Context-dependent impact of the invasive *Impatiens glandulifera* on native vegetation

DISSERTATION

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2 Abstract

Biological invasions are an important aspect of anthropogenic global change and considered to be one of the major threats to biodiversity worldwide. Invasive species can change native species abundance, community structure, and ecosystem processes in invaded communities. However, due to context-dependencies it is often difficult to generalize the impact of invasive species. The outcome of an invasion is for example influenced by species traits, the invaded ecosystem, and invasion stage. Developmental stages and site-specific conditions can modify the performance of the invader and its interaction with other organisms. Another challenge is to disentangle cause and effect of an invasion. An alien species can cause changes in a previously intact ecosystem, thus be the "driver" of the changes. Alternatively, it can be a "passenger" which is facilitated by previous ecosystem changes. Context-dependencies as well as causality of invasions are important issues to understand and evaluate invasions, and to develop more targeted management plans.

Thus, I investigated context-dependencies and causality of the impact of invasions using the model plant species *Impatiens glandulifera*. It heavily invaded several habitat types in Central Europe, but its impact on native plant communities is rated ambiguously, pointing towards context-dependencies. In an experimental study under controlled conditions I assessed the competitive and allelopathic effects of *I. glandulifera* on native co-occurring plant species. I found that seedlings and juvenile plants were negatively affected by a combination of allelopathy and competition. Native species differed in their susceptibility to *I. glandulifera,* and juveniles were more affected than seedlings. 2-metoxy-1,4-naphtoquinone (2-MNQ), the supposed main allelochemical, led to minor reductions in plant growth, suggesting that it may not be the only allelopathic substance of *I. glandulifera*. With two field studies I tested whether this species-specific response of native plants to allelopathy and competition of *I. glandulifera* leads to changed community patterns. I performed an observational vegetation survey within heterogeneous riparian meadows and alder forests in Germany. The vegetation was recorded in summer and spring because of seasonal species turnover and thus potentially different impact of *I. glandulifera*. The abundance of *I. glandulifera* as well as its impact on native vegetation depended on the environmental conditions at a particular patch. Plant species α-diversity was found to be not affected, but native plant cover was reduced specifically to species and season. To see whether the impact of *I. glandulifera* is causal and thus *I. glandulifera* a driver of ecosystem changes, I conducted a field experiment within the same study sites. Invaded and uninvaded plots were compared with plots from which *I. glandulifera* was removed and plots where *I. glandulifera* was planted. A negative impact of planting *I. glandulifera* and a concurrent positive effect of removal on native vegetation biomass and *Urtica dioica* performance indicated a causal but low effect of *I. glandulifera*. Species α-diversity was again not affected. I suggest that *I. glandulifera* is a "back-seat driver" of changes, which is facilitated by previous ecosystem changes but is also a driver of further changes. In summary, I found that the impact of *I. glandulifera* depended on the native target species, their developmental stage, on the habitat, and season. Dominant plant species, especially *U. dioica* were most affected, species α-diversity was not affected, species composition only under specific conditions. I conclude that the impact of *I. glandulifera* on native vegetation is only minor to moderate. However, from literature it is known that *I. glandulifera* has a negative impact on several additional ecosystem properties such as mycorrhiza, soil properties, and herbivores.

The results of my studies are also relevant to develop management strategies for *I. glandulifera*. Generally, eradication measures are not feasible at large scales because of the wide distribution of *I. glandulifera*. They should primarily be applied to sites which are valuable in terms of nature conservation and to sites, where the strongest impact of *I. glandulifera* is to be expected. This is the case in habitats with high light conditions in combination with high soil moisture. Attention should also be paid to habitats with distinct spring communities, because they were also affected by *I. glandulifera*. The understanding that *I. glandulifera* is not a clear driver of ecosystem changes, but has some characteristics of a back-seat driver, indicates that removal is not sufficient for management of an *I. glandulifera* population. Additionally, habitat-restoration is required to counter those changes that benefited the invasion of *I. glandulifera*.

3 Zusammenfassung

Biologische Invasionen sind ein wichtiger Aspekt des anthropogenen globalen Wandels und wohl eine der größten Bedrohungen der Biodiversität weltweit. Invasive Arten können einheimische Arten verdrängen und Strukturen und Prozesse von Ökosystemen verändern. Allerdings ist es aufgrund von Kontext-Abhängigkeiten schwierig, den Einfluss invasiver Arten zu verallgemeinern. Der Einfluss hängt beispielsweise von den einheimischen Arten, dem betroffenen Ökosystem und dem Stadium der Invasion ab. Umweltbedingungen und Entwicklungsstadien einer invasiven Art bestimmen deren Wachstum und Interaktion mit einheimischen Arten. Eine weitere Herausforderung ist es, Ursache und Wirkung einer Invasion zu unterscheiden. Eine invasive Art kann ein vormals intaktes Ökosystem verändern, also der „Treiber“ von Ökosystemveränderungen sein. Alternativ ist es möglich, dass die invasive Art durch vorangegangene Veränderungen des Ökosystems begünstigt wird und damit nur deren „Passagier“ ist. Sowohl Kontext-Abhängigkeiten als auch die Kausalität von Invasionen sind wichtige Aspekte, um Invasionen verstehen und beurteilen zu können, aber auch um adäquate Managementstrategien entwickeln zu können.

Aus diesem Grund war es das Ziel dieser Dissertation, Kontext-Abhängigkeiten und die Kausalität von Pflanzen-Invasionen zu untersuchen. Als Modellart wurde *Impatiens glandulifera*, das Drüsige Springkraut, verwendet. Es ist in Europa in vielen Habitaten weit verbreitet. Sein Einfluss auf die einheimische Vegetation wird aber kontrovers beurteilt, was auf Kontext-Abhängigkeiten hinweist. Mithilfe eines Experiments unter kontrollierten Bedingungen wurde der Effekt von Konkurrenz und Allelopathie von *I. glandulifera* auf mehrere einheimische Begleitarten untersucht. Es zeigte sich, dass Keimlinge und Jungpflanzen der Begleitarten durch eine Kombination aus Konkurrenz und Allelopathie von *I. glandulifera* im Wachstum gehemmt wurden. Die Pflanzenarten reagierten unterschiedlich stark, Jungpflanzen wurden stärker gehemmt als Keimlinge. 2-metoxy-1,4-naphtoquinone (2-MNQ), von dem angenommen worden war, dass er der wichtigste allelopathische Stoff des Springkrauts ist, bewirkte nur eine geringe Wachstumshemmung. Dies lässt darauf schließen, dass das Springkraut weitere allelopathische Stoffe besitzt. In zwei Freilandstudien wurde geprüft, ob der artabhängige Einfluss von *I. glandulifera* auch zu einer Veränderung der Vegetation führt. In heterogenen Bruchwäldern und Feuchtwiesen entlang von Flüssen wurden im Frühjahr und im Sommer Vegetationsaufnahmen durchgeführt. Sowohl die Abundanz von *I. glandulifera* als auch dessen Einfluss auf die einheimische Vegetation hingen von den Umweltbedingungen ab. Die Artendiversität wurde durch *I. glandulifera* nicht reduziert, wohl aber die Deckung der einheimischen Pflanzen, und zwar abhängig von Pflanzenart und Jahreszeit. Um herauszufinden, ob dieser Effekt kausal und *I. glandulifera* damit der “Treiber” der Veränderungen ist, wurde ein Freilandexperiment durchgeführt. Dabei wurden Plots mit *I. glandulifera* und Plots ohne *I. glandulifera* mit Plots verglichen, in denen *I. glandulifera* entfernt oder eingepflanzt wurde. Das Entfernen von *I. glandulifera* wirkte sich positiv auf die Biomasse der einheimischen Vegetation und auf das Wachstum von *Urtica dioica* aus, das Einpflanzen dagegen negativ. Dies belegt einen kausalen Effekt von

I. glandulifera, der allerdings nicht stark war. Die Artendiversität wurde wiederum nicht von *I. glandulifera* beeinflusst. Ich leite aus den Ergebnissen ab, dass *I. glandulifera* ein “Trittbrettfahrer” von Ökosystemveränderungen ist, der sowohl von vorangegangenen Veränderungen profitiert, als auch weitere Änderungen verursacht. Insgesamt ergaben meine Untersuchungen, dass der Einfluss von *I. glandulifera* von den jeweiligen einheimischen Arten, deren Entwicklungsstadium, vom Habitat und von der Jahreszeit abhängt. Dominante Arten, wie vor allem *U. dioica*, sind besonders betroffen, während die Artendiversität nie von *I. glandulifera* verändert wurde und die Artenzusammensetzung nur unter bestimmten Bedingungen. Aus diesen Ergebnissen kann geschlossen werden, dass *I. glandulifera* nur einen geringen bis moderaten Einfluss auf die einheimische Vegetation nimmt. Aus der Literatur ist allerdings bekannt, dass *I. glandulifera* auch Auswirkungen auf viele andere Ökosystemkomponenten hat, wie Mykorrhiza, Herbivore oder Bodeneigenschaften.

Die Ergebnisse dieser Dissertation können helfen, eine zielgerichtete Managementstrategie für *I. glandulifera* zu entwickeln. Grundsätzlich sind großflächige Bekämpfungsmaßnahmen aufgrund der weiten Verbreitung von *I. glandulifera* nicht zu empfehlen. Sie sollten daher prioritär nur auf Flächen von hohem naturschutzfachlichem Wert durchgeführt werden, oder nur in Habitaten, in denen ein starker Einfluss von *I. glandulifera* zu erwarten ist. Dies sind Habitate mit hoher Bodenfeuchte und hoher Lichtverfügbarkeit. Aufmerksamkeit sollte man auch Flächen mit einer ausgeprägten Frühjahrsgeophyten-Vegetation schenken, da auch diese von *I. glandulifera* verändert wurde. Da *I. glandulifera* kein eindeutiger Treiber von Ökosystemveränderungen ist, sondern einige Eigenschaften eines Trittbrettfahrers hat, reicht es bei der Bekämpfung eines Bestandes nicht aus, *I. glandulifera* zu entfernen. Zusätzlich sollte das ursprüngliche Ökosystem wiederhergestellt und die Veränderungen, die *I. glandulifera* gefördert haben, möglichst rückgängig gemacht werden.

4 Synopsis

4.1 Introduction

4.1.1 Biological Invasions

Human-mediated biological invasions are part of the ongoing global change. Among land use, climate change, pollution, and nitrogen deposition, they are considered to be one of the main threats to nature worldwide (Sala et al. 2000, Díaz et al. 2019). Invasive species can alter ecosystems processes, change native community structure and reduce biodiversity (Ehrenfeld 2010, Vilà et al. 2011). Natural migrations overcoming geographical barriers have been common during earth history and have also gone along with tremendous changes in species pools and ecosystems (Stigall 2019). For example, tectonic movements and climate changes opened pathways and changed vectors. However, human mediated invasions reach unprecedented extent of distances, propagule numbers and dispersal rates (Ricciardi 2007). They have occurred already for thousands of years since men have carried for instance lifestock and crop plants along with their own movements (Anderson 2009, Hulme 2009). However, with increasing mobility, international trade, and globalization, intentional and unintentional transport of biota accelerated drastically in modern times (Ricciardi 2007). This resulted in the consideration of human mediated invasions separately from natural migrations and in the rise of invasion science. Out of all introduced species only a small fraction becomes invasive, because the process of naturalization and invasion implicates several filters (Richardson et al. 2000, Richardson and Pyšek 2006, Gallien and Carboni 2017): to establish, invading species have to be able to exist and reproduce within the biotic and abiotic conditions of the area they have been introduced to, and plants need dispersal vectors to spread. Thereby, the interplay of traits of the invader with the biotic and abiotic environment determines the invasiveness of the invader, as well as invasibility of the native community (Richardson and Pyšek 2006, Gallien and Carboni 2017). Additionally, human activities are not only responsible for the transport of alien species but also affect invasion dynamics in the introduced range. Invaders benefit e.g. from anthropogenic dispersal, disturbances, or climate change while they can be prevented by any kind of regulations and management (Ricciardi et al. 2017, Sinclair et al. 2020). Ultimately, a naturalized alien species is defined to be invasive if it exerts any kind of negative impact on human health, human economy or native ecosystems (see Box 1 for terms and definitions). Risks to health and economy as caused by pathogens or weeds and human interest for prevention are rather obvious. Nevertheless, it is quite difficult to define and detect negative ecological impacts.

Box 1: Terms and definitions.

alien species

A taxon is alien if it was intentionally or unintentionally introduced by humans into an area outside its natural range. The transport overcomes biogeographical barriers the taxon would not be able to overcome by natural dispersal. Synonyms: non-native, non-indigenous, exotic. (Blackburn et al. 2014, EuropeanUnion 2014, IUCN 2020)

invasive

Concerning the definition of the term "invasive" there have been discrepancies. Several authors referred it to species with high reproduction and spread, irrespectively of impact (Richardson et al. 2000, Kowarik 2010). In recent literature, "invasive" is usually restricted to species with a negative impact on native ecosystems. Especially in political contexts, threat to diversity is emphasized (EuropeanUnion 2014, IUCN 2020). Although also native species could meet this definition, the term "invasive" is usually reserved for alien species, while native species are often referred to as "pest" species (Pyšek et al. 2004).

invasibility

Invasibility is the vulnerability of a recipient ecosystem to invasion. It is determined by biotic and environmental conditions of the ecosystem (Perkins et al. 2011). For example communities with high species diversity are generally considered to be less susceptible to invasion.

archeophyte vs. neophyte

In Central Europe alien species are commonly classified by their residence time (Pyšek et al. 2004). Archaeophytes have been introduced before 1492 when America was discovered. They comprise several species that came along with human agriculture, often already in prehistoric times. Separation of archaeophytes from natives is often difficult and people became so familiar with them that they are often seen as natives. Neophytes in contrast, have been introduced after 1492. Interestingly, in the European Union regulation on invasive alien species, there is no separation between archeophytes and neophytes.

