix vegetation will likely mitigate or even reverse our observed changes in species richness and composition.

The shift in precipitation regime at our lowest site highlights the uncertainty of precipitation regimes in future climate scenarios and how they are coupled to the effects of temperature on productivity and diversity of grasslands (Backhaus et al. 2014; Grant et al. 2014a, 2014b). Our results underline the importance of understanding the interplay of temperature and precipitation (Easterling et al. 2000; Schär et al. 2004) in driving grassland community dynamics, especially for abrupt climatic changes. These findings highlight that water supplementation at our lowest and driest site may yield additional insights onto the interactive effects of precipitation and temperature and will be an avenue of future research in this study. This study suggests that climate warming may increase aboveground biomass of montane grasslands as long as it is not coupled with a decrease in precipitation or sustained periods of drought. These montane grasslands are likely not adapted to drought stress during the growing season. The consistent loss of species in the first year indicates significant and rapid reordering of competitive outcomes in these communities, which may lead to unpredictable outcomes in the future at larger temporal and spatial scales. Shifts in composition can lead to challenges for conservation as well as for economy. Species loss or homogenization decreases community asynchrony (Gross et al. 2014; Hautier et al. 2018) and stability (Hautier et al. 2015), and the ability of those communities to buffer extreme events is also reduced, causing less secure ecosystem services in future climates (Wilcox et al. 2017). As disparities in responses of biomass production and richness to environmental changes in these systems remain, continued observational and experimental studies are warranted, and joint consideration of temperature and precipitation are critical.

Acknowledgments

We thank Christian Körner, Erika Hiltbrunner, and Michael Bahn for giving valuable feedback during the process of writing, and Ralf Hafner for kindly visualizing the experimental setup.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was supported by the German Federal Ministry of Education and Research (BMBF) in the framework of the BonaRes project SUSALPS (Sustainable use of alpine and prealpine grassland soils in a changing climate) under Grant (project number: 031B0027C).

Author contributions

BB, PW, MS, and AJ conceived the ideas; BB, MS, and AJ designed methodology; BB, PW, MAS, MASAK, PE, AH, and JI collected and processed data; BB, PW, and PE analyzed data; BB led the writing of the manuscript; PW, MASAK, PE, AH, JI, MS, MAS, and AJ assisted writing the manuscript. All authors critically contributed to the drafts and gave final approval for publication.

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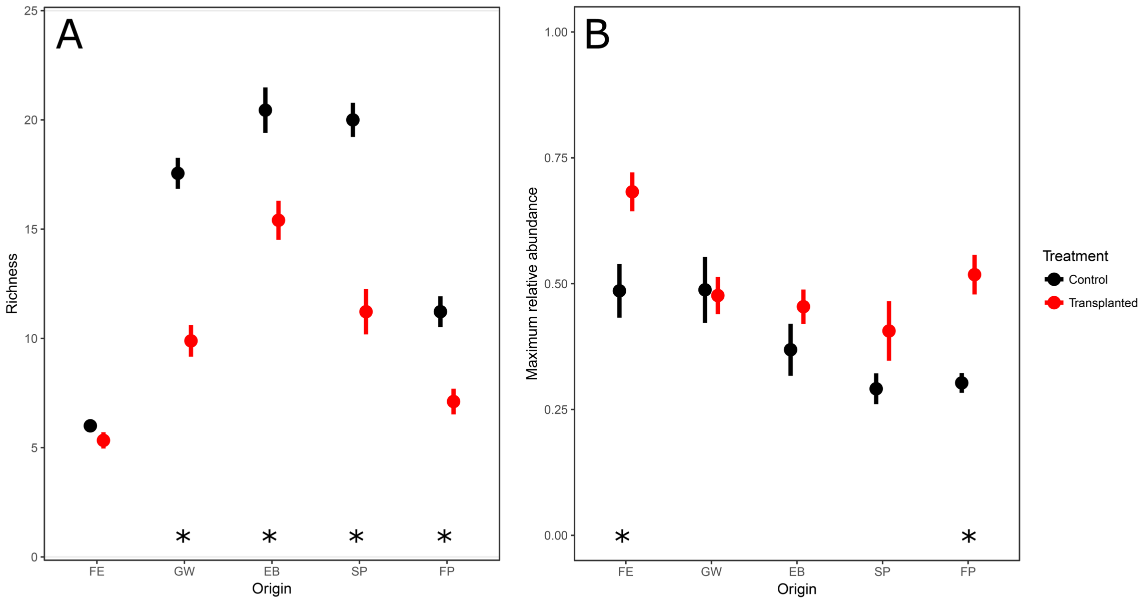
Supplementary Material to Manuscript 4:



Supplementary Figure 1: A) Species richness and B) Maximum relative abundance of the most abundant species per mesocosm at different origins and the effects of translocation in 2017. Both variables differed significantly between origins ($p < 0.0001$). Species richness decreased following translocation ($p < 0.0001$), and interacted with origin ($p < 0.01$). Maximum relative abundance differed between origins ($p < 0.0001$) and generally increased following translocation ($p < 0.0001$); there was no significant interaction between origin and treatment ($p = 0.064$). Asterisks indicate significant differences between treatments of the different origins following a Tukey-HSD post-hoc comparison test.

Supplementary Table 1: Effect of environmental change by downslope translocation on relative proportion to community aboveground biomass of plant functional groups. No deterministic trend with none of the analysed environmental parameters was detected. The shown numbers are p-Values of linear models.

Environmental change / Plant functional group	**Elevational difference [m]**	**Growing Degree Days**	**Precipitation [mm]**
Graminoids	0.33	0.17	0.07
Forbs	0.24	0.18	0.1
Legumes	0.88	0.69	0.82

Supplementary Table 2: Analysis of 2016 (year of experimental set up) data showing no significant differences between control and translocated communities regarding aboveground biomass and species richness. If shown p-value below 0.05 the parameter was always increasing. Hence, excavation, transportation and installation had no influence on translocated communities.

Recipient / Origin	**Furka**		**Stubai**		**Esterberg**		**Graswang**		**Fendt**	
Parameter	*Aboveground biomass*	*Species richness*	*Aboveground biomass*	*Species richness*	*Aboveground biomass*	*Species richness*	*Aboveground biomass*	*Species richness*	*Aboveground biomass*	*Species richness*
Grasswang	-	-	-	-	NA	NA	-	-	-	-
Fendt	-	-	-	-	NA	NA	0.87	0.039	-	-
Bayreuth	0.016	0.63	0.76	0.95	NA	NA	0.026	0.91	0.73	0.052

Supplementary Table 3: Species list of all occurring species within the here reported experimental set-up of SUSALPS found in 2016 and 2017 during peak biomass harvest.

Species	Family	Functional Group	Bayreuth	Fendt	Graswang	Esterberg	Stubai	Furka
Achillea millefolium	Asteraceae	Herb	1	1	1	1	1	NA
Agrostis capillaris	Poaceae	Grass	1	NA	1	1	1	NA
Agrostis gigantea	Poaceae	Grass	NA	NA	1	NA	NA	NA
Agrostis rupestris	Poaceae	Grass	NA	NA	NA	NA	1	NA
Agrostis stolonifera	Poaceae	Grass	1	1	1	1	1	NA
Alchemilla monticula	Rosaceae	Herb	NA	NA	1	1	1	NA
Alchemilla vulgaris	Rosaceae	Herb	1	NA	1	1	1	NA
Alopecurus pratensis	Poaceae	Grass	1	1	1	NA	NA	NA
Anthoxanthum alpinum	Poaceae	Grass	NA	NA	NA	NA	NA	1
Anthoxanthum odoratum	Poaceae	Grass	1	NA	1	1	1	NA
Arrhenatherum elatius	Poaceae	Grass	NA	NA	1	NA	NA	NA
Barbarea vulgaris	Brassicaceae	Herb	1	NA	NA	NA	NA	NA
Bellis perennis	Asteraceae	Herb	1	NA	NA	NA	NA	NA
Bistorta officianilis	Polygonaceae	Herb	NA	NA	1	1	NA	NA
Campanula barbata	Campanulaceae	Herb	NA	NA	NA	NA	NA	1
Campanula pratensis	Campanulaceae	Herb	NA	NA	NA	NA	1	NA
Campanula scheuchzeri	Campanulaceae	Herb	NA	NA	NA	NA	1	1
Capsella bursa-pastoris	Brassicaceae	Herb	NA	NA	NA	1	NA	NA
Carduus crispus	Asteraceae	Herb	NA	NA	NA	NA	1	NA
Carex curvula	Cyperaceae	Grass	NA	NA	NA	NA	NA	1
Carex montana	Cyperaceae	Grass	NA	NA	1	NA	NA	NA
Carex pallescens	Cyperaceae	Grass	NA	NA	NA	NA	1	NA
Carex spicata	Cyperaceae	Grass	NA	NA	1	NA	NA	NA
Carex sylvatica	Cyperaceae	Grass	NA	NA	1	1	1	NA
Carum carvi	Apiaceae	Herb	NA	NA	NA	1	1	NA
Centaurea jacea	Asteraceae	Herb	1	NA	1	1	NA	NA
Cerastium holosteoides	Caryophyllaceae	Herb	1	NA	1	1	1	NA
Chaerophyllum hirsutum	Apiaceae	Herb	NA	NA	NA	1	1	NA
Chaerophyllum temulum	Apiaceae	Herb	NA	NA	NA	1	NA	NA
Cirsium oleraceum	Asteraceae	Herb	NA	NA	NA	NA	1	NA
Convolvulus arvensis	Convolvulaceae	Herb	1	NA	NA	NA	NA	NA
Crepis aurea	Asteraceae	Herb	NA	NA	NA	1	1	NA
Crepis biennis	Asteraceae	Herb	1	NA	NA	NA	NA	NA
Crepis conyzifolia	Asteraceae	Herb	NA	NA	NA	NA	NA	1
Crocus albiflorus	Iridaceae	Herb	NA	NA	NA	NA	1	NA
Cynosurus cristatus	Poaceae	Grass	1	NA	NA	1	NA	NA
Dactylis glomerata	Poaceae	Grass	1	1	1	1	1	NA
Deschampsia cespitosa	Poaceae	Grass	NA	NA	NA	1	1	NA
Deschampsia flexuosa	Poaceae	Grass	1	NA	1	1	1	NA
Elymus caninus	Poaceae	Grass	NA	1	NA	NA	NA	NA
Elymus repens	Poaceae	Grass	NA	1	NA	1	NA	NA

Epilobium dubium	Onagraceae	Herb	1	NA	NA	NA	NA	NA
Equisetum arvense	Equisetaceae	Herb	NA	NA	1	1	NA	NA
Euphrasia minima	Scrophulariaceae	Herb	NA	NA	NA	NA	NA	1
Festuca pratensis	Poaceae	Grass	1	NA	1	1	1	NA
Festuca rubra	Poaceae	Grass	1	NA	1	1	1	NA
Filipendula ulmaria	Rosaceae	Herb	NA	NA	NA	1	NA	NA
Gentiana punctata	Gentianaceae	Herb	NA	NA	NA	NA	NA	1
Geranium pratense	Geraniaceae	Herb	NA	NA	NA	NA	1	NA
Geum montanum	Rosaceae	Herb	NA	NA	NA	1	NA	1
Geum rivale	Rosaceae	Herb	NA	NA	NA	1	1	NA
Geum urbanum	Rosaceae	Herb	NA	NA	NA	1	NA	NA
Glechoma hederacea	Lamiaceae	Herb	NA	1	NA	NA	NA	NA
Helictotrichon pubescens	Poaceae	Grass	1	NA	1	1	NA	NA
Helictotrichon versicolor	Poaceae	Grass	NA	NA	NA	NA	NA	1
Heracleum sphondylium	Apiaceae	Herb	NA	1	1	NA	NA	NA
Hieracium alpinum	Asteraceae	Herb	NA	NA	NA	NA	NA	1
Holcus lanatus	Poaceae	Grass	1	NA	NA	NA	NA	NA
Homogyne alpina	Asteraceae	Herb	NA	NA	NA	NA	NA	1
Hypochaeris radicata	Asteraceae	Herb	1	NA	NA	NA	NA	NA
Knautia arvensis	Dipsacaceae	Herb	NA	NA	1	NA	NA	NA
Lactuca serriola	Asteraceae	Herb	NA	NA	NA	NA	1	NA
Lathyrus pratensis	Fabaceae	Legume	1	NA	1	1	NA	NA
Leontodon autumnalis	Asteraceae	Herb	1	NA	NA	1	NA	NA
Leontodon helveticus	Asteraceae	Herb	NA	NA	NA	1	1	1
Leontodon hispidus	Asteraceae	Herb	1	NA	NA	1	1	NA
Leucanthemopsis alpina	Asteraceae	Herb	NA	NA	NA	NA	NA	1
Leucanthemum ircutianum	Asteraceae	Herb	1	NA	1	1	1	NA
Ligusticum mutellina	Apiaceae	Herb	NA	NA	NA	NA	NA	1
Lolium multiflorum	Poaceae	Grass	NA	1	1	1	NA	NA
Lolium perenne	Poaceae	Grass	1	1	1	1	1	NA
Luzula alpina	Juncaceae	Herb	NA	NA	NA	NA	NA	1
Luzula campestris	Juncaceae	Grass	1	NA	1	NA	NA	NA
Luzula lutea	Juncaceae	Grass	NA	NA	NA	NA	NA	1
Lychnis flos-cuculi	Caryophyllaceae	Herb	NA	NA	1	NA	NA	NA
Lysimachia nemorum	Primulaceae	Herb	NA	NA	NA	NA	1	NA
Medicago lupulina	Fabaceae	Legume	1	NA	NA	NA	NA	NA
Myosotis alpestis	Boraginaceae	Herb	NA	NA	NA	1	NA	NA
Nardus stricta	Poaceae	Grass	NA	NA	NA	NA	NA	1
Persicaria maculosa	Polygonaceae	Herb	1	NA	NA	NA	NA	NA
Phleum pratense	Poaceae	Grass	NA	1	NA	1	1	NA
Pilosella aurantiaca	Asteraceae	Herb	1	NA	1	NA	NA	NA
Pilosella piloselloides	Asteraceae	Herb	1	NA	1	NA	NA	NA
Pimpinella major	Apiaceae	Herb	NA	NA	1	NA	1	NA
Plantago lanceolata	Plantaginaceae	Herb	1	NA	1	1	1	NA
Poa alpina	Poaceae	Grass	NA	NA	NA	NA	NA	1
Poa angustifolia	Poaceae	Grass	1	1	1	1	1	NA