4.1.2 Invasions, nature conservation and the society

OFFICIAL VIEW ON INVASIONS. The threat by invasive alien species to nature and human well-being is officially recognized at international level. Based on the United Nation Convention on Biological Diversity (CBD 1992), the Aichi target number 9 (COP-CBD 2010), as well as the United Nation Sustainable Development Goals (United Nations 2015) declare that invasions should be prevented, prioritized, and threatening species eradicated by the year 2020. Despite the importance of invasions and increasing number of publications, the impact of invasions remains still poorly understood and quantified (IPBES-6 2018). This is why IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Weltbiodiversitätsrat) and IUCN (International Union for Conservation of Nature) maintain specialist groups dealing with invasion assessments, management opportunities and policy making. The commitments within the CBD are reflected in the "European Union Biodiversity Strategy to 2020" (European Commission 2011). The aim is to halt biodiversity and ecosystem service loss, which includes controlling invasions. For this purpose, a new regulation on invasive alien species was released, covering prevention, restrictions, and management of invasive species (European Union 2014). Subsequently, "the Union list" was adopted. This is a regularly updated list of invasive alien species of European concern, implying that action at Union level is required for their management. Currently the list contains 30 animal and 36 plant species, including *Impatiens glandulifera*, the model species of my studies (European Commission 2019). The European national states have to implement the regulation in their own legislation and practical nature conservation measures, as Germany did in 2017 (Nigmann and Nehring 2020). In addition to the Union list national states can also compile their own list of invasive species. Germany has not done so since the release of the Union list, but there is an older detailed invasion assessment for 80 invasive and potentially invasive plant species in Germany (Nehring et al. 2013). By the year 2020 the CBD as well as European Biodiversity Strategy have not come to an end, but will be continued with new programs still including a focus on invasions.

THE SOCIETY AND RESPONSIBILITY FOR ACTIONS. To prevent and manage invasions, the effort of private citizens, policy makers, and different stakeholders such as agriculture, trade, and nature conservation is required. However, it is a challenge to mobilize their effort in a reason-based way (Courchamp et al. 2017). Lack of citizen knowledge, uncertainty of scientific evidence and low generality of impact can lead to invasive species denialism (Russell and Blackburn 2017). Sympathy for pets and ornamental plants can hinder prevention programs, and lethal eradication often induces oppositions such as in the case of shooting of wild horses in Australia (Crowley et al. 2017). On the other hand, promoting actions against invasions can have the potential to raise xenophobia or racism (Simberloff 2003) and can be misused by right-wing policy. It is a problem that there is no global face of efforts against invasions, such as e.g. the iconic orang-utan is for efforts against deforestation (Courchamp et al. 2017). I think such a global face has to be positively connotated. Human beings' actions arise from emotions: people commit theirselves only to something they like, or against something they fear. This is one reason for science to create knowledge on invasions and their impact, to develop suitable management and to involve the public in a dialogue knowledge transfer (Courchamp et al. 2017). Management actions should take place at early invasion stages to be as successful as possible and to avoid difficult and controversial eradication. Therefore, invasive species have to be prioritized by their impact which has to be evaluated. With the knowledge of already successful invasions it will hopefully be possible to avoid future invasions.

4.1.3 Impact of invasions

WHAT IS IMPACT? Invasive species can have an impact on human well-being such as health or economy, and on native ecosystems. Here I only focus on the latter. The ecological impact means any kind of change of ecosystem properties caused by the invader (Pyšek and Richardson 2010, Ricciardi et al. 2013, Jeschke et al. 2014). This can be for example change of native vegetation, animal communities, species diversity and interactions, food webs, soil properties, microbial communities, and fire regimes (Dogra et al. 2010, Pyšek and Richardson 2010). Indeed, every (non-native) species should have some impact just due to integrating into the community (Ricciardi et al. 2013). According to Parker et al. (1999) the total impact of an invader has three dimensions: the invaders range, abundance and per-capita impact. This is crucial because invasiveness in the sense of dispersal and establishment does not necessarily correlate with per-capita impact (Ricciardi and Cohen 2007, Rumlerová et al. 2016). A species with a small range can have a high local impact, while widespread species can have a low impact (Ricciardi et al. 2013). Another type of impact of invasions is biotic homogenization on a genetic and functional level (Lövei 1997, Clavel et al. 2011). Human-mediated dispersal overcomes geographical isolation which is crucial for maintenance of global diversity. Without barriers a few generalist species spread globally, leading to a “Macdonaldization” of the biosphere (Lövei 1997). Locally, species number, including aliens, can increase, but globally, total species number as well as distinctiveness (β-diversity) declines. Especially native specialists decrease because they are more prone to extinction (Clavel et al. 2011, Stigall 2019). However, in most studies “impact” means the local change of ecosystem properties in the sense of abundance × per-capita impact. Per-capita impact is usually not separately considered. Thus, here I use the term “impact” as change of ecosystem properties due to abundance × per-capita impact unless it is explicitly stated.

MECHANISMS OF IMPACT. There are numerous hypotheses explaining how alien species become invasive having a negative impact on native ecosystems (Catford et al. 2009, Ricciardi et al. 2013, Enders et al. 2019). Some of them focus on properties of the receiving ecosystem making it invasible, some focus on properties of the invader making it invasive, and others focus on interactions between the invader and other species. Ecosystems are considered to be prone to invasions if they are for example characterized by low biotic diversity (diversity-invasability hypothesis), by disturbances, high resource availability, high heterogeneous environment, or if they possess empty niches (Enders et al. 2019). If an invader occupies an empty niche it is likely to establish, but without strong impact on native species (MacDougall et al. 2009). If the invader in contrast occupies the same or a similar niche than native species, and concurrently has a higher fitness, it can exert a strong impact, replacing the native species. Thus, a combination of niche differences and fitness differences determines whether invasive and native species exclude each other or whether they can co-exist (MacDougall et al. 2009). The ideal weed hypothesis implies that specific traits enhance the fitness of the invader and thus, benefit its invasiveness. Such traits include rapid growth, rapid exploitation of resources, high plasticity, high fecundity, small seed size (Rejmanek and Richardson 1996). However, traits of the invader have to be considered in relation to properties of the invaded ecosystem. To establish, the invader has to be adapted to the conditions of the receiving ecosystem, pre-adapted at the best. Invasion success is higher if the traits of the invader are different from those of the native community (Catford et al. 2009, Ricciardi et al. 2013, Enders et al. 2019). It is also possible that traits benefiting the early stage of invasion can turn into a disadvantage for the invader at a later stage, if the conditions of the native ecosystem change over time (for example trade-off between ruderal characteristics and stress tolerance). Finally, this can lead to the invaders' population decline, so called boom-bust dynamics (reckless invader hypothesis, Simberloff and Gibbons 2004). Superiority of the invader can also be due to species interactions as for example explained by the enemy-release hypothesis (Keane and Crawley 2002). Enemy-release occurs when an alien species escaped from natural enemies (predators, herbivores, pathogens) restricting its growth in the home range. In the exotic range without those enemies, the invader benefits from reduced damage. No longer required to invest into defense, the now available resources can be allocated to growth and reproduction, resulting in a higher competitive ability (EICA hypothesis, evolution of increased competitive ability, Blossey and Notzold 1995). Generally, new associations with native species can influence the alien species, for example if native generalistic pollinators contribute to its reproduction (Enders et al. 2019). Furthermore, invasive species can gain a large advantage by novel weapons (novel weapon hypothesis, Callaway and Ridenour 2004). Such weapons can be chemicals, physical properties or behavior against competitors who are not adapted to them. The most well-known example is plant allelopathy, the release of chemicals that negatively affect other plant species (Hierro and Callaway 2003, Levine et al. 2003, Callaway and Ridenour 2004). Textbook examples are *Centaurea maculosa* and *C. diffusa* that have a higher impact on the growth of plant species co-occurring in their invasive range in North America than in their Eurasian native range due to the roots exudates 8-hydroxyquinoline and (±)-catechin (Hierro and Callaway 2003, Inderjit et al. 2006). Allelopathy along with resource competition plays also a decisive role for the impact of *Impatiens glandulifera* on native plants, which is subject of manuscript 1. Assigning the three components of invasion impact sensu Parker (1999) to these hypotheses, invader range should be mostly determined by dispersal and habitat invasibility and invader abundance by habitat invasibility, invader traits, and adaption to the habitat. Per-capita impact should in a large part result from invader traits and species interactions. However, the mechanisms of impact explained by these hypotheses are interrelated with each other. The impact of invasions always results from interaction between properties of the invader and the recipient ecosystem.

4.1.4 Assessing the impact of invasions

MEASURING IMPACT. Impact of invasive species can be detected measuring any kind of change of ecosystem properties caused by the invader. For this, a situation with the invader is compared with a situation without the invader. This can be done by observational, experimental or modeling-based methods and their combinations (Stricker et al. 2015). Observational methods include the most often used comparison of invaded and uninvaded field sites, less commonly along a gradient of invader abundance, or along a chronosequence of different invasion stages (Kumschick et al. 2015b). Experimental studies remove or add the invader, and can be done in different stages of artificiality from lab-experiments with single species or ecosystem components, over mesocosms, to field studies within the natural ecosystem (Kumschick et al. 2015b, Stricker et al. 2015). Parameters measured are mostly biomass, species composition and diversity (at least for plants, (Armas et al. 2004)), but all organizational levels and processes in an ecosystem could be taken into account. This includes molecular processes, traits, species and individual performance, populations, communities, species interactions such as pollination or interactions in trophic networks, but also environmental properties and interactions between species and the abiotic environment. Diversity is not only species diversity, but also diversity on the genetic, functional, taxonomic, and trait level (Kumschick et al. 2015b). Additionally the different taxonomic groups such as microbes, plants, animals, and functional guilds like pollinators, predators, etc., and even ecosystem services can be considered (Charles and Dukes 2007, Kumschick et al. 2015b). Design, analysis, and interpretation of studies on the impact of invasions on ecosystems face the problem that the ideal control treatment should represent the original ecosystem state prior to invasion, but in most cases it is not very well-known (Parker et al. 1999). Hence, it is not clear what the best control is, especially for field studies. Experimental approaches removing or adding the invader can reduce this problem compared to pure observation of invaded and uninvaded sites because they can show the direct response of the native ecosystem. It is also a possibility to combine different controls like invaded site vs. uninvaded site and invader removal, or invader addition. I applied this in manuscript 3. Additional removal or addition of a native species can show whether an observed effect is caused by the invader or just by the treatment. However, practicability and necessary effort often restrict the dimension of studies. If this results in a low sample size, differences between treatments are often not significant, although the effect size is large. Thus, invasion impacts are often not detected in spite of being present (Davidson and Hewitt 2014). Furthermore, interactions between different species within an ecosystem can lead to indirect effects making the impact more complex and its detection more complicated (White et al. 2006).

CONTEXT-DEPENDENCY OF IMPACT. Complexity of nature entails that the impact of an invasion does not only depend on properties of the invader but also on the context of the invasion. Because context-dependency is a quite recently arising topic and very important for the understanding, evaluation, and management of invasions, it is a central subject of this thesis. Context-dependencies can occur at all levels of intrinsic (e.g. species, traits, interactions) and extrinsic (environmental) ecosystem properties, as well as space, time, and invasion stage or intensity (Parker et al. 1999, Jeschke et al. 2014, Kumschick et al. 2015b, Sapsford et al. 2020). Different native species in different developmental stages can be differently sensitive to the impact of an invader. Based on niche theory it is straightforward that species perform and interact depending on the environment and thus, interactions of native with invasive species also do. As a result, the impact of an invasion can depend on ecosystems, habitats, or environmental gradients. For example, the Zebra mussels (*Dreissena polymorpha*) showed habitat-dependency with its impact differing between environmental conditions (Strayer 2020). Kueffer et al. (2013) use the term “species x ecosystem interactions” with “ecosystem” referring to the broad ecological context of an invasion. Dependence on time can occur if the native species composition changes due to seasonal variation, succession, or changing environmental conditions. Time since invasion is crucial if an effect of the invader accumulates (e.g. allelopathic substances, litter), if the invader shows boom-bust cycles, if the invader changes its interactions with native species (e.g. predator of the invader arises) or finally undergoes post-introductional evolution (Sapsford et al. 2020). For nature conservation, knowledge of context-dependent impacts can help to prioritize those contexts with the highest impact for management measures.