Poa pratensis	Poaceae	Grass	1	1	1	1	1	NA
Poa trivialis	Poaceae	Grass	1	1	1	1	1	NA
Polygonum aviculare	Polygonaceae	Herb	NA	NA	NA	1	NA	NA
Potentilla aurea	Rosaceae	Herb	NA	NA	NA	NA	NA	1
Primula veris	Primulaceae	Herb	NA	NA	1	1	1	NA
Prunella vulgaris	Lamiaceae	Herb	NA	NA	1	NA	1	NA
Ranunculus acris	Ranunculaceae	Herb	1	1	1	1	1	NA
Ranunculus alpestris	Ranunculaceae	Herb	NA	NA	NA	1	1	NA
Ranunculus montanus	Ranunculaceae	Herb	NA	NA	NA	1	1	1
Ranunculus nemorosus	Ranunculaceae	Herb	NA	NA	NA	1	NA	NA
Ranunculus repens	Ranunculaceae	Herb	NA	NA	1	1	NA	NA
Rhinanthus minor	Scrophulariaceae	Herb	1	NA	NA	1	NA	NA
Rhinanthus serotinus	Scrophulariaceae	Herb	NA	NA	NA	1	NA	NA
Rumex acetosa	Polygonaceae	Herb	1	1	1	1	1	NA
Rumex alpestris	Polygonaceae	Herb	NA	NA	NA	NA	1	NA
Rumex sanguineus	Polygonaceae	Herb	NA	1	NA	NA	NA	NA
Sibbaldia procumbens	Rosaceae	Herb	NA	NA	NA	NA	NA	1
Stellaria longifolia	Caryophyllaceae	Herb	NA	NA	NA	1	NA	NA
Taraxacum officinale	Asteraceae	Herb	1	1	1	1	1	NA
Tragopodon pratensis	Asteraceae	Herb	1	NA	1	1	NA	NA
Trifolium alpinum	Fabaceae	Legume	NA	NA	NA	NA	NA	1
Trifolium dubium	Fabaceae	Legume	1	NA	1	1	NA	NA
Trifolium pratense	Fabaceae	Legume	1	1	1	1	1	NA
Trifolium repens	Fabaceae	Legume	1	1	1	1	1	NA
Trisetum flavescens	Poaceae	Grass	1	NA	1	1	1	NA
Trollius europaeus	Ranunculaceae	Herb	NA	NA	NA	1	NA	NA
Vaccinium vitis-idaea	Ericaceae	Herb	NA	NA	NA	NA	NA	1
Veronica arvensis	Scrophulariaceae	Herb	1	NA	NA	1	NA	NA
Veronica bellidioides	Scrophulariaceae	Herb	NA	NA	NA	NA	NA	1
Veronica chamaedrys	Scrophulariaceae	Herb	NA	NA	1	1	1	NA
Veronica filiformis	Scrophulariaceae	Herb	NA	NA	1	1	1	NA
Veronica montana	Scrophulariaceae	Herb	NA	NA	NA	NA	1	NA
Veronica polita	Scrophulariaceae	Herb	NA	NA	1	1	NA	NA
Veronica serpyllifolia	Scrophulariaceae	Herb	NA	NA	1	NA	NA	NA
Vicia angustifolia	Fabaceae	Legume	1	NA	NA	NA	NA	NA
Vicia cracca	Fabaceae	Legume	NA	NA	1	1	NA	NA
Vicia hirsuta	Fabaceae	Legume	1	1	NA	1	NA	NA
Vicia sepium	Fabaceae	Legume	NA	NA	NA	1	NA	NA
Vicia tetrasperma	Fabaceae	Legume	1	NA	NA	NA	NA	NA
Viola spec	Violaceae	Herb	NA	NA	1	NA	1	NA

Manuscript 5

Stable plant community biomass production despite species richness collapse (2023, *Science of the Total Environment* ; doi: 10.1016/j.scitotenv.2022.161166)

Yujie Niu, **Max A. Schuchardt**, Andreas von Heßberg, Anke Jentsch

Science of the Total Environment 864 (2023) 161166

Contents lists available at ScienceDirect

Science of the Total Environment

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Short Communication

Stable plant community biomass production despite species richness collapse under simulated extreme climate in the European Alps

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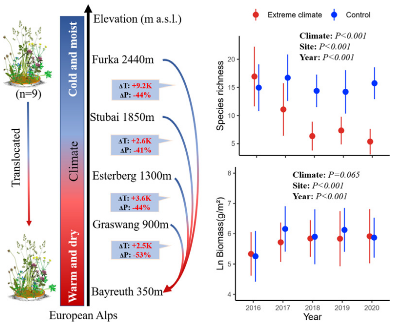
HIGHLIGHTS

- Tracking real plant species loss by pushing grasslands beyond their ecological thresholds
- The decline in native species richness did not lead to a decrease in the biomass contribution of native species.
- Reframing our perception of non-native colonization by focusing towards the beneficial impacts of novel communities

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Elena Paoletti

Keywords:
Climate change
Mountain plant community
Species loss
Colonization
Biodiversity loss-productivity relationship

ABSTRACT

Direct observation of biodiversity loss in response to abrupt climate change can resolve fundamental questions about temporal community dynamics and clarify the controversial debate of biodiversity loss impacts on ecosystem functioning. We tracked local plant species loss and the corresponding change of aboveground biomass of native and non-native species by actively pushing mountain grassland ecosystems beyond their ecological thresholds in a five-year, multisite translocation experiment across the European Alps. Our results show that species loss (ranging from a 73 % to 94 % reduction in species richness) caused by simulated climate extremes (strong warming interacting with drought) did not decrease community biomass. Even without non-native species colonization, the community biomass of native species remained stable during native species richness collapse. Switching our research focus from local extinction in the face of climate change towards the beneficial impacts of persisting native species (in addition to novel plant-plant interactions) might yield insights on transformative opportunities for boosting climate resilience.