CAUSALITY OF IMPACT. Another challenge in assessing the impact of an invader is to disentangle cause and effect of an invasion, as addressed in manuscript 3. It is not necessarily clear that a change of ecosystem properties observed along with a species invasion is really caused by the invader. An alien species can invade an intact ecosystem and cause changes there, and thus be the "driver" of the changes (MacDougall and Turkington 2005, Didham et al. 2005). Alternatively, invasion may be facilitated by earlier ecosystem changes, such as global warming, land use change, pollution, nutrient input or altered disturbance regimes. Then the invasion is only a symptom, and the invader a "passenger" of the underlying change (MacDougall and Turkington 2005, Didham et al. 2005). In other words, the invasion is possible because the ecosystem invasibility was changed by anthropogenic factors. Bauer (2012) added the "back-seat driver" to this model. Back-seat drivers are in between the extreme positions of the continuum from drivers to passengers. In the back-seat driver model ecosystem changes and invasion interact. Like passengers, invasion of back-seat drivers is facilitated by previous ecosystem changes, and like drivers the invasion leads to further changes. Thus, back-seat drivers are a contribution, not the cause of species decline and ecosystem changes (Bauer 2012). Similar to context-dependencies the question of causality is a crucial point of invasion biology and has only rarely been studied yet. For nature conservation measures it is important, because a proper management method of a specific invasive species depends on its driver-passenger behavior (Bauer 2012). In case of a driver, removal of the invader which is the only reason for changes is ideally sufficient. In case of a passenger, removal can not be expected to be sufficient for ecosystem recovery but ecosystem restoration can. However, in case of a back-seat driver both is needed, removal of the invader combined with ecosystem restoration. Thus, management of a back-seat driver is more complicated because the previous changes that facilitated invasion have to be known and countered.

EVALUATION OF IMPACT. To compare the impact of invasions between different alien species, different invasion contexts, or different response variables, it is not sufficient to measure a response variable only, but a comparable metric without units is required to quantify the impact. While there are several such indices Armas et al. (2004) recommended the use of the relative interaction index (RII) which I also used in manuscript 1 and 3. RII was developed for the study of species interactions, especially competition and facilitation between plants. It is bound to the range from -1 to +1, it is symmetrical around zero (no effect), and the algebraic sign shows whether the effect of the manipulation is negative or positive (Armas et al. 2004). Per-capita impact and abundance of the invader can be integrated with impact-abundance curves. A response variable or a measure of impact (e.g. RII) is plotted against abundance of the invader (Pearse et al. 2019, Sapsford et al. 2020, Strayer 2020). Comparisons of shape, slope, and goodness of fit can be used to compare species and contexts. I applied this in manuscript 1 and 2, plotting growth of native plants against allelopathic material of *I. glandulifera* and cover of natives against cover of *I. glandulifera*, respectively (Bieberich et al. 2018, 2020). Impact-abundance curves can also show whether the per-capita effect is equal over the gradient of abundance of the invader, or whether it is non-linear, thus having thresholds, which is also a context-dependency (Sapsford et al. 2020). However, quantification of impact is not sufficient for management decisions and communication with policy makers (Simberloff 2011). An impact score is required per invasive species to rank their total impact on the different ecosystem components and perhaps also on economy and health. There are two main scoring frameworks among several less established ones (Vimercati et al. 2020). The General Impact Standard Scoring system (GISS) comprises environmental and socio-economic impacts and is mostly used in Europe (Kumschick et al. 2015a, Nentwig et al. 2016, Rumlerová et al. 2016). However, the European Union did not use the GISS scoring but their own assessment to compile the Union list. Blackburn et al. (2014) and Hawkins et al. (2015) processed the environmental impact of the standard scoring system (GISS) into the Environmental Impact Classification for Alien Taxa (EICAT) for application for the IUCN where it was adopted as standard in 2020 (IUCN 2020). With some differences both frameworks evaluate the impact of an invasive species into several impact categories (e.g. competition, disease transmission, impact on plants) and several defined levels of impact intensity. When evaluating the overall impact of an invader, conflicts can arise when different guilds (pollinators vs. plants) are controversially affected or when human stakeholders have different interests. For example, increasing alien plant biomass may be harmful to the native ecosystem but increases the ecosystem service of carbon sequestration; the decrease of large native predators by a toxic alien amphibian is detrimental for nature conservation but beneficial for livestock farmers (Vimercati et al. 2020). Similarly, there can be a conflict between agricultural use of alien species and nature conservation as in the case of the Black Locust *Robinia pseudoacacia* which is a favored forest tree but is considered invasive (Vítková et al. 2017). Generally, nature conservation aims are a question of perspective and wishes. Even the increase of diversity can be evaluated as "good" because the aim is a high diversity, or it can be evaluated as "bad" because the aim is preservation of an unchanged ecosystem state.

4.1.5 Model species *Impatiens glandulifera* in Europe

MODEL GENUS IMPATIENS. *Impatiens glandulifera* is one of the most common invasive plant species in Central Europe and an excellent model species to study plant invasions (Fig. 2). It belongs to the large genus *Impatiens* (Balsaminaceae, Ericales) that consists of more than 1000 species, mainly from the Old World tropics and subtropics and a few from temperate regions (Yu et al. 2016). *Impatiens* species have beautiful flowers with high diversity of colors and shapes, thus sometimes regarded as 'the dicot counterpart of the orchid' (Yuan et al. 2004). For this reason, several members of the species are cultivated as ornamentals, also outside their home-range where some became invasive in different parts of the world (Čuda et al. 2016). In

Europe, there is one native species, *I. noli-tangere*, and the two invasive species *I. glandulifera* and *I. parviflora* (Fig. 1). Additionally, *I. balfourii, I. balsamina, I. capensis, I. edgeworthii*, and *I. scabrida* rarely occur in Europe covering a range from casual occurrence to potentially invasive (Čuda et al. 2016). *I. walleriana*, the Busy Lizzie (Fleißiges Lieschen), is cultivated as a popular ornamental, but not escaped into the wild (Fig. 1). Some studies used this setting to study intrageneric competition and habitat requirements, and to identify which traits are associated with invasiveness within the genus. The invasive species, especially *I. glandulifera*, are highly productive in growth and show a high phenotypic plasticity in reaction to shading, nutrients and soil moisture (Skálová et al. 2012, 2013, Minden and Gorschlüter 2016). Traits regarding early plant development have a major importance for invasiveness. For example, naturalized-invasive species have heavy seeds, need long time for germination, allocate biomass in shoots rather than roots, and are similar to the native *I. noli-tangere*. However, planting frequency seems to be more important for naturalization than traits (Čuda et al. 2016).

INVASION PROCESS. *I. glandulifera* is native to the Himalaya mountains where it occurs in field and forest edges, along roads, in pastures, shrublands, mixed forests and forest gaps up to 4000 m a.s.l. (Beerling and Perrins 1993, Čuda et al. 2020). Its first introduction to Europe for ornamental purposes is known to have taken place in 1839 to Kew Gardens in England where the first naturalization was recorded in 1855, but multiple introductions from multiple origins are indicated by population genetics (Perrins et al. 1993, Hagenblad et al. 2015, Nagy and Korpelainen 2015, Kurose et al. 2020). Approximately since the mid 20th century, *I. glandulifera* has been spreading exponentially over Europe (Pyšek and Prach 1995). Now it is very common and its distribution ranges from Scandinavia to Mediterranean countries up to an elevation of at least 1200 m a.s.l (Fig. 2F-G, Larsson and Martinsson 1998, Pacanoski and Saliji 2014, Laube et al. 2015). Also other parts of the world such as North America, Argentina, Russia, New Zealand, and Japan were invaded by now (Fig. 2F, Čuda et al. 2020). In Europe, *I. glandulifera* first spread mainly in riparian habitats, settlements and along roads (Pyšek and Prach 1993). Due to large amounts of pollen and sugar-containing nectar, the flowers of *I. glandulifera* are very attractive to several pollinators, enabling a high reproduction (Titze 2000, Chittka and Schürkens 2001, Nienhuis and Stout 2009, Nienhuis et al. 2009, Vervoort et al. 2011). The numerous seeds are very well dispersed, primarily by an effective ballistic short-distance dispersal mechanism of the fruit capsule (Fig. 2B). It opens explosively catapulting the 500 – 800 seeds per plant over about 6 meters (Beerling and Perrins 1993, Chapman and Gray 2012, Deegan 2012). Secondarily, rivers serve as corridors for hydrochoric long-distance dispersal carrying the seeds within the sediments (Lhotská and Kopecký 1966, Love et al. 2013). Additionally, human-mediated long-distance dispersal plays an important role (Walker et al. 2009, Zybartaite et al. 2011). With increasing time since invasion of a river, *I. glandulifera* spreads laterally from the river bank to adjacent, mostly riparian wet habitats, as well as upstream along the tributaries (Malíková and Prach 2010). Thereby, spread of *I. glandulifera* is also enhanced by flooding (Čuda et al. 2017a).

Figure 1. Photographs of *Impatiens*-species occurring in Europe. Sources: photo of the native *I. noli-tangere* taken by J. Bieberich. Photos of all other alien species from GBIF (www.gbif.org) and iNaturalist (www.inaturalist.org), published under the CC BY-NC license. *I. balfourii* © soniafabrega, *I. edgeworthii* © Cordula Bernert, *I. capensis* © Judy Gallagher, *I. scabrida* © karoconniff, *I. parviflora* © DougSponsler, *I. balsamina* © Prajwal Ullal, *I. walleriana* © kgammons. Photographs of *I. glandulifera* are shown in Fig. 2.

Typical riparian habitats are inundation communities, fens, mesotrophic grasslands and woodlands (Beerling and Perrins 1993). They often comprise tall herbaceous vegetation with e.g. *Urtica dioica*, *Galium aparine*, *Phalaris arundinacea*, *Calystegia sepium*, *Rumex obtusifolius*, *Alliaria petiolata*, *Anthriscus sylvestris*, *Heracleum mantegazzianum*, *Aegopodium podagraria*, and *Lamium maculatum* (Beerling and Perrins 1993, Cockel et al. 2014, Diekmann et al. 2016, Bieberich et al. 2020). Over the last 20 years *I. glandulifera* has increasingly invaded deciduous and mixed forests, also distantly from riversides (Čuda et al. 2017b, 2020). To be able to succeed in such different habitats, high tolerance to environmental conditions and a trait plasticity are beneficial as shown for *I. glandulifera* in experimental studies (Skálová et al. 2013, Minden and Gorschlüter 2016).

IMPACT OF *IMPATIENS GLANDULIFERA*. In invaded vegetation, *I. glandulifera* can often become dominant (Fig. 2C – E) and have a negative impact on several components of the ecosystem such as plants, mycorrhiza, herbivores, pollination networks, and soil properties. This is comprehensively addressed in the discussion section. Massive establishment is enabled by the high reproductive potential and competition with native vegetation. *I. glandulifera* possesses several growth-related traits that are linked to the high competitive effect. As an annual species it develops from seeds every year (Beerling and Perrins 1993). Though without any storage organ, it grows very fast in spring and reaches a remarkable height of up to 3 m; higher than any native annual and at least as high as the native perennial herbs (Beerling and Perrins 1993, Bieberich et al. 2020). This vigorousness is due to an economic growth strategy. The plant mainly consists of water rather than biomass (Koenies and Glavac 1979, Beerling and Perrins 1993), the root system provides high anchorage relative to low allocation of dry biomass into roots (Ennos et al. 1993). Under shade the cost-effective NO_3- is used as osmoticum rather than expensive organic sugars or acids, and a large leaf area with high chlorophyll content enables high photosynthesis rates even under shade (Andrews et al. 2005). Only a relatively low number of invertebrates is known to feed on *I. glandulifera* such as Gastropoda, Cercopoidea (Froghoppers, Schaumzikaden), Miridae (Mirid bugs, Weichwanzen), and Aphidae (Schmitz 1991). Damage by insect herbivores and parasitic rust fungi in the invaded range is lower than in the native range and lower than damage in native *I. noli-tangere* (Schmitz 1991, Tanner et al. 2014). This meets the enemy-release hypothesis and can contribute to high performance of *I. glandulifera* in the invaded range (EICA hypothesis). However, larvae of the Geometridae moth *Xanthorhoe biriviata*, a specialist herbivore of *I. noli-tangere*, that was long assumed to reject *I. gandulifera* was now also found to feed on it (Schmitz 1991, 2005, 2007). In addition to vigorous growth, *I. glandulifera* has allelopathic potential. *I. glandulifera* as well as other members of the genus produce substances such as naphtoquinones, other phenolic compounds, steroids, several flavonoids, or essential oils that could act as allelochemicals (Bohm and Towers 1962, Lobstein et al. 2001, Tříska et al. 2013, Cimmino et al. 2016, Szewczyk et al. 2016a, b, Vieira et al. 2016). Often the naphtoquinones 2-methoxy-1,4-naphthoquinone (2-MNQ) and 2-hydroxy-1,4-naphthoquinone (lawson) are recorded, whereby 2-MNQ is the major quinone and considered to be the main allelopathic substance (Bohm and Towers 1962, Chapelle 1974, Lobstein et al. 2001, Tříska et al. 2013, Ruckli et al. 2014a). In *I. glandulifera,* it is present in manifold higher amounts than in other

Impatiens species (Lobstein et al. 2001). Results are contradictory whether 2-MNQ is also produced by the native *I. noli-tangere* (Chapelle (1974) and Ruckli et al. (2014) no, versus Lobstein et al. (2001) yes). Thus, it is unclear whether 2-MNQ can be considered a novel allelopathic weapon. Interestingly, also juglone, the famous allelochemical of *Juglans regia*, is a naphtoquinone with a structure related to 2-MNQ and lawson (Rietveld 1983, Lobstein et al. 2001, Terzi 2008). 2-MNQ is known to get rinsed off the leaves of *I. glandulifera* by rainwater, to be present in the soil and to inhibit mycorrhiza growth (Ruckli et al. 2014a). Simultaneously, *I. glandulifera* litter and plant material extracts can reduce seed germination of other species (Vrchotová et al. 2011, Ruckli et al. 2014a, Loydi et al. 2015). Thereby the concentration of 2-MNQ in the extracts correlated with their inhibitory effect (Ruckli et al. 2014a) but the direct role of 2-MNQ was still unclear prior to my study on allelopathy and competition of *I. glandulifera* (Bieberich et al. 2018). Resource competition and allelopathy interact with each other and can lead to suppression of other plants. In pot experiments it was shown that *I. glandulifera* has a negative impact on growth of *Urtica dioica* (Tickner et al. 2001, Bottollier-Curtet et al. 2013, Gruntman et al. 2014) and conspecifics such as *I. noli-tangere* (Skálová et al. 2013, Čuda et al. 2015). Results of field studies are more contradictory. Del Fabbro et al. (2014) found no effect of *I. glandulifera* invasion on germination of experimentally sown seeds but on germination from natural seed bank. Also in Bavarian forests, recruitment in agroforests was not hindered in invaded sites (Ammer et al. 2011). Considering plant communities of field sites, negative effects on plant diversity and species composition were reported by Cockel et al. (2014) and Hulme and Bremner (2006) in riparian habitats, Rusterholz et al. (2017) in a deciduous forest, and by Kiełtyk and Delimat (2019) in the Tatra Mountains. A negligible effect in contrast, was found in riparian habitats by Hejda and Pyšek (2006), Hejda et al. (2009), Diekmann et al. (2016), in forests by Čuda et al. (2017b), and in mixed habitats by Künzi et al. (2015). Sometimes the weak effect of *I. glandulifera* is thought to be due to high fluctuations in its population size (Kasperek 2004, Diekmann et al. 2016). However, it is not clear what determines the varying effect. Context-dependencies, such as dependency on habitat, environmental conditions, seasons, native plant species, and plant developmental stages, could be reasons and are addressed in all manuscripts of this thesis.

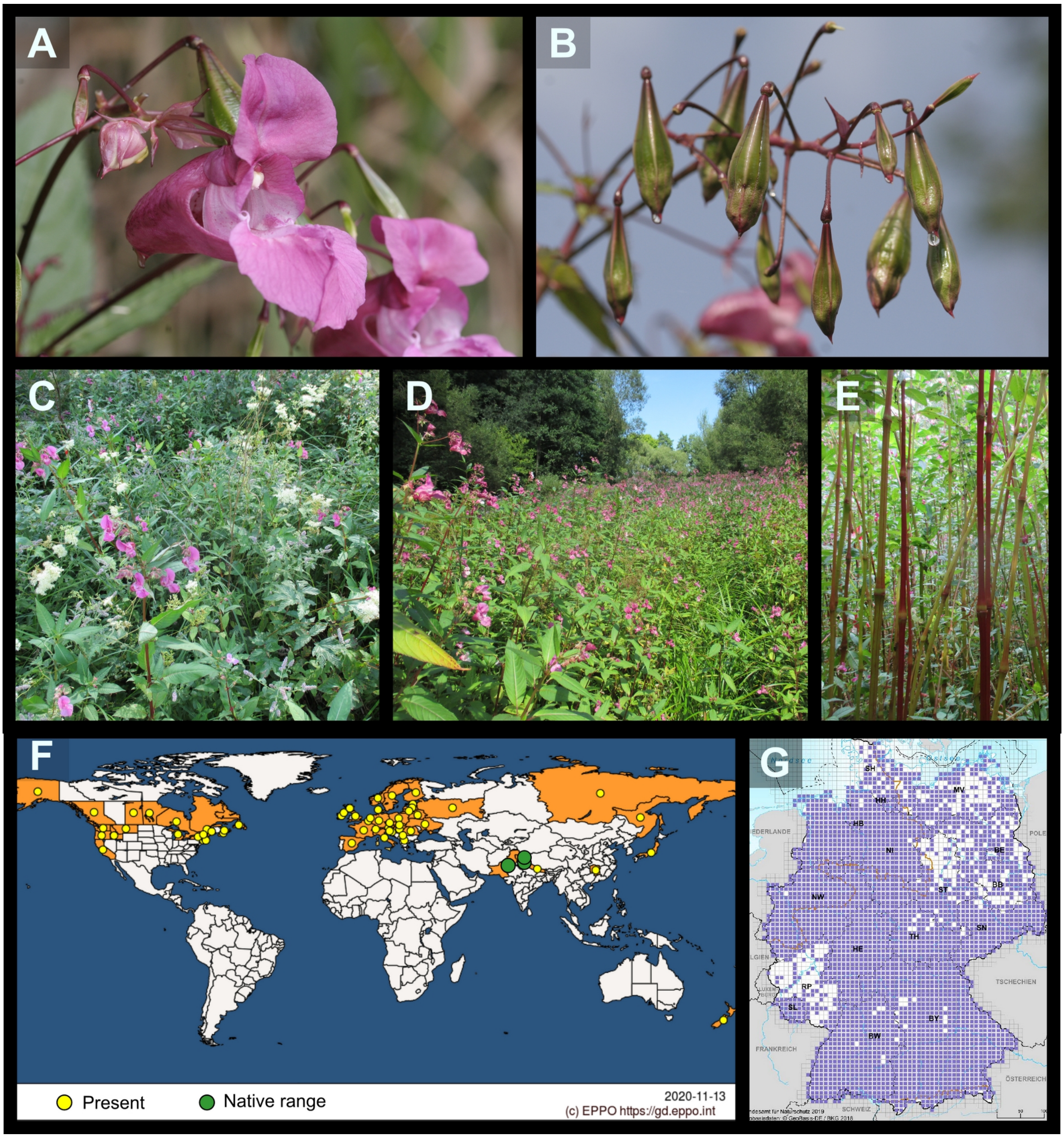

Figure 2. Photographs and distribution of *I. glandulifera*. A) flowers, B) seed capsules, C-E) field sites invaded by *I. glandulifera* with the cover ranging from low C), medium D), to very high E). A-E) All pictures taken by Judith Bieberich. F) Global distribution map based on occurrence per country. Source: EPPO database (European and Mediterranean Plant Protection Organization, https://gd.eppo.int). G) Distribution of *I. glandulifera* in Germany based on a 10 × 10 km grid. Source: Nigmann and Nehring (2020).

4.2 Synopsis of the manuscripts of the thesis

MAIN OBJECTIVES. The motivation of my studies was to understand mechanisms and processes of impact of plant invasions. This is one general aim of invasion biology and important for prediction of invasions and development of management strategies (Bartz and Kowarik 2019). Specifically, my aim was to study context-dependencies in terms of species-, developmental stage-, season- and habitat-specific impact, which is a purpose of invasion biology that has arisen only recently. Within the framework of context-dependencies, competition and allelopathy as mechanisms of impact, interactions of invader × environment, and causality of impact were the subjects of my studies. *I. glandulifera* was chosen as model species because ambiguous study results from literature suggest that its impact may be context-dependent. Deepening the knowledge on extensively studied model species also improves the general understanding of invasions (Kueffer et al. 2013).

STUDY CONCEPT. The designs of the three manuscripts covered a gradient of closeness to nature, control and complexity. A laboratory and pot experiment with selected target organisms (manuscript 1 on allelopathy and competition) is appropriate to study mechanisms, because it provides high control over interfering factors, but is rather artificial. Field experiments increase complexity and closeness to nature, but provide lower control of interfering factors. By conducting field experiments it is possible to consider natural communities, and the experimental design allows to study causality of impacts (manuscript 3). The natural situation is best reflected in the observational approach of manuscript 2 (correlation between environmental conditions, *I. glandulifera*, and native vegetation cover) but without deduction of causality. These three approaches serve as controls for each other. Consistent results can confirm the impact of *I. glandulifera* on native vegetation. In all field studies on the impact of *I. glandulifera* on native vegetation existing so far, only species composition and diversity based on cover per species were considered. I expanded these classical parameters by the performance of selected native target species in order to be able to study species-dependencies and gain more insights into community interactions. The target species were chosen as they regularly co-occur with *I. glandulifera* in different habitats and were used consistently in all studies as far as possible. The most important ones are *Urtica dioica* and *Filipendula ulmaria*, which co-occur with *I. glandulifera* very commonly and are also capable of forming dominant stands. In the experimental field study of manuscript 3, biomass was used as parameter for species abundance because it is more exact than estimated cover. Additionally, performance of individual plants of *U. dioica* was measured because, like species biomass, it can show a fast response to experimental removal and addition of *I. glandulifera*.

MANUSCRIPT 1. The first question was how *I. glandulifera* affects native plants by allelopathy and competition and whether 2-MNQ is its main allelochemical. In the framework of context-dependencies, native species and their developmental stages are expected to differ in their susceptibility to *I. glandulifera* allelopathy and competition. In the experimental study of manuscript 1 (Bieberich et al. 2018) I used seedlings and juvenile plants (first year growth) of *I. glandulifera* and the native target species *Geum urbanum*, *Filipendula ulmaria*, *Urtica dioica*, and *Salix fragilis*. Plants were grown in competition with *I. glandulifera*, treated with *I. glandulifera* leaf material, or 2-MNQ. Seedlings were grown on agar for 6 days from germination onwards. Juvenile plants were potted into soil for ten weeks. I found that overall *I. glandulifera* had a negative effect on the growth of all target species depending on the species and plant developmental stage. *F. ulmaria* was the least affected and *U. dioica* the most, and juveniles were more suppressed than seedlings, especially by competition. 2-MNQ had a negative impact on the growth of the target plants but its effect was rather small compared to competition in juveniles, and compared to the effect of *I. glandulifera* leaf material on seedlings. Thus, 2-MNQ acts as allelochemical, but may not be the only substance responsible for the allelopathic effect of *I. glandulifera*. To disentangle resource competition of *I. glandulifera* seedlings from allelopathy, I added active charcoal to the agar. It is expected to absorb allelopathic substances released from *I. glandulifera* roots and thus reverses the negative allelopathic impact. This revealed that *I. glandulifera* seedlings had a competitive effect on *U. dioica,* but no allelopathic effect. In the juvenile stage, competition with *I. glandulifera* had a strong effect on all species and this should reflect a combined effect of resource competition and allelopathy. However, I found that the competitive effect of *I. glandulifera* was of comparable strength to the competitive effect of the natives on their conspecifics (intraspecific competition). This indicates that *I. glandulifera* may act similarly to dominant native species in the field. Surprisingly, *I. glandulifera* seedlings were tolerant to their own allelochemicals, but juveniles not. I suggest that the tolerance of seedlings can enable a massive recruitment in spring suppressing other species. During further development allelopathic self-inhibition ("autotoxicity") and density-dependent mortality may lead to spacing between individuals and reduce intraspecific resource competition among the remaining individuals. The autotoxicity may also be connected to declines of a population and thus play a role in observed population fluctuations of *I. glandulifera*.

MANUSCRIPT 2. If the species-specific response of native plants to allelopathy and competition of *I. glandulifera* is also relevant in the field, it may lead to changes on plant species composition, α-diversity, and abundance. This was addressed in the field study of manuscript 2 (Bieberich et al. 2020). In a heterogeneous riparian habitat, the environmental conditions can change from patch to patch on a very small spatial scale. For this reason, also abundance of *I. glandulifera* and its impact on native vegetation was expected to depend on the environmental conditions at a particular patch (subsequently named micro-habitat). Another changing property of riparian habitats can be species composition due to seasonal species turnover. Especially in riparian forests, plant communities are often characterized by early flowering geophytes. In order to test whether abundance of *I. glandulifera* and its impact on native plant species depend on environmental conditions and season, I performed a vegetation survey within heterogeneous riparian meadows and alder forests in Germany. Per study site, plots were arranged on a grid. This systematic design of the observational study allowed a representative sampling over the whole gradient of environmental conditions and *I. glandulifera* cover, and regression analysis instead of comparison between invaded and uninvaded plots only. Using a piecewise structural equation modeling approach, effects of the environment on *I. glandulifera* and in turn on the native vegetation were directly linked. I found that high soil nutrients, moderate light and moderate soil moisture benefited *I. glandulifera* resulting in a patchy occurrence. Impact depended on micro-habitat and season. The native vegetation was most affected under high light conditions, especially with high soil moisture. Comparing seasons, plant species composition was not affected in summer but in spring. That might be explained by a high allelopathic effect of *I. glandulifera* on young native plants as found in manuscript 1 (Bieberich et al. 2018) and by legacy effects from the previous year. Impact on plant cover was species-specific whereby per season and micro-habitat always the most dominant species were most affected. These were *U. dioica* in summer, by contrast *Ranunculus ficaria* and *Anemone nemorosa* in spring, and *U. dioica* in the moist-bright habitat while *F. ulmaria* in bright habitats independently of soil moisture. Plant species α-diversity was not affected at all. Thus, native plant species were reduced in cover but not excluded from the communities. This might be due to population dynamics. The patchy occurrence and year-to-year changes in abundance of *I. glandulifera* can lead to co-existence with native species at a larger spatial and temporal scale, because the native vegetation can persist in uninvaded patches and recover when *I. glandulifera* declines.

MANUSCRIPT 3. To see whether these observations from the vegetation survey represent a causal impact, and thus *I. glandulifera* being a "driver" of ecosystem changes, I additionally conducted a field experiment within the same study sites (Bieberich et al. 2021). *I. glandulifera* was removed from invaded plots and transplanted to uninvaded plots. The response of the native vegetation was quantified by the relative interaction index (RII) that allowed a direct comparison between the two trials (removal and planting) and between the habitats riparian meadows and alder forests. A negative impact of planting *I. glandulifera* and a concurrent positive effect of removal on the native vegetation indicated a causal effect of *I. glandulifera* on total native biomass and growth of *Urtica dioica*. However, this effect was rather low. Species α-diversity and composition, as well as vegetation height and biomass of the most frequent native species were not affected by *I. glandulifera* manipulations. Habitat-dependency was very weak because only the effect of *I. glandulifera* planting on total biomass was slightly stronger in alder forests than meadows. This is contrary to the observational study (manuscript 2). *I. glandulifera* only partially met the criteria of a "driver" of ecosystem changes that would easily establish and clearly suppress natives, while removal would lead to recovery of the native vegetation. I suggest that *I. glandulifera* is a "back-seat driver" whose invasion is favored by previous ecosystem changes until it becomes a driver of further changes itself.