1. Introduction

Global biodiversity loss due to climate change is exposing the need to understand the impacts of declining species richness on ecosystem productivity (Duffy et al., 2017; Urban, 2015). Over the past decade, there has been a shift in research focus from the richness-productivity relationship (Duffy et al., 2017; Fraser et al., 2015) towards experiments testing the effects of richness loss on ecosystem functioning (Jochum et al., 2020).

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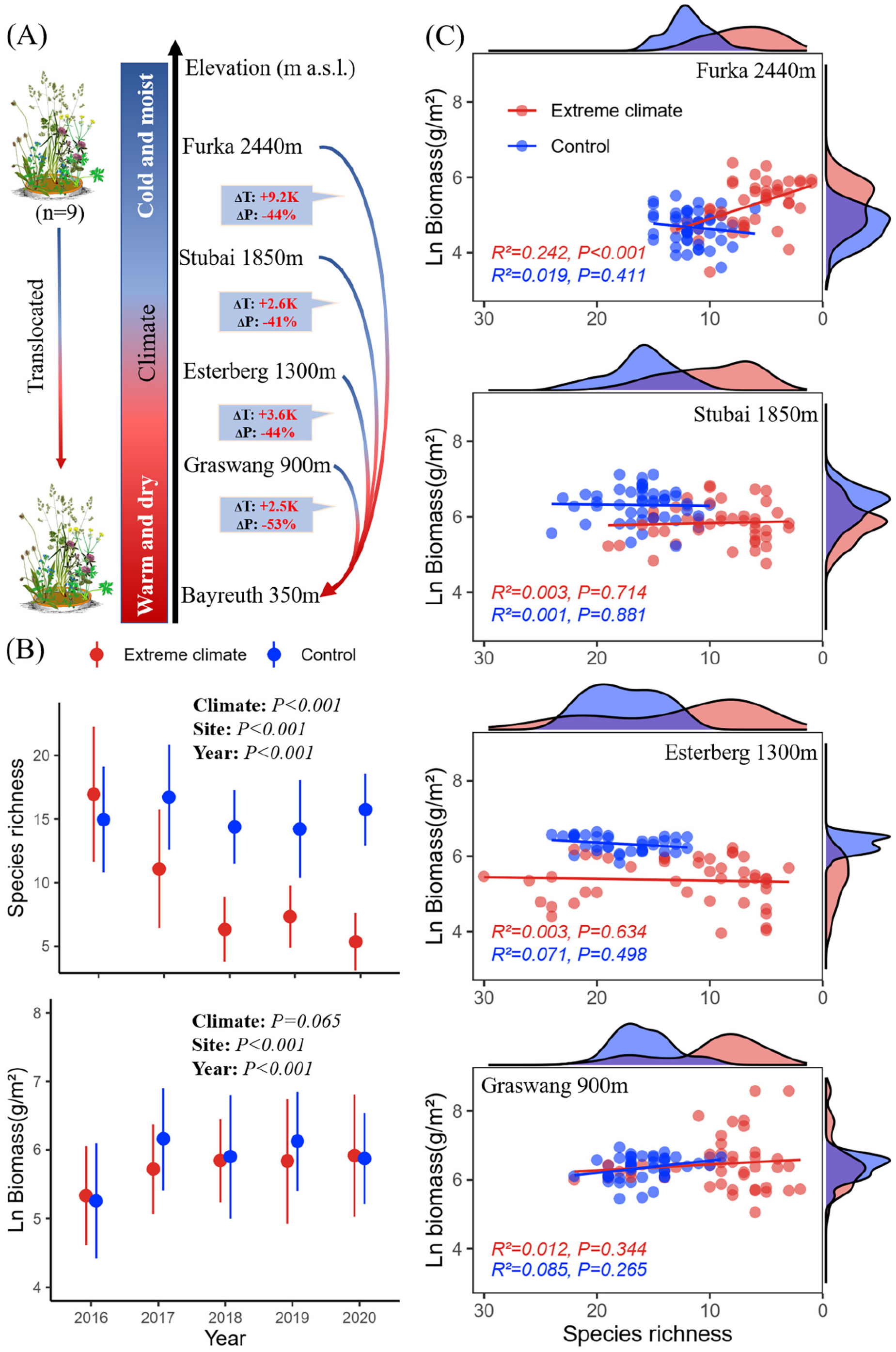
http://dx.doi.org/10.1016/j.scitotenv.2022.161166
Received 6 September 2022; Received in revised form 20 December 2022; Accepted 20 December 2022


(A)
(n=9)
Translocated
Cold and moist
Climate
Warm and dry
Elevation (m a.s.l.)
Furka 2440m
ΔT: +9.2K
ΔP: -44%
Stubai 1850m
ΔT: +2.6K
ΔP: -41%
Esterberg 1300m
ΔT: +3.6K
ΔP: -44%
Graswang 900m
ΔT: +2.5K
ΔP: -53%
Bayreuth 350m
(B)
Extreme climate
Control
Species richness
Climate: P<0.001
Site: P<0.001
Year: P<0.001
Ln Biomass(g/m²)
Climate: P=0.065
Site: P<0.001
Year: P<0.001
2016
2017
2018
2019
2020
Year
(C)
Furka 2440m
Extreme climate
Control
R²=0.242, P<0.001
R²=0.019, P=0.411
Stubai 1850m
R²=0.003, P=0.714
R²=0.001, P=0.881
Esterberg 1300m
R²=0.003, P=0.634
R²=0.071, P=0.498
Graswang 900m
R²=0.012, P=0.344
R²=0.085, P=0.265
Ln Biomass(g/m²)
Ln biomass(g/m²)
Species richness