CONCLUSION. In summary, I found that the impact of *I. glandulifera* depended on the native target species, their developmental stage, on the habitat, and season. Suppression of neighboring plants was due to a combination of allelopathy and competition. The species-specific impact could be observed under artificial experimental conditions as well as under field conditions. In all cases *U. dioica* was the most affected species, followed by other common and dominant species such as *F. ulmaria*. Species α-diversity was not affected, species composition only under specific conditions. From our results I conclude that the impact of *I. glandulifera* on native vegetation is only minor. I do not expect that native plants are threatened, in the sense of full replacement of a species, or total change of a community. However, suppression of abundant dominant plant species could lead to changes in ecosystem processes because dominant plants account for functions such as primary production and nutrient cycles. *I. glandulifera* had a causal impact on the native vegetation. However, it was not a clear driver of ecosystem changes but should be considered a back-seat driver that benefited from previous changes.

4.3 Discussion

4.3.1 Impact of *Impatiens glandulifera* on native vegetation

Considering all available field studies on the impact of *I. glandulifera* on native vegetation, more studies conclude a minor than a major impact (Tab. 1). Thus, the impact of *I. glandulifera* on vegetation can be rated as minor to moderate. Species abundance seems to be clearly affected (Hulme and Bremner 2006, Cockel et al. 2014, Bieberich et al. 2020, 2021), but impact on species diversity and composition is ambiguous (Tab. 1). A clear pattern which factor determines the impact is not visible. Most of the studies pool data of different habitats, or do not describe the habitats examined in detail. Riparian habitats for example could comprise meadows, river banks, or flooded sites. According to our results, they should differ in their susceptibility to *I. glandulifera*. The impact of *I. glandulifera* can vary strongly between years, sites, and even patches within one site (Cockel et al. 2014, Čuda et al. 2017b, Rusterholz et al. 2017, Bieberich et al. 2020). Temporal variations of impact can represent a steadily increasing impact as indicated by Rusterholz et al. (2017), which may result from accumulating allelochemicals or tipping points in response of the native ecosystems (Sapsford et al. 2020). Alternatively, the variations can represent ups and downs of the impact. Annual changes of the impact of *I. glandulifera* could for example result from varying environmental conditions caused by precipitation and temperature. *I. glandulifera* was observed to vary in its abundance from year-to-year on a small spatial scale (Bieberich et al. 2020) but also in its population sizes over several years (Kasperek 2004). Boom-bust dynamics – a rapid population expansion followed by strong decline – is sometimes observed in invasion biology. For example, the pondweed *Elodea canadensis* spread massively over Europe in the 19th century and reached such high population densities, that the river Thames was reported to be impassible. Then suddenly, without an obvious reason, the populations declined to a minor status (Simberloff and Gibbons 2004). Boom-bust dynamics can result from interactions with enemies (e.g. release from enemies followed by integration into native food webs), density-dependent interactions, disturbances, succession, environmental changes, or exhaustion of resources (Simberloff and Gibbons 2004, Strayer et al. 2017). For *I. glandulifera,* I found that it was not fully tolerant to its own allelochemicals and suggest that this may contribute to a decline of abundances (Bieberich et al. 2020). Boom-bust dynamics can recur with several population up-and-downs (Strayer et al. 2017). Native ecosystems may then have the opportunity to recover during down-phases, as I also discuss for *I. glandulifera* (manuscript 2). Alternatively, the boom-bust dynamics can occur with only one rise and one fall (Strayer et al. 2017). This is of special importance for nature conservation as it would possibly give the opportunity for just waiting until the population declines strongly in a bust phase, instead of taking management measures. In case of *I. glandulifera* it would be interesting whether there are busts that even lead to extinction of populations. I suggest that at least in riparian meadows it is possible that *I. glandulifera* may be replaced by natural succession.

Table 1. Scientific field studies on the impact of *I. glandulifera* (Imp.gla) on native vegetation.

Habitat and study region	**Method**	**Impact of *I. glandulifera* on investigated parameters**	**Concluded overall impact**	**Reference**
riparian vegeation, Czech Republic	1) observational: invaded vs. uninvaded 2) experimental: invaded vs. removal	insignificant reduction of alpha-diversity; no or marginal change of species composition	negligible	Hejda and Pyšek (2006)
riparian vegetation, England	experimental: invaded vs. removal	strong reduction of α- and γ-diversity and seedling density; high impact on light demanding species; positive impact on non-native species	negative	Hulme and Bremner (2006)
riparian river banks, England	experimental: invaded vs. two methods of removal; over 3 years	reduction of species number and cover, very high variation between sites and years make evaluation of results difficult	negative, increasing with time and cover of Imp.gla	Cockel et al. (2014)
riparian meadows and forests, Germany	observational: regression between environmental variables, cover of Imp.gla and native vegetation	no effect on alpha-diversity but species-specific reduction of plant cover; correlations depended on environmental conditions (micro-habitat) and season	no threat but reduction of cover of dominant species	Bieberich et al. (2020) manuscript 2
riparian meadows and forests, Germany	observational and experimental: invaded vs. removed vs. uninvaded vs. planted	negative causal impact on vegetation biomass and performance of *Urtica dioica*; no effect on alpha-diversity; very slight habitat-dependency	causal but low	manuscript 3
managed mixed forest, Czech Republic	observational and experimental: invaded vs. uninvaded vs. removal; over 3 years	variation higher between years than between treatments; effect on soil and litter characteristics (minimal), species composition, mainly on light demanding ones; no effect on plant α-diversity	minimal	Čuda et al. (2017b)

Table 1. continued

Habitat and study region	Method	Impact of *I. glandulifera* on investigated parameters	Concluded overall impact	Reference
mixed deciduous forest, Switzerland	observational and experimental: invaded vs. uninvaded vs. removal; correlation with Imp.gla density; over 5 years	reduction of α-diversity of above ground vegetation and seedbank; no correlation with Imp.gla density; no effect on aboveground species composition and seedbank	negative impact, increasing over time	Rusterholz et al. (2017)
various communities pooled, Czech Republic	observational: invaded vs. uninvaded; Imp.gla along with other invasive species	insignificant reduction of α-diversity; high similarity between invaded and uninvaded plots; smallest impact compared to the other invasive plant species	very low effect	Hejda et al. (2009)
various habitats pooled, Switzerland	observational: sampling along a gradient of the invader cover; Imp.gla along with other invasive species	no impact on α-diversity; no interaction of impact with environmental variables	no impact	Künzi et al. (2015)
various habitats partly separated, Germany	observational: invaded vs. uninvaded; Imp.gla along with Imp.par	significant reduction of α-diversity but only by a low amount; significant but weak shift of species composition; light demanding species especially affected; higher impact in open vegetation indicated; soil K-content reduced, other chemicals not affected	low	Diekmann et al. (2016)
various habitats pooled, montane belt, Poland	observational: invaded vs. uninvaded; invaded plots sampled along a gradient of Imp.gla cover	considerable change in species composition and reduction of α-diversity, especially if Imp.gla cover exceeded 80%	strong negative impact	Kiełtyk and Delimat (2019)

4.3.2 Impact assessment of *Impatiens glandulifera*

My assessment according to GISS and EICAT. To evaluate the environmental impact of *I. glandulifera* on native ecosystems, I applied the General Impact Scoring System (GISS, (Kumschick et al. 2015a, Nentwig et al. 2016)) and the EICAT scheme (IUCN 2020). The GISS is commonly used in Europe and well suited to present all available data on *I. glandulifera* impacts (Tab. 2). In addition to plants, *I. glandulifera* affects several ecosystem properties such as pollinators, herbivorous insects, soil- and litter-dwelling invertebrates, mycorrhiza, and soil chemicals (Tab. 2). The allelopathic effect of *I. glandulifera* can even encroach upon neighboring aquatic ecosystems. Only transmission of disease and hybridization with native species are not known. In all concerned categories I rate the impact as minor to medium (category 2-3) but differentiation between levels is difficult. A major problem is that it is crucial to know the spatial scale of impact, and whether several and also less abundant species are affected. The wide distribution of *I. glandulifera* could indicate that the impact is relevant for a larger scale, but response of the natives is only studied locally or in pot experiments. Also knowledge on impact on rare species is lacking. Summarizing over all categories, I came up with 10 of 30 environmental scores. Also Rumlerová et al. (2016) applied the GISS scheme to *I. glandulifera* along with several other invasive species and came up with a total sum of 10 environmental scores for *I. glandulifera*. However, they do not provide an explanation of their assessment and cite only four journal articles that report the highest mentioned impact of *I. glandulifera*. In the EICAT scheme, impact is evaluated for several impact mechanisms (IUCN 2020). For *I. glandulifera* the mechanisms 1) competition, 9) impact on chemical ecosystem characteristics, and 12) indirect impacts through interactions with other species (e.g. pollination and mycorrhiza) are relevant. Impact in all these categories can be rated minor or moderate (category 2 or 3, out of 5 effect sizes). The decision between these categories depends on whether *I. glandulifera* causes only performance of native species or also populations of native species to decline ("reduction in the number of mature individuals of a native species"). The impact is clearly not major because in no case, local or sub-population extinction is known. Thus, for the GISS and the EICAT scheme, knowledge on large-scale impacts (spatially, population level) would be required, but even for the well-studied *I. glandulifera* this knowledge is lacking. I conclude, that assessments are often conducted without such studies available. In both scoring systems the highest reported impact per category has usually to be taken into account for scoring. In the EICAT system, even only the highest rated category alone represents the global assessment. This is according to the precautionary principle but makes the consideration of context-dependencies and differently affected guilds impossible. In case of *I. glandulifera* interaction with insect pollinators rises a critical question. Pollinators can benefit from food provided by *I. glandulifera* flowers, especially in autumn in flower-poor agricultural landscapes or in habitats where *U. dioica* increased due to nitrification. This may be a positive argument for *I. glandulifera*, compensating for a negative impact on other organisms, at least in degraded sites.

Table 2: Scoring environmental impact of *I. glandulifera* according to the Generic Impact Scoring System GISS.

Category	Score and justification	
1.1. Impacts on plants or vegetation through mechanisms other than competition	2	Experimental studies, show that *I. glandulifera* produces allelochemicals, mainly the allelopathically active 2-MNQ, and reduces germination and growth of neighboring species. The only field study has ambiguous results on germination. (Vrchotová et al. 2011, Del Fabbro et al. 2014, Gruntman et al. 2014, Ruckli et al. 2014a, Loydi et al. 2015, Bieberich et al. 2018)
1.2. Impacts on animals	2	*I. glandulifera* provides food to pollinators as it produces a high amount of pollen, nectar and sugar, even in autumn when other flowering plants decline. It can only have negative effects on specialist pollinators if it replaces their obligatory food plants. (Starý and Láska 1999, Tanner et al. 2013, Ruckli et al. 2013, Horáčková et al. 2014, Starý et al. 2014) There is a relative low number of invertebrates feeding on *I. glandulifera*. Correspondingly number of e.g. Coleoptera, Heteroptera, and gastropods can be reduced in invaded sites. However, some snails seem to benefit as well as native syrphid flies and parasitoid wasps relying on aphids that feed on *I. glandulifera*. (Schmitz 1994, Titze 2000, Lopezaraiza-Mikel et al. 2007, Nienhuis and Stout 2009, Nienhuis et al. 2009, Bartomeus et al. 2010, Vervoort et al. 2011, Konusova et al. 2016) Also larvae of the Geometridae moth *Xanthorhoe biriviata*, specialist herbivor of *I. noli-tangere* that was long assumed to reject *I. glandulifera* was now also found to feed on it (Schmitz 1991, 2005, 2007).
1.3. Impacts on species through resource competition	3	Competitive effect on plants is shown in experimental studies. Several field studies show a negative impact on vegetation (Tab. 1). Mainly, abundance and performance of common dominant species are reduced. However, results of the studies are ambiguous, especially regarding species diversity and composition which are only sometimes affected. Overall there are more studies indicating minor than major impact. (Tickner et al. 2001, Hejda and Pyšek 2006, Hulme and Bremner 2006, Hejda et al. 2009, Cockel et al. 2014, Gruntman et al. 2014, Diekmann et al. 2016, Rusterholz et al. 2017, Čuda et al. 2017b, Bieberich et al. 2018, 2020, 2021, Kiełtyk and Delimat 2019) *I. glandulifera* can compete with native plants for pollinators because it has very attractive flowers. Lower flower visitation rates can result in lower reproduction of native plants, but results are controversial. (Chittka and Schürkens 2001, Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2010, Cawoy et al. 2012, Thijs et al. 2012, Emer et al. 2015)

Table 2. continued.

Category	Score and justification	
1.4. Impacts through transmission of diseases or parasites to native species	0	(no impact known or detectable) Virus infection was observed with symptoms like Tobacco Rattle Virus (Kollmann et al. 2007) but there is no information on transmission from or to native plants. The rust *Puccinia komarovii* var. *glanduliferae* was intentionally introduced to England for biocontrol of *I. glandulifera*. Previously, resistance of native plants was ensured. (Kollmann et al. 2007)
1.5. Impacts through hybridization	0	(no impact known or detectable)
1.6. Impacts on ecosystems	3	In invaded sites soil chemistry and litter characteristics can be changed, also for the benefit of *I. glandulifera.* However, results are ambiguous. (Dassonville et al. 2008, Rusterholz et al. 2014, Pattison et al. 2016, Čuda et al. 2017b) Due to its allelochemicals *I. glandulifera* can suppress growth of mycorrhizal fungi and its colonization of tree and herb species (Tanner and Gange 2013, Ruckli et al. 2014a, b, 2016). This can also lead to an indirect negative impact on vegetation. Soil and litter-dwelling organisms seem to be more affected in their composition than in abundance. Results on specific groups are rated ambiguously, thus there are winners and loosers (Greenwood and Kuhn 2014). Succession of forest trees is not restricted by *I. glandulifera* (Tanner et al. 2013, Rusterholz et al. 2014, Pattison et al. 2016). In contrast, *I. glandulifera* itself seems to be outcompeted by succession within forests (Čuda et al. 2020). There are no data on succession in riparian habitats. *I. glandulifera* can enhance erosion from river banks because in winter, it freezes to dead and due to a lacking root system leaves the soil unprotected (Ammer et al. 2011). The allelochemical 2-MNQ has a negative impact on the development of aquatic daphnia and algae (Diller et al.). Thus, *I. glandulifera* can negatively affect aquatic food networks if growing along water bodies.

Explanation of impact levels (Nentwig et al. 2016): 0) No data available, no impacts known, not detectable or not applicable. 1) Minor impacts, only locally or on abundant species. 2) Minor impacts, not only locally or on abundant species. 3) Medium impacts, large-scale, several species concerned, relevant decline (this includes decrease in species richness or diversity). 4) Major small-scale destruction of the vegetation, decrease of species of concern. 5) Major large-scale destruction of the vegetation, threat to species of concern, including local extinctions.

CURRENT OFFICIAL STATUS. Currently, *I. glandulifera* is officially recognized as invasive with negative effects on native ecosystems. It is listed on the Global Invasive Species Database of the IUCN Invasive Species Specialist Group (GISD). This is reasoned by the rapid spread of *I. glandulifera*, its thick stands dominating landscapes, competition, and displacement of native plant species. In Europe, *I. glandulifera* is included in the Union list, the list of invasive alien species of European concern (European Commission 2019). Criteria for inclusion of an already established invader are 1) that it exerts a negative impact, 2) action at Union level is required for its management, and 3) inclusion on the Union list will likely effectively prevent, minimize or mitigate the impact (EuropeanUnion 2014). Prior to inclusion in the Union list, risk assessment of *I. glandulifera* was conducted by (Pisarczyk and Tokarska-Guzik 2015), according to a protocol specific to the European Union. Therein, they describe its invasion in detail and rate the environmental impact as moderate. Their justification is similar to my assessment, but is less detailed and based on considerably less scientific literature. Invasive alien species of European concern are prohibited to introduce, transport, keep and trade intentionally. Unintentional transport has to be prevented and the member states have to develop management plans based on a risk evaluation and cost effectiveness. Thus, in response to the EU regulation, Germany published a management plan with risk assessment (LANa 2019). It rates the risk of *I. glandulifera* with some caution considering that no population of rare species is known to have become extinct, and considering the ambiguous results of field studies. Unfortunately, only a few and rather old studies are cited while the increasing number of publications is not considered, which seems to be a general problem. Already in the old German regulation on invasive plants that was published prior to the Union list, *I. glandulifera* is rated only as potentially invasive (Nehring et al. 2013). In contrast, Switzerland assumed a very negative impact listing *I. glandulifera* on the black list of plants evidentially harming native biodiversity (Info Flora 2014).

CONCLUSION OF IMPACT. Personally, I think that the perception of the impact of *I. glandulifera* may be biased by the appearance of its stands. Due to its tall growth, conspicuous flowers, and high abundance, native species within its stands are readily overlooked, even if they are present. Thus, objective research is needed and its results have to be taken into account. Local impact in the sense of abundance × per-capita impact is minor to moderate, depending on extrinsic contexts (environment, space, time) and intrinsic contexts (species, functional groups). However, total impact sensu Parker et al. (1999) considering also the range of the invader as well as large scale impact on native populations as required by GISS and EICAT scoring has not been explicitly studied yet. From the wide distribution of *I. glandulifera* one might derive a stronger impact. Furthermore, *I. glandulifera* affects a lot of different ecosystem properties such as mycorrhiza, soil properties, and herbivores. In summary, the total impact of *I. glandulifera* can be rated as moderate.

4.3.3 Management recommendations

The European Union assumes that it is still possible to control *I. glandulifera* in protected areas and to prevent spread from intentional introductions (Pisarczyk and Tokarska-Guzik 2015). The German management plan in response to the EU regulation recommends programs related to public awareness, hand pulling of small stands, and mowing larger stands for 2-3 consecutive years as measures against *I. glandulifera*. Such measures have to be appropriate in terms of environmental effects and monetary costs. In flooded riparian sites, eradication is not recommended if recolonization is expected (LANa 2019). Within the first national report, German nature conservation authorities state that there was no management action done in the years 2015-2018 (Nigmann and Nehring 2020). In the UK, there is a biological control program using the introduced rust fungus, *Puccinia komarovii var. glanduliferae* as specialist enemy against *I. glandulifera* but it has not proved very successful up to now (Tanner et al. 2015b, Currie et al. 2020, Kurose et al. 2020, Tanner and Gange 2020). I consider the introduction of natural enemies to be risky, because even despite taking precautions, transmission to native plants is possible. Eradication is not feasible for most *I. glandulifera* populations. Due to its high monetary costs (Leblanc and Lavoie 2017) it should primarily be applied to sites which are valuable in terms of nature conservation and especially sensitive to the impact of *I. glandulifera*. Eradication has to be repeated over several years because I showed that *I. glandulifera* removal had only a low effect within one season. The habitat-dependent impact is a great opportunity to develop more targeted management plans. I found the highest correlative impact at bright conditions such as abandoned meadows, but especially in combination with high soil moisture such as in marshes or open patches of swamp-forests. Special attention should also be paid to habitats with distinct spring communities. However, impact on rare communities still has to be studied. The understanding that *I. glandulifera* is not a clear driver of ecosystem changes, but has some characteristics of a back-seat driver benefiting from previous changes, provides further opportunities. This is also discussed in manuscript 3. In case of a back-seat driver removal of the invader is not sufficient but additionally habitat-restoration is required (Bauer 2012). Invasion of *I. glandulifera* often follows intentional tree cutting or river restorations (Lapin et al. 2016, Čuda et al. 2020). For this reason, measures to prevent invasion should be considered already while planning such an anthropogenic habitat change (D'Antonio and Meyerson 2002). For example, the Bayreuth state water authority reported positive experience with planting sods of *Phalaris arundinacea* at restored riversides (personal communication). This perennial dominant plant species can close the otherwise raw soil, leaving less space for *I. glandulifera*.

4.3.4 *Impatiens glandulifera* – one of the worst invasive plants?

THE INVASIVE CON-GENERIC. *Impatiens parviflora* originating from Middle Asia is a second member of the genus *Impatiens* that is very widespread and (at least potentially) invasive in Central Europe (Nehring et al. 2013). Like *I. glandulifera*, it is annual but clearly smaller reaching only about one meter in height (Kowarik 2010). More than *I. glandulifera, I. parviflora* is associated with anthropogenic ruderal sites, forests, and forest edges (Kowarik 2010, Čuda et al. 2014). In invaded forests, often a negative correlation between native plant cover and species diversity is found (Obidziński and Symonides 2000, Chmura and Sierka 2006, Dobravolskaitė 2012). According to Diekmann et al. (2016) this negative effect of *I. parviflora* is smaller than that of *I. glandulifera*. It is often assumed that *I. parviflora* mainly colonizes empty sites that are disturbed or comprise a light availability too low for most native species. Dense native vegetation is considered to be less invasible (Obidziński and Symonides 2000, Chmura and Sierka 2006, Dobravolskaitė 2012, Hejda 2012) suggesting that *I. parviflora* may have some characteristics of a passenger of changes. There are two experimental removal studies that could be used as reference for causality of impact, but they have controversial results (Hejda 2012, Florianová and Münzbergová 2017). As with *I. glandulifera*, controversial results could be due to context-dependencies. Spread and plant growth of *I. parviflora* depend on habitat and environmental conditions, whereby the plant developmental stages differ in their dependence on the environment (Florianová and Münzbergová 2018). Indeed, Chmura and Sierka (2006) found the correlation between *I. parviflora* abundance and native plant diversity differing between forest types, like I found with *I. glandulifera*. Overall, the impact of *I. parviflora* can be rated as lower than the impact of *I. glandulifera*.

THE MOST INVASIVE PLANTS IN GERMANY AND EUROPE. According to the GISS scoring of Rumlerová et al. (2016), *I. gandulifera* is not within the top 24 European invaders with the potentially highest environmental impact. In contrast, *Fallopia japonica, Heracleum mantegazzianum,* and *Solidago canadensis,* as well as for example *Lupinus polyphyllus,* the aquatic plants *Eichhornia crassipes and Elodea canadensis,* and the tree species *Robinia pseudoacacia* and *Acacia ssp.* are included in this list of top invader. The first three places are taken by *Lantana camara, Arundo donax,* and *Carpobrotus edulis* having the highest potential impact in Europe. They are problematic invaders in several Mediterranean regions of the world, but in Europe they are restricted to the Mediterranean basin and currently not on the Union list. In Germany, the knotweed species (*Fallopia japonica, F. sacchalinensis,* and their bastard *F. x bohemica,* Synonym *Reynoutria ssp.*), Giant hogweed (*Heracleum mantegazzianum*), and the goldenrot species *Solidago canadensis* and *S. gigantea* are probably among the most widespread herbaceous plant invaders, also rising public awareness. They occur partly in the same habitats as *I. glandulifera,* and also form dominant stands (Kowarik 2010, Nehring et al. 2013). Like *I. glandulifera, H. mantegazzianum* and *Solidago ssp.* were favored as bee plants providing nectar (Davis et al. 2018). They all are very tall herbs. *Fallopia ssp.* and *H. mantegazzianum* grow up to 4 m tall, meaning that they are higher than *I. glandulifera* and produce a lot of biomass (Pyšek and Prach 1993). In contrast to *I. glandulifera,* they are perennial. *Fallopia ssp. and Solidago ssp.* repeatedly resprout tall stems from rhizomes and spread clonally, while *H. mantegazzianum* forms a rosette until it flowers and dies (Kowarik 2010). In a comparative field study Hejda et al. (2009) found that *Fallopia ssp.* and *H. mantegazzianum* reduced the native plant species number more strongly than several other European plant invaders, such as *Aster novi-belgii, Helianthus tuberosus,* and *S. gigantea*. Out of all considered species, *I. glandulifera* had the smallest effect. *Fallopia ssp.* stands harbor up to ten times less plant species than uninvaded reference sites (Mincheva et al. 2016, Lavoie 2017). In comparison, the highest estimated reduction of species richness by *I. glandulifera* is only 25 % (Hulme and Bremner 2006). Native plant growth is suppressed by resource competition (Mincheva et al. 2016, Lavoie 2017). According to my own observations, in *Fallopia ssp.* stands light availability is very strongly reduced. Allelopathy has been considered but not clearly shown (Lavoie 2017). Like *I. glandulifera, F. japonica* can reduce mycorrhiza colonization of native plants (Tanner and Gange 2013). *Fallopia ssp.* species have a deep rhizome and produce a large amount of litter, which both changes soil properties. However, impact on soil is rated ambiguously, indicating that the impact depends on the invaded community (Lavoie 2017). Various guilds are found to be differently affected by knotweeds. For example, fungi and detrivors benefit from the high amount of biomass, while soil bacteria and some gastropods, frogs, and birds are loosers (Lavoie 2017). In direct comparisons, negative effects of *F. japonica* on foliage dwelling arthropods and snails are more pronounced than the effects of *I. glandulifera* (Beerling and Dawah 1993, Horáčková et al. 2014). Studies on the environmental impact of *H. mantegazzianum* are less often done than one might expect. *H. mantegazzianum* reduces native plant species richness and productivity. It is highly competitive because its leaves widely expand over neighboring plants, reducing light availability (Thiele and Otte 2007, Jandová et al. 2014). Allelopathy is considered, but the effect does not differ from that of the native *H. sphondylium* (Jandová et al. 2015). Invasion in field sites as well as impact on vegetation depends on the habitat: roadsides have the highest frequency of occurrence whereas abandoned meadow the highest frequency of dominant stands (Thiele and Otte 2008). The impact is highest in ruderal grasslands and other ruderal vegetation, but native vegetation is only reduced if the cover of *H. mantegazzianum* is at least 50 % (Thiele and Otte 2007, Thiele et al. 2010). Furthermore, the impact changes over time and this correlation is nonlinear: native vegetation declines for 30 years after invasion, and soil biotic and abiotic characteristics change. In the further process *H. mantegazzianum* declines and the native ecosystem recovers, maybe due to a negative soil-feedback (Dostál et al. 2013, Jandová et al. 2014). In conclusion, *H. mantegazzianum* seems to show boom-bust dynamics. More than for its environmental impacts *H. mantegazzianum* is renowned for its socioeconomic impact due to phytotoxicity. Skin contact causes severe burns after exposition to sun light (Kowarik 2010). Species with a high socioeconomic impact are often the focus of eradication programs causing huge economic costs. The costs in turn increase the socioeconomic impact. Also *I. glandulifera* has a high socioeconomic impact if eradication costs are considered. Additionally, it is sometimes thought, to hinder access to angling areas (Pisarczyk and Tokarska-Guzik 2015). However, I do not think that crossing an *I. glandulifera* stand is more difficult than crossing native tall herbaceous vegetation with *U. dioica*. Like the other invasives, the North American *Solidago* species are associated with reduction of native vegetation due to competition and allelopathy, as well as change of soil chemical properties and disruption of mycorrhiza (Fenesi et al. 2015, Pal et al. 2015, Bielecka et al. 2020). Similar to *I. glandulifera*, *Solidago ssp.* produce a very large amount of seeds. Long distance dispersal is enabled by wind (Kowarik 2010). *S. canadensis* often invades disturbed sites such as abandoned fields and urban ruderal areas (Kowarik 2010, Fenesi et al. 2015) potentially indicating that it could be a passenger of land use change. Fenesi et al. (2015) found that the driver-passenger behavior of *S. canadensis* depends on the competing native plant species. *S. canadensis* can act as a driver, or alternatively as a back-seat driver whose competitive effect is enhanced by disturbance. German nature conservation authorities rated *H. mantegazzianum* as well as *Fallopia ssp.* as invasive species evidently harming native diversity, while *Solidago ssp.*, like *I. glandulifera*, as potentially invasive only (Nehring et al. 2013). The Union list currently only contains *H. mantegazzianum*, while *Fallopia ssp.* and

Solidago ssp are not listed. The genus *Heracleum* is represented not only by *H. mantegazzianum* but also by the less common *H. sosnowskyi* and *H. persicum* to focus on prevention of their spread. To explain why *Fallopia ssp.* are not included, it has to be born in mind that the Union list is dynamic. The member countries continually discuss inclusion of additional invasive species. Thus, *Fallopia ssp.* may be added anytime.