Prior studies at regional and global scales focused on the role of primary productivity in regulating plant species richness through richness-productivity experiments (Fraser et al., 2015). Concerns over the consequences of biodiversity loss under climate change have triggered interest in the research of biodiversity loss on productivity (Jochum et al., 2020; Wardle, 2016), yet, much of the evidence for biodiversity loss negatively affecting productivity is drawn from comparisons or linear regressions of experimental communities with low vs. high species richness (Duffy et al., 2017; Jochum et al., 2020; Wardle, 2016). Biodiversity loss is often studied or simulated using assembled communities with varying species richnesses (Jochum et al., 2020; Manning et al., 2019), instead of studying real richness loss along a time series in semi-natural and natural plant communities. There is little consensus on how climate change-induced biodiversity loss affects productivity of grasslands (Manning et al., 2019; Wardle, 2016). Two possible reasons are: (I) Although accelerated species loss has been apparent since the mid-twentieth century (Alstad et al., 2016; Steinbauer et al., 2018) and is projected with high probability for future climate scenarios (Urban, 2015), data and empirical evidence tracking species loss (Niu et al., 2019; Wolf et al., 2021) and the corresponding productivity changes (Duffy et al., 2017; Wardle, 2016) of plant communities under pressure are still lacking. (II) Additionally, the compensatory dynamics of the surviving species under novel climates (Bai et al., 2004; Barry et al., 2019) and the colonization of non-native species offsetting species losses (Steinbauer et al., 2018) make the effects of biodiversity loss on productivity (Duffy et al., 2017) less predictable.

Over the past two decades, a growing body of studies has explored the impacts of extreme climate on grassland plant communities through observations and experiments (De Boeck et al., 2018a). Extreme climate, such as increased temperatures and drought, have the potential to have devastating impacts on population dynamics and community composition, with cascading effects on ecosystem functioning (Smith, 2011). However, there is still no consensus regarding the effects of extreme climate on primary productivity. As an example, various studies across different grasslands suggest a negative effect (Bastos et al., 2020), no effect (Kreyling et al., 2008) or even a positive effect (Gharun et al., 2020) of extreme climate on productivity. Considerable evidence from theoretical and experimental studies suggests that biodiversity plays a key role for biomass production in the face of extreme climate (De Boeck et al., 2018a; Isbell et al., 2015). However, taking species richness loss along time series into account, the driving mechanisms behind this response remain unclear. Furthermore, climate extremes, such as increased temperature and drought, are likely to co-occur in the near future (Field et al., 2012). These co-occurrences are expected to have the strongest impact on ecosystems in the near future. Field multifactor experiments are especially valuable for exploring the independent and combined effects of different extreme climates (Smith, 2011) on ecosystems, but are unlikely to consider all aspects in one experiment. Direct observation of biodiversity loss and changes in biomass production in response to experimentally abrupt and lasting combined extreme climate along a time series provides unique insights to elucidate the mechanisms of plant community dynamics under severe environmental stress. Pushing grassland ecosystems beyond their ecological thresholds via experimental downslope translocations to simulate extreme climate through simultaneously increased temperature and lowered precipitation (Fig. 1A) may intensify the collapse of species richness and promote the colonization of non-native species in the short term. Here, we use such an experimental approach to study the response of community biomass to species richness collapse in the face of extreme climate. We hypothesize that a decline in plant species richness along a time series caused by climate change will decrease plant community biomass.

2. Materials and methods

2.1. Study sites

This study was conducted within the framework of the SUSALPS project (https://www.susalps.de/). Five representative sites from alpine (high elevation), subalpine, montane, and mesic (low elevation) grasslands along an elevational gradient ranging from 2440 m a.s.l. (above sea level) to 350 m a.s.l. across Switzerland, Austria, and Germany in the European Alps were selected for plant-soil mesocosm translocations to simulate different extreme climates (Fig. 1A, Table S1). Specifically, these five sites were located at Furka (46°34′N, 08°25′E, 2440 m a.s.l.), Stubai (47°07′N, 11°18′E, 1850 m a.s.l.), Esterberg (47°30′N, 11°09′E, 1300 m a.s.l.), Graswang (47°34′N, 11°01′E, 900 m a.s.l.), and Bayreuth (49°55′N, 11°34′E, 350 m a.s.l.), from highest to lowest elevation. The mean annual temperatures were 0.3 °C, 6.9 °C, 5.9 °C, 7.1 °C, and 9.6 °C, and the mean annual precipitation measurements were 1096 mm, 1031 mm, 1095 mm, 1306 mm, and 608 mm during the experimental period, respectively. The mean growing season temperatures were 8.8 °C, 9.9 °C, 10.7 °C, 11.3 °C, and 13.2 °C, and the mean growing season precipitation measurements were 181.1 mm, 397.2 mm, 380.7 mm, 503.0 mm, and 165.6 mm, respectively. The first two dominant species according to the relative biomass in the plant communities were: *Carex curvula*, *Poa alpina*; *Agrostis capillaris*, *Alchemilla vulgaris*; *Festuca pratensis*, *Trifolium pratense*; *Festuca rubra*, *Pimpinella major*; and *Festuca rubra*, *Agrostis capillaris*, respectively. In the summer of 2016, a total of 72 intact plant-soil mesocosms were extracted from four higher-elevation experimental sites. Nine mesocosms originating from each higher elevation site were translocated downslope to the lowest elevation site (Bayreuth) to simulate an extreme climate treatment (increased temperature interacting with drought). We manipulated the interacting effect of increased temperature and lowered precipitation as this synergy will most likely have the strongest effect on mountain grasslands in the near future (Stephan et al., 2021). We buried translocated mesocosms into existing local grassland communities without any buffer zones to allow for competition from the local colonization and increase the potential of seed-input to the soil. At each site of origin, one set of mesocosms (n = 9) was reburied as climatic control. The mesocosms were 30 cm in diameter and 40 cm in depth, except at the high elevation site, Furka, where a depth of 25 cm was used (for detailed translocation methods, see Berauer et al. (2019)).