CONCLUSION. All these mentioned worse invaders possess properties typical for invasive species. They have a high reproduction, high competitive effect, and are often considered to possess allelopathy. Context-dependencies seem to be common, although they are mostly not addressed in particular. Generally, perennial plants have a higher impact than annual ones (Gaertner et al. 2014). Clonal growth can benefit invasion as in the case of *Fallopia ssp.*, *Solidago ssp.* and *Carpobrotus sp.* This is because connected clones can perform as cooperative systems, ensure persistence at an invaded site, and complicate eradication (Kowarik 2010, Roiloa 2019). Often fragments of rhizomes or stolons also serve as dispersal units (Roiloa 2019). *I. glandulifera*, the only species of those with a considerable environmental impact, is annual, indicating a lower impact. However, it seems to “compensate” for the annual life form with high reproduction, fast growth, and clearly shown allelopathy. Generally, those species have a high impact, that cause regime shifts such as altering fire regime (e.g. *Acacia ssp.*), accumulating litter (*Fallopia ssp., Arundo donax, Carpobrotus edulis*), or changing nutrients. In consequence, they can turn the invaded ecosystem into another. The impact is higher the more a species’ traits differ from those of the invaded community (Gaertner et al. 2014). *Solidago ssp.* have a higher impact in nutrient poor grasslands compared to tall herbaceous vegetation (Kowarik 2010), *Heracleum mantegazzianum* in grasslands (Thiele and Otte 2007). The nutrient fixing tree *Robinia pseudoacacia* has a higher effect in dry grasslands compared to forests (Vítková et al. 2017). *I. glandulifera* is not very different from the tall herbaceous native species, except for being annual. It does not turn the vegetation type into another. However, it affects several components of the invaded ecosystem, like the other most invasive plants do. Unfortunately, it is not clear whether invaders considered to be less invasive affect ecosystem properties less, or whether they are only less studied.

4.3.5 *Impatiens glandulifera* – a predictor of other invasions?

“NEW” IMPATIENS INVADERS. One aim of invasion biology science is to gain knowledge to predict further invasions. The more species are similar to each other, the more they can be expected to share their invasion behavior. This is most likely the case with closely related species. Additionally to *I. glandulifera* and *I. parviflora*, there are five members of the genus *Impatiens* that rarely occur in Europe and may become more widespread (Fig. 2, Čuda et al. 2016). *I. balfourii, I. edgeworthii*, and *I. scabrida* share their origin in the Himalaya Mountains with *I. glandulifera* (Morgan 2007). *I. balsamina* is one of the most widespread species in Asia. This wide distribution is assumed to be connected to long seed viability (Morgan 2007) which also could benefit invasion. *I. capensis*, is native to various North American habitats such as marshy ground, forest edges, and dumps (Morgan 2007). German nature conservation authorities rate *I. balfourii* and *I. edgeworthii* as potentially invasive (Nehring et al. 2013). In experimental studies *I. balfourii* and *I. capensis* showed a reproductive potential similar to *I. glandulifera* (Perglová et al. 2009, Ugoletti et al. 2011, Skálová et al. 2011). Regarding biomass production and with a height of circa 1 m the "new" *Impatiens* invaders are in between *I. glandulifera* and *I. parviflora* (Morgan 2007, Ugoletti et al. 2011, Skálová et al. 2012). This may indicate that their competitive effect might also be in between *I. glandulifera* and *I. parviflora*. Indeed, Skálová et al. (2013) found *I. capensis* to be competitively inferior to *I. glandulifera*. An allelopathic effect can be assumed because bioactive substances are generally common in the genus *Impatiens* (Bohm and Towers 1962, Lobstein et al. 2001, Tříska et al. 2013, Cimmino et al. 2016, Szewczyk et al. 2016a, b, Vieira et al. 2016). Some species, especially *I. balsamina,* are used for medical purposes (Szewczyk et al. 2016a). The medically active substances may possibly also possess allelopathic potential. *I. capensis* and *I. balsamina*, are known to contain 2-MNQ (Lobstein et al. 2001, Mori et al. 2011), but in smaller amounts than *I. glandulifera*. However, I found, that 2-MNQ seems not to be the only allelochemical, but other substances should also be important. Thus, a lower amount of 2-MNQ does not necessarily result in a lower allelopathic effect. Field studies on the new *Impatiens* invaders are still scarce. *I. balfourii* occurs in several European countries like Germany with single, at least casual occurrences. Reported habitats are roadsides, along streams, minor urban and ruderal areas, disturbed sites, forest margins (Schmitz and Dericks 2010, Najberek et al. 2020). *I. edgeworthii* has been spreading in several German forests since approximately the year 2000 (Weiss 2013). There it shows similar habitat requirements than *I. parviflora* and the native *I. noli-tangere*. It preferentially invades open sites from where it spreads into the adjacent area. Established stands can be dominant and are even capable of suppressing *U. dioica* and *Aegopodium podagraria* (Weiss 2013). In conclusion, this new *Impatiens* invaders have some invasion potential. Resource competition could be less strong than in *I. glandulifera*, but allelopathy may be a decisive factor. The wide natural distribution of *I. balsamina* and the wide habitat range of *I. capensis* and *I. balfourii* may indicate that they show habitat-dependency of their interaction with native ecosystems.

A COMPARABLE ANNUAL. Knowledge on *I. glandulifera* may be transferred to one other plant species of the Union list. *Humulus scandens* (syn. *H. japonicus*) is an annual vine from Asia that was introduced to Europe and America for ornamental purposes (EPPO 2019). By now, only some occurrences have been reported, but it is currently spreading. Its seeds are dispersed by wind and water, and germinate in a large number. It is considered established for example in France, where it was first introduced to, as well as in Italy and Hungary. The invaded habitats are similar to those of *I. glandulifera*: mainly riparian and disturbed sites, also woodlands, wet meadows, floodplain forests, and roadsides from lowlands to higher elevations. Climbing over the neighboring plants, it forms dense stands and can suppress the native vegetation (EPPO 2019). This is a strategy different from *I. glandulifera*, but allelopathy was also observed (Xu et al. 2020). Dying back in winter, it can enhance erosion of riverbanks, like *I. glandulifera* does (EuropeanCommision and Sundseth 2020). I suggest that dispersal and habitat invasion along rivers could be similar to *I. glandulifera*, including potential habitat dependencies. However, wind dispersal can lead to a faster spread in habitats far from rivers. Affinity to disturbance can indicate some characteristics of a passenger. The climbing growth form can lead to a competitive effect even stronger than that of *I. glandulifera*.

HABITAT-DEPENDENCY CANDIDATES. Habitat-dependencies of invasions and their impact can basically be assumed for all invasive species. They are often generalists occurring in different habitats where they could behave differently. Striking candidates could be *Crassula helmsii*, an amphibious plant ranging from free water floating to terrestrial forms (Smith and Buckley 2020, van der Loop et al. 2020), the tree species *Acer negundo* that undergoes a secondary invasion from wetlands into more dry lands (Erfmeier et al. 2011), or *Robinia pseudoacacia* invading for example dry grasslands and forests, alluvial habitats, agricultural landscapes, and urban areas (Vítková et al. 2017). Also *Ailanthus altissimus* occurs in a wide habitat range from semi-dry grasslands, xeric Mediterranean to alluvial forests and urban to natural areas (Sladonja et al. 2015). Indeed, in Croatia, it was shown to be more aggressive in coastal than in continental areas (Novak and Novak 2018).

4.3.6 Future perspectives

FUTURE RESEARCH QUESTIONS. Based on my study results several subsequent research questions arise. I suggest addressing the following subjects: 1) For *I. glandulifera*, up to now, only local impact on common native plants was studied. Large scale studies are lacking and it is not known whether *I. glandulifera* leads to plant community homogenization. Knowledge on the impact on rare species and habitats with special nature conservation value is necessary for nature conservation. Competitive superiority over rare or generally less competitive species can be expected, because experimental studies showed a high competitive and allelopathic effect on native species with a generally high competitive ability. Further experimental studies with rare species could verify this. However, the important question is whether *I. glandulifera* invades sites with rare species or protected sites at all. According to the European Union risk assessment, the Netherlands and Poland fear for their nature conservation areas (Pisarczyk and Tokarska-Guzik 2015). Investigating invasion in valuable areas, the question of causality has to be considered. If *I. glandulifera* is only found in sites without rare species, it can be due to a low invasibility of such sites or due to suppression of the rare species by *I. glandulifera*. 2) The driver-passenger behavior determines the required management strategy for an invader. However, in the case of a passenger it has to be figured what drives the passenger. This ecosystem change underlying the invasion has to be countered to be able to prevent invasions or to restore native ecosystems. 3) Impact assessment frameworks such as EICAT are an important tool to rank invasive species based on literature evidence. However, it is not designed for an empirical comparison of different contexts. To gain deeper knowledge on species- and habitat-dependent impact, different invaders in different habitats should be directly compared within one standardized design. To study the impact of plant invaders on native vegetation, I suggest a combined observational and experimental approach like I applied with invaded and uninvaded patches, as well as removal and addition of the invader. Investigated habitats have to comprise those invaded by the specific invader of interest, but concurrently standardized for all investigated species. Anyhow, they should include the riparian habitat, grasslands, deciduous and coniferous or mixed forests, and ruderal areas. A concept similar to the Biodiversity Exploratories with several regions each comprising all habitats, would be desirable. With a common garden experiment within field sites several invasive species could be compared at one site. However, this would imply intentional introduction of invasive species into sites they have not invaded. It can be questioned if this is ethically correct and it requires careful handling of the invaders. 4) The habitat-dependent impact of an invader has three interacting components, the habitat requirements of the invader, the invasibility of the recipient ecosystem, and the per-capita impact of the invader which differs between habitats. Disentangling these components would be important to understand habitat-dependencies. For a corresponding field study *I. glandulifera* could serve as model organism. Planting the invader into experimental bare soil indicates environmental habitat suitability, planting it into existing vegetation shows invasibility, and planting it in different frequencies shows the per-capita impact of the invader. Additionally, an artificial community with a standardized species pool can show changes in competitive interactions along an environmental gradient (similar to the “Hohenheimer Grundwasserversuch”). Like mesocosm experiments, this would enable high complexity and control.

NOVEL SPECIES FOR A FUTURE WORLD? Globally, the increase of recorded invasions steadily increases and an accumulation is not expected in the near future (Seebens et al. 2017). Thus, we have to think about dealing with that. Prevention should have the highest priority and is an aim of the current global nature conservation efforts. Their implications may be visible in some years. Bringing non-native species into the wild is prohibited and also using them in semi-natural sites, such as for landscape architecture should clearly be avoided. A drastic, but reasonable measure would be the use of white instead of black lists to regulate invasions. Thus, only non-native species that are known to have a low invasion potential would be allowed to introduce and use (Courchamp et al. 2017). However, non-native species are not necessarily “bad”. They can contribute to ecosystem services and even have a nature conservation value providing for example food or shelter to other species, especially in destroyed ecosystems. In fragmented Brazilian forests native pollinators are absent, but the non-native African honey bee pollinates across the forest fragments (Schlaepfer et al. 2011). However, it should be considered that such non-natives may have contributed to the decline of those native species they now substitute. Against the background of climate change it is the question, whether non-native species are even necessarily required, because native species and community compositions are not able to change fast enough to resist. In forestry, this is currently an urgent question, because loosing ecosystem services of forests would have drastic effects. Integration of non-native species leads to so called novel ecosystems. As a result of human ecosystem changes, they comprise a novel combination of species and have the potential for novel ecosystem function (Hobbs et al. 2006). In an increasingly human-modified world, they will increase in frequency and importance for ecosystem services. However, they are subject of an ongoing debate on whether they are valuable, or whether original habitats have to be restored – if possible at all (Hobbs et al. 2009). Not only non-invasive alien species, but also invasive aliens can provide ecosystem services, complicating discussions on their management. An excellent example is *Robinia pseudoacacia* which is considered invasive but has such an economic value in forestry that some EU member states vetoed against its inclusion in the Union list. It is indeed so popular that it became part of the cultural identity of some countries such as Hungary, and is not seen as alien (Vítková et al. 2017). Like nature conservation in general, invasion biology raises the question which nature we do want to conserve, or the nature of which point of time. Are new species welcome, or do we bear the responsibility to compensate and avoid human caused ecosystem changes including alien invasions? It is a philosophical question whether animal dispersal is natural but human-driven dispersal is not, or in general whether humans are part of nature. It is clear, that invasions are part of the human-caused global change and that we are responsible. Evidence-based research can help to understand, prevent and manage invasions and introductions in the future.