2.2. Measurement of meteorological parameters and plant community monitoring

Onsite weather station data (2 m above ground) was used to calculate climatic parameters, including mean annual temperature (MAT), mean annual precipitation (MAP), growing season temperature and precipitation, and growing degree days (GDDs). GDDs with a lower bound of 5 °C were calculated as a proxy for thermal time available for plant growth using the R package "*pollen*" (Nowosad, 2019). We recorded climatic data during the entire experimental period from 2016 to 2020, except for Esterberg in 2016 due to a weather station failure. The growing season was defined as the number of days between the first five consecutive days with a mean air temperature above 5 °C and the date of harvest, which depended on the yearly seasonality of each respective site (Menzel et al., 2003). The differences of mean annual temperature and precipitation of each higher elevation site compared to the recipient site, Bayreuth, during experimental exposure (2016–2020) are shown in Fig. 1A. We defined the extreme climate using the absolute temperature thresholds (warming of 2 °C) of the IPCC report (Allen et al., 2019; Hoegh-Guldberg et al., 2019) for extremely severe impacts on global natural ecosystems and ecosystem collapse. In our

Fig. 1. (A) To simulate extreme climate, four subalpine and alpine grassland sites along an elevational gradient in the European Alps ranging from 900 m a.s.l. (above sea level) to 2440 m a.s.l. across Germany, Austria, and Switzerland were selected for a downslope translocation experiment to Bayreuth at 350 m a.s.l. Extreme climate in our experiment refers to a temperature increase of 2.5–9.2 K and a precipitation decrease of 41–53 % across all sites of origin compared to the recipient site (Bayreuth). (B) Extreme climate change decreased species richness over time but showed no effect on community biomass. (C) Species richness effects on community biomass per experimental site. Reversed x-axis order indicates the process of species loss (same Fig. 2C). Red and blue lines are general linear models fit for extreme climate and control. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

treatments, we abruptly increased the annual temperature by 2.5–9.2 °C and decreased annual precipitation by 41–53 % simultaneously to push the grassland communities beyond their ecological thresholds (Fig. 1A). The downslope translocation of intact plant-soil mesocosms provides an ideal study system to gather in-depth insights on the collapse of species richness under abrupt extreme climate and the linked responses of plant community biomass.

Aboveground biomass was clipped at 3 cm above ground level between mid-June and the beginning of August (depending on site-specific peak biomass). Plants were sorted to individual species, then oven-dried at 60 °C for a minimum of 48 h and weighed. Here, we take aboveground net primary production (ANPP) as one key measure of ecosystem productivity. The number of species present within each replicate was recorded as species richness. Based on whether the species appeared within all the replicate plant communities of the same origin site in the year of experimental setup (2016), each species was assigned a treatment-level resident status ("native" or "non-native"). Then, based on local expert knowledge, we double-checked the resident status of every species each year for each treatment.

2.3. Statistical analysis

Three-way repeated ANOVAs were performed to analyze the main effects of extreme climate change on species richness and community biomass. A general linear model was performed to assess the relationship between community biomass and decreasing species richness under climate extremes. Fig. 1B The effects of extreme climate, site, and year on species richness and community biomass production (quantified as the natural logarithm (Ln)) were analyzed using three-way repeated measures ANOVAs with two "between" factors (Climate and Site) and one "within" factor (Year). Fig. 1C We used a general linear model—with mean community biomass as a response variable and species richness as explanatory variables—for each site of origin to test the relationship between community biomass and species richness under both extreme climate and climate control (Pinheiro et al., 2017). Fig. 2A and B One-way ANOVA was used to examine the interannual change of species richness and biomass production of native and non-native species through time by using Tukey's method for each site separately under extreme climate. Fig. 2C To test how native species biomass changed with decreasing native species richness, we used a general linear model with mean native species biomass as the response variable and native species richness as the explanatory variable for each site under extreme climate.

All calculations and statistical analyses of the data and figure plotting were performed using R (version 4.0.3, R Foundation for Statistical Computing, Vienna, Austria), with the 'ez' package (Lawrence and Lawrence, 2016) and 'rstatix' package (Kassambara, 2021) for ANOVAs, and the 'lme4' package (Bates et al., 2007) for general linear models with different subgroups.

3. Results

3.1. Extreme climate effects on species richness and community biomass

Over the five-year experimental exposure period (Fig. 1A), extreme climate decreased mean species richness (Fig. 1B, $P < 0.001$) across all sites (Figs. S1–S4), while mean species richness remained stable at climatic control sites. Interestingly, we found no difference in the mean biomass of climatic control sites and extreme climate sites (Fig. 1B, $P = 0.065$) across all locations. We found significant effects of sites on species richness ($P < 0.001$) and community biomass ($P < 0.001$, Fig. 1B). General linear models for each site further revealed that decreased species richness had no effect on community biomass for three of the four sites ($P_{Stubai} = 0.714$, $P_{Esterberg} = 0.634$, $P_{Graswang} = 0.344$) and had a positive effect on plant community biomass at the highest-elevation site ($P_{Furka} < 0.001$). The stable community biomass was attributable to the compensatory dynamics of both the surviving species under novel climates and the colonization of non-native species.

3.2. Native and non-native species dynamic under extreme climate

Across all sites, native species richness decreased with time under extreme climate (Fig. 2A), finally reaching a stable state of depleted plant communities (with no significant difference compared to the previous year after the dry year in 2018). Depleted plant communities triggered the colonization of non-native species, further amplifying plant community re-assembly (Figs. S1–S4). Non-native species were able to colonize warmed plant communities, interestingly not due to reduced community biomass, but rather due to a decline in native species richness (Fig. 2A, B). On average, 94 %, 74 %, 81 %, and 73 % of the native species were lost within three years upon translocation from high to low elevation from Furka, Stubai, Esterberg, and Graswang, respectively. Despite the significant decline of native species richness across all sites until 2018, we found no significant differences in native species community biomass between any two consecutive years. The only significant decrease in native species biomass was found in the alpine plant community of highest elevation origin between 2018 and 2019 (ANOVA, $P_{2018–2019} < 0.05$). Interestingly, despite the significant decrease in native species richness, we did not detect a decrease in native species contribution to community biomass ($P_{Stubai} = 0.290$, $P_{Esterberg} = 0.057$, $P_{Graswang} = 0.475$, Fig. 2C). For alpine plant communities originating from the highest elevation site, we even found a weak increase in biomass under the extreme climate of the low elevation site ($P_{Furka} < 0.049$) before it collapsed to only one species (*Nardus stricta* L.) in the last two years of the experiment. Moreover, biomass contribution by non-native species also ensured that the total community biomass did not further decrease.

4. Discussion

The species richness-productivity relationship is fundamental in understanding the impacts of current biodiversity loss on ecosystem functioning (Duffy et al., 2017) and is the key to nature-based, diversity-driven climate solutions (Mori et al., 2021). Climate change impairs the relationship between species richness and biomass production (De Boeck et al., 2018a). It is generally believed that extreme climates dramatically reduce diversity and productivity. However, counterexamples exist (Arnone III et al., 2011; Gharun et al., 2020) depending on the grassland type and climatic extremity (Smith, 2011). For example, De Boeck et al. (2018b) found that increased temperature alone did not have a significant effect on plant biomass production and species richness of alpine grasslands but warming interacted with drought reduced biomass production and led to community reshuffling from depressed states. Our study provides two remarkable key findings countering our initial hypothesis. First, species assemblages in plant communities of low-species richness, which were exposed to extreme climate (increased temperature coinciding with drought) and subsequently went through high local species loss and low colonization of non-native species, did not experience reduced biomass production under conditions that caused massive species loss. Second, the decline in native species richness did not lead to a decrease in the biomass production of native species. In our study, the commonly found decline in species richness adversely effecting community biomass was less consistent than many previous experiments suggested (Duffy et al., 2017; Mori et al., 2021; Wardle, 2016). Likely, these contrasting signals are due to a focus on defined levels of species richness (Jochum et al., 2020; Wardle, 2016) instead of studying realized species loss (Jochum et al., 2020). To more precisely predict the response of ecosystem function to future plant species loss, there is a need for research to focus on: (i) the complementary effects of a few surviving species buffering the collapse of ecosystem functioning through resource partitioning, biotic feedbacks (biotic interactions with other trophic levels), and abiotic facilitation (the ability of some native species to alter environments to benefit other species) (Barry et al., 2019); (ii) the non-random, adaptive re-assembly and temporal stability of plant communities

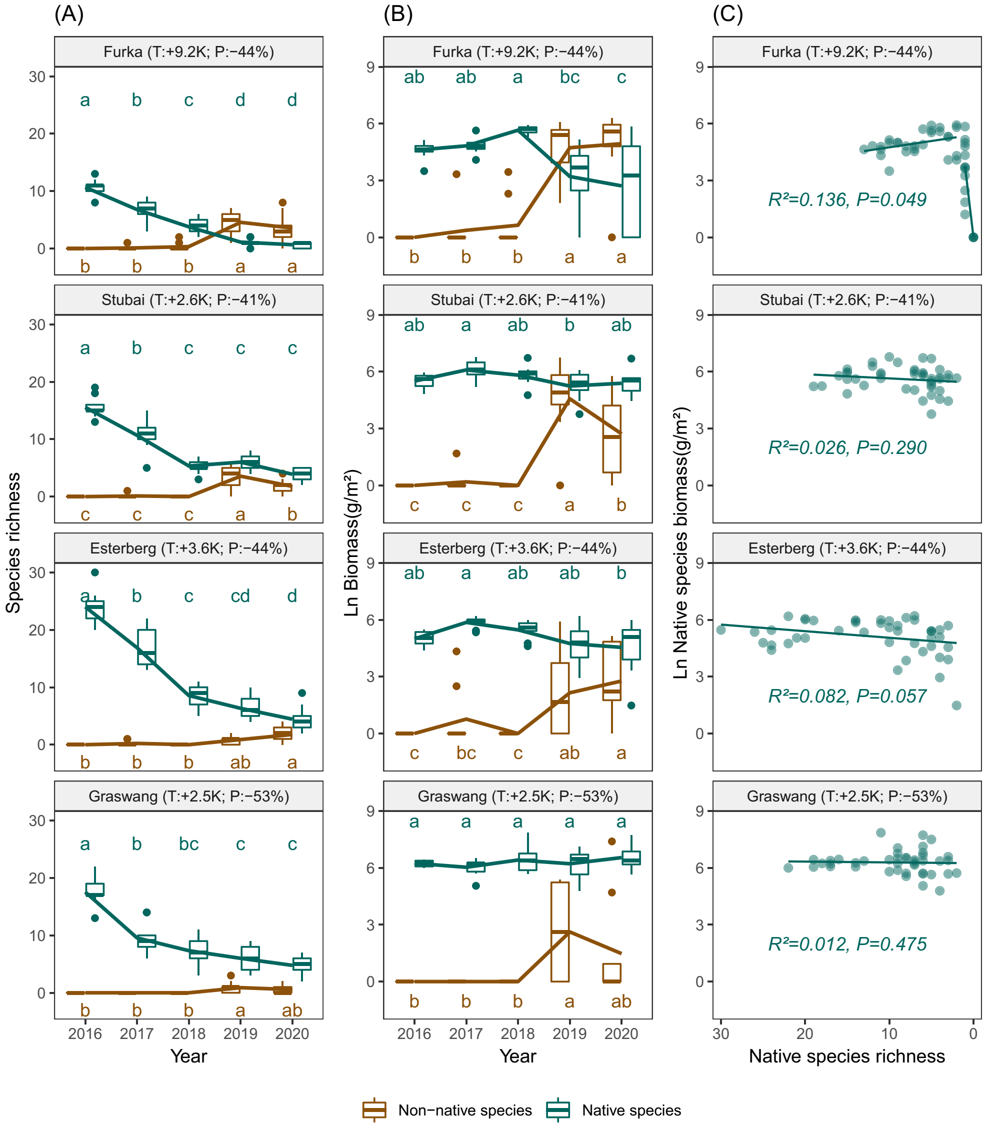


Fig. 2. Temporal dynamics of species richness (A) and community biomass (B) of native and non-native species under extreme climate change. Lowercase letters along years indicate significant differences within the respective treatment at $P < 0.05$. (C) Native species richness contribution to native community biomass. Regression lines represent a linear model. Note that the linear model was split into two for the alpine plant communities (Furka) under extreme climate (Bayreuth) due to the collapse to only one species in the last two years of the experiment, making native species modelling across time unreliable.

dominated by non-native species under climate change, revealing mechanisms of increasing climate resilience (Pearson et al., 2018); and (iii) the effects of climate-induced biodiversity loss (in contrast to experiments with manipulated richness levels) on ecosystem multifunctionality (Hector and Bagchi, 2007). The stability of critical ecosystem functions like net primary production, and thus carbon fixation, is one positive outcome under a possibly extremely warmed and drought-generating future climate. Future climate change may not be as extreme and as sudden as experimental scenarios, and the time lag between native species decline and non-native species colonization may be long due to community resistance to colonization, providing more time for dispersal and colonization of non-native species. On a larger temporal scale and under relatively mild climate change, the relationship between the loss of native species and the dispersal and colonization of non-native species in the process of novel plant community assembly

(Alexander et al., 2015) will be more complex. This complexity will in part be due to the collective effect of abiotic (climate and soil) and biotic (resistance of native species) filters, especially in alpine grassland ecosystems undergoing variations in growing season length, delayed germination of soil seed banks (Hoyle et al., 2013), and clonal reproduction strategies of alpine plants (Körner and Hiltbrunner, 2021). If a warmer future is inevitable, we may need to reframe our critical perception of biodiversity loss and non-native colonization by shifting our focus towards the beneficial impacts of natural reorganization and the formation of novel plant communities. These communities may accelerate ecosystems' transformations to a climate-resilient future (Coleman and Wernberg, 2020), particularly in the realm of biomass-related functioning (Soliveres et al., 2016). The role of persisting native species in maintaining productive ecosystems should figure prominently in global change science and policy (Duffy et al., 2017). However, we should be aware that biomass production is only one part of ecosystem multifunctionality. As shown by our most extreme case, from Furka to Bayreuth, the complementary dynamics of a few surviving species and the colonization of non-native species can offset native species biomass reduction. More data is needed to understand whether the presence of non-native species may help recover multifunctionality in a collapsed native species ecosystem. Thus, including measures like fodder quality (Berauer et al., 2021) or multi-trophic interactions (Schuchardt et al., 2021) besides primary production must be considered in future work for a more holistic understanding of the question.

CRediT authorship contribution statement

A.J. designed the project; Y.N. conceived the paper and wrote the first draft; Y.N., M.S., A.H., and A.J. collected data; Y.N., M.S., and A.H. analyzed data; and Y.N., M.S., A.H., and A.J. revised the manuscript.

Data availability

All species-specific data used for analyses is available on figshare via https://doi.10.6084/m9.figshare.20973790. All code and data products used for analyses in this study are also available from the corresponding author upon request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to the Federal Ministry of Education and Research (BMBF) for funding this research (SUSALPS; grant numbers 031B0027C, 031B0516C, 031B1067C). This study is also part of A.J.'s research project MindTheGap!, financed by the Upper Franconian Trust (Oberfrankenstiftung; grant number: OFS FP00237). Y. Niu is a Humboldt fellow funded by the Alexander von Humboldt-Foundation (AvH). We thank J. Feys for checking the statistical models, J. Schug and M. De Giuli for editing grammar, as well as four anonymous reviewers for their insightful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.161166.

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9 Acknowledgements

First of all, I have to thank Anke Jentsch for accompanying me on my way from a student assistant during my Master program in Bayreuth to a PhD student in her Disturbance Ecology lab. From day one, she took me along on international conferences and field work - thus offering great opportunities to collaborate internationally and develop a critical mindset as a scientist. Additionally, I have to thank Anke for giving me the most possible creative freedom for this thesis with all the curves I've taken; in the end, I decided to focus on our shared personal and professional interest: understanding pristine mountain ecosystems!

The work of this thesis and the underlying publications would not have been possible without the work of the many interns helping with fieldwork, weighing heaps of biomass, scanning thousands of leaves (literally), and enjoying the beauty of the European Alps: Addie, (US), Ragini (India), Gloria (Ghana), Christine (Norway), Francesco (Portugal), Franklin (US), Gabriel (Spain), Lena (US), Sara (Colombia), Gisele (Brazil). A special thanks go out to Jenna (US), my DAAD 2022 intern, who offered, among various other things, to read an earlier version of this thesis as a native speaker. The same is true for all the students of my Experimental Ecology classes that helped with field and lab work in the various global change experiments of the Disturbance Ecology Lab. I have to thank the KIT Garmisch-crew, mainly Rainer Gasche, for all the car rides to the Esterberg site—I don't take this for granted and really appreciate it (and the ice-cream in Oberammergau). Furthermore, I would like to thank Christian Körner, Erika Hiltbrunner and Michael Bahn for offering their field sites to the Disturbance Ecology lab to establish the underlying experiments of this thesis and for providing valuable feedback during field work and during the writing process of the various manuscripts.

The same is true for Christine Pilsl. She always knew the right people at the right time (both within the Geo building, on campus or in Bayreuth). Similarly, Reinhold Stahlmann knew how to communicate with WIFI or printers, while I lost my patience a long time ago. It was a great team effort or, ecologically speaking, there was great complementarity within the team.

Furthermore, I've spent two hilarious field seasons with Justyna, Jana, and Negin. It didn't matter if we were in the botanical garden of UBT, the Kaserstatt Alm in the Stubai valley, Furkapass, or one of the local beer gardens in Bayreuth. Ice cream, beer, and snacks – girls, what are the odds? Justyna, we still have to go for breakfast in Interlaken (not too sure who lost the bet, but we won't pay anyways)! But first of all, I'm going to come visit your beautiful island to explore some crags, mountain tops, beaches, forests, and lakes (but for sure not your caves). Thanks for all your advice, comments on manuscripts, and fun times with the strongest woman in the world that happens to be my girlfriend now (rock-climbing insider). And apologies for making you sleep downhill on the second floor of my camper van your second week of being in Germany. In the end, Jana provided her Master's thesis co-supervisor with Prinzenrolle and Fred-Ferkel—always keeping up the office-mood. Negin was awesome just for being Negin.

Of course, I have to thank all my friends outside the PhD life. This would have never been possible without all of you. Most importantly, my flat mates, the Badgers, developed a pretty high level of resistance to me talking nonsense at home after coming home from the office (the 'intelligent' part of my daily life). Sorry for being in a crazy mood sometimes and many thanks for sugar-support in the final steps of this thesis ☺. A special thanks goes out to my longest friend and kind-of relationship: Butz, you are awesome, not only because we love going out for dinner in the best restaurant of Bayreuth (da Corrado: which is obviously not a Franconian restaurant but Italian), but also for all the rest. It doesn't matter if we watch fire brigades at Christmas Eve, listen to our favorite Beats (Yo Kurt) or just hang out at yours or at my parents' place. The same is true for Bernd. It started with a van trip to establish the SusAlps experiment in GAP in 2016. You, as the new PhD student, and me as a Hiwi with a car and two practical hands. In between, we shared an office for ~2years and tough times in the Geo building ("mit allem was dazugehört"). And it ended with me visiting you quite often in Hohenheim to collaborate on 6 awesome, groundbreaking papers on alpine ecology.

Moreover, thank you to Andy Heßberg, Philipp Kohler and Pia Eibes, who truly became my friends over the years as we shared a lot of things outside the academic life: outdoor activities, pizza, honeybees, bicycles, swimming, ice cream and the life of a PhD student. Special thanks for helping me with all the species identification when I found myself lost somewhere in the mountains (which mostly happened via WhatsApp: "Max, can you send some close-ups of the ligules?" etc…).

And then, there is my Family and Ulli. Where shall I start and end? I mean, it's obvious that none of this would have been possible without your support. You helped me through all the ups and downs of such a crazy PhD life. Kisses to all of you three.

And finally, I have to thank Zora & Toni (my camper vans) for always keeping me warm and cozy, and for keeping the beer and Spezi cold for me and the team during fieldtrips and conferences.

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