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5 Manuscripts

5.1 Manuscript 1

Species- and developmental stage-specific effects of allelopathy and competition of invasive *Impatiens glandulifera* on co-occrring plants

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Authors contributions: JB, ML, and HF had the idea. JB, ML, MD, and HF developed the study design. JB, MD, JH, and SM performed the experiments, collected, analyzed, and visualized the data, and wrote the initial draft. JB curated the data, prepared the figures and analyses as shown in the manuscript. JB, ML, and HF reviewed the manuscript. ML and HF supervised the study and provided resources.

Author contributions adopted literally from the manuscript webpage:
JB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing
ML: Conceptualization, Methodology, Resources, Supervision, Writing – original draft, Writing – review & editing
MD: Formal analysis, Investigation, Methodology, Visualization, Writing – original draft
JH: Formal analysis, Investigation, Visualization, Writing – original draft
SM: Formal analysis, Investigation, Visualization, Writing – original draft
HF: Conceptualization, Methodology, Resources, Supervision, Writing – original draft, Writing – review & editing

PLOS ONE

RESEARCH ARTICLE

Species- and developmental stage-specific effects of allelopathy and competition of invasive *Impatiens glandulifera* on co-occurring plants

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Abstract

Background

Impacts of invasive species on native communities are often difficult to assess, because they depend on a range of factors, such as species identity and traits. Such context-dependencies are poorly understood yet, but knowledge is required to predict the impact of invasions.

Materials and methods

We assessed species- and developmental stage-specificity of competitive and allelopathic effects of the invasive plant *Impatiens glandulifera* on different developmental stages of four native plant species. While some studies have shown a reduction in plant growth caused by *I. glandulifera*, the magnitude of its impact is ambiguous. For our study we used seedlings and juveniles of *I. glandulifera* and the native target species *Geum urbanum*, *Filipendula ulmaria*, *Urtica dioica*, and *Salix fragilis* (seedlings only of the latter), which often co-occur with *I. glandulifera* in different habitats. Plants were grown in competition with *I. glandulifera* or treated with *I. glandulifera* leaf material, or 2-metoxy-1,4-naphtoquinone (2-MNQ), its supposedly main allelochemical.

Results and conclusions

Overall *I. glandulifera* had a negative effect on the growth of all target species depending on the species and on the plant's developmental stage. *F. ulmaria* was the least affected and *U. dioica* the most, and seedlings were less affected than juveniles. The species-specific response to *I. glandulifera* may lead to an altered community composition in the field, while growth reduction of seedlings and juveniles should give *I. glandulifera* an advantage in cases where plant recruitment is crucial. 2-MNQ led to minor reductions in plant growth, suggesting that it may not be the only allelopathic substance of *I. glandulifera*. Surprisingly, *I. glandulifera* was not fully tolerant to 2-MNQ. This autotoxicity could contribute to *I.*

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glandulifera population dynamics. We conclude that *I. glandulifera* reduces the growth of native vegetation and alters early successional stages without fully hindering it.

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Introduction

Invasive species are considered to be among the most important drivers of biodiversity loss worldwide [1]. They affect native ecosystems negatively in many ways. They can suppress growth of native species and alter ecosystem processes and structures [2,3]. However, it is difficult to comprehensively assess the impact of invasive species due to context-dependencies. The outcome of an invasion is influenced by the invaded ecosystem, invasion stage and species traits [4]. Depending on the invaded ecosystem the invasive species interacts with different native species. Basically, different species should react differently to the invasion and the interaction between native and invasive plants could depend on their developmental stage. Such developmental-stage specific interactions are rarely studied but such knowledge would improve our ability to understand and predict the overall effect of a particular invasive species as well as invasion processes in general.

The plant genus *Impatiens* is an ideal model taxon for the study of context-dependencies [4] such as species- and developmental stage specificity. Several species of this genus are widely introduced and constitute a broad range of invasiveness. In Central Europe *Impatiens glandulifera* Royle is one of the most famous alien plants with its strikingly tall growth of more than 2 m height and its large, purple flowering stands [5]. Introduced to England in the 19th century, it has spread over nearly the whole of Europe and is nowadays very common [6–9]. It mainly followed river systems but subsequently also invaded sites at a distance from the rivers [8]. Invaded habitats are riparian sites, mesotrophic grasslands and woodlands, semi-natural sites but also forests out of the riparian zone [5,7,9,10]. Generally *I. glandulifera* is favored by disturbances [5,11]. In 2017 *I. glandulifera* was added to the list of invasive alien species of Union concern [12,13] However, the degree of invasiveness is perceived differently in different countries. In 2014 it was included in the black list of plants evidentially harming native biodiversity in Switzerland [14]. In contrast German nature conservation authorities rate *I. glandulifera* as potentially invasive, with an assumed threat to native species [15]. This moderate ranking was justified with the mixed results from field studies on the impact of *I. glandulifera* on native plant communities [11,16–19]. Thus, a deeper understanding of the interaction between *I. glandulifera* and its co-occurring plant species is required.

Possible mechanisms for the suppression of co-occurring plants are allelopathy and competition [20]. *I. glandulifera* produces 2-methoxy-1,4-naphthoquinone (2-MNQ), which is considered to be its main allelopathic substance. [21–25]. 2-MNQ gets rinsed off the leaves by rainwater, is present in the soil and inhibits mycorrhiza growth [21]. *I. glandulifera* litter leachates and plant material extracts reduce the germination of other species such as *Leucosinapis alba* [26] or *Scrophularia nodosa* [21], with the concentration of 2-MNQ in the extracts correlating with their inhibitory effect [21]. *I. glandulifera* litter reduces seed germination species-specifically [27], and tree saplings suffer in invaded field sites [28,29]. It is also a strong competitor of *Urtica dioica* [30] and conspecifics as *Impatiens noli-tangere* [31,32]. In contrast, other studies did not find such negative effects. Thus, seed germination [33], and forest recruitment were not restricted in invaded forest sites [34]. These varied outcomes may be caused by context-dependencies, because all these studies were conducted with different

settings regarding study conditions, target plants, their developmental stages and the parts of *I. glandulifera* plants considered.

Native species co-occrring with *I. glandulifera* are expected to differ in their susceptibility to the invasive plant, due to differences in their traits and autecology. Additionally, life stages are known to affect interactions between species [35]. Thus, seedlings could respond differently to *I. glandulifera* than juvenile plants. Both developmental stages are important for the recruitment of plants and a negative impact on either of the stages or both may result in altered plant community composition. Overall, the direct role of 2-MNQ in mediating plant-plant interactions is still unclear, including its effect on *I. glandulifera* itself. If *I. glandulifera* benefits from inhibiting growth of co-occurring plants via 2-MNQ it should be less sensitive to 2-MNQ than native plants in order to have an advantage by suppressing growth of co-occurring plants. To comprehensively explore species- and developmental stage specific effects and the mechanisms of the impact of the invasive *I. glandulifera* we investigated competitive and allelopathic effects on different co-occurring native species. Here, we asked the following questions: 1) Are competitive and allelopathic effects species-specific? 2) Do these effects depend on plant developmental stage, in particular do the effects on seedlings and juveniles differ? 3) Is 2-MNQ the substance responsible for the allelopathic effects of *I. glandulifera*? 4) Is *I. glandulifera* tolerant to its own chemical weapons? To answer these questions we experimentally tested the effect of competition by *I. glandulifera* as well as leaf material and pure 2-MNQ on the growth of seedlings and juveniles of selected native species that co-occur with *I. glandulifera* in different habitats.

Materials and methods

Plant species

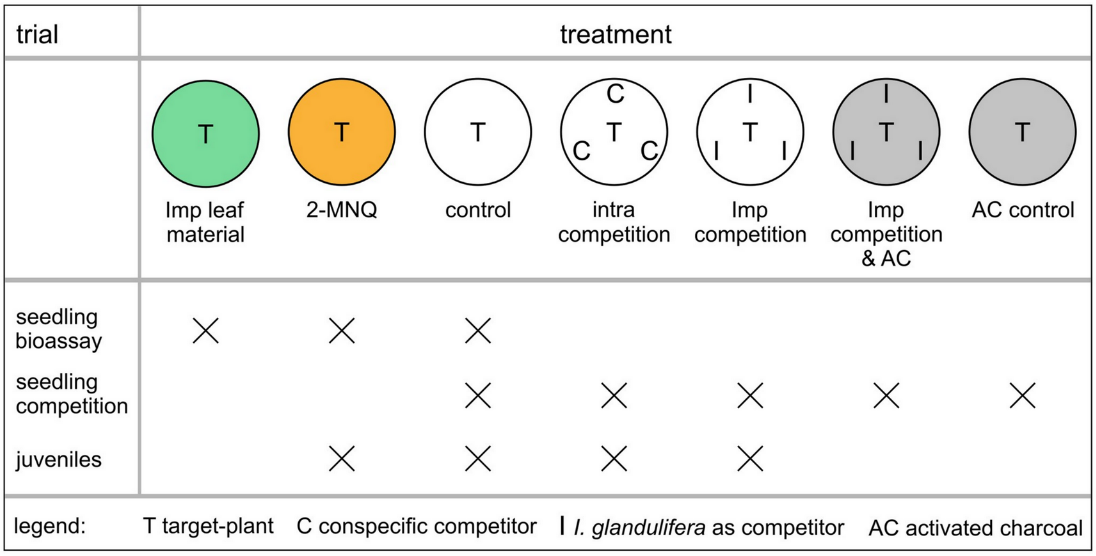
As native target species species we used plant species that regularly co-occur with *I. glandulifera* in riparian habitats or deciduous woodlands in Germany: *Filipendula ulmaria* (L.) Maxim. is common in tall herbaceous vegetation of elder woods and meadows, *Geum urbanum* L. in woodlands and disturbed habitats. *Urtica dioica* L. is typical for tall herbaceous vegetation especially in nutrient rich sites [36,37]. All target species are perennial and can form dominant stands. We therefore expected that they should cope with competition by *I. glandulifera* relatively well. In the seedling trial *Salix fragilis* L., a tree from wetlands and early successional stages at riversides [38], was used additionally, as well as *Lepidium sativum* L., a control species not co-occrring with *I. glanduifera* but often used in allelopathy experiments [39]. *I. glandulifera* was used as target species and to test its impact on other plants. No permission was required to use this invasive plant species because all trials were conducted before it was included in the list of invasive alien species of Union concern [12,13]. Flowers of *I. glandulifera* juveniles were removed prior to seed set and all its plant material was destroyed after the trials.

Seedling trials

Seeds of all species except for *L. sativum* were collected in 3–8 field sites per species in the region of Bayreuth (Germany). We were permitted by the government of Upper Franconia (Regierung von Oberfranken) to collect plant material in this region. Neither one of the sites nor one of the species is under nature protection. In these sites, *I. glandulifera* was mostly absent, except for a few occasions where it was moderately intermixed with the native vegetation. Seeds of each species were pooled for the experiment. Seeds of *I. glandulifera*, *F. ulmaria*, *U. dioica*, *G. urbanum* were collected in autumn 2014 from a minimum of 20 plants per site. They were dry stored under refrigeration (8 ˚C). Seeds of *S. fragilis* were collected in early June from 3 sites and 3–6 trees per site, mixed with the hybrid *Salix x rubens* Schrank. These seeds

were stored under refrigeration (4 ˚C). Seeds of *L. sativum* were commercially obtained (Kiepenkerl, article number 2498, year 2014/2015). To overcome dormancy in seeds they were warm–cold stratified within wet quartz sand, *G. urbanum* and *F. ulmaria* (2 weeks at 30 ˚C and 4–11 weeks at 4 ˚C) and seeds of *I. glandulifera* (10–12 weeks at 4 ˚C). The trials with seedlings were conducted from beginning of June (when *S. fragilis* fructified in this particular year) to August 2015. Seeds of all species were sown every couple of days as required to obtain as many germinating seeds of the different species at the same time. They were placed on wet filter paper in petri dishes close to window exposed to natural light at room temperature and kept moist with a fungicide solution (Previcur N 1.5 ml / 1 l water; Bayer). As soon as radicles emerged (one day to several weeks, depending on the species) the germinated seeds were used for the trials. Maximum length of the radicle was 4 mm for *I. glandulifera* and 3 mm for all other species chosen for trials.

To test the competitive and allelopathic effects of *I. glandulifera* seedlings, we grew the target seedlings on agar (0.5% w/v) either solitarily (control), surrounded by three conspecific seedlings (intraspecific competition), or in competition with three *I. glandulifera* seedlings (Fig 1). Hereafter, the plant that is subjected to the treatments is defined as target plant or target seedling. To distinguish between a growth reduction due to an allelopathic or a competitive effect we additionally added activated charcoal (0.05% w/v) to the agar. The activated charcoal is expected to absorb allelopathic substances potentially released by *I. glandulifera* seedlings [40]. To control for general impacts of the activated charcoal on the seedlings' growth we included a treatment with one single target seedling on agar containing just the activated charcoal. The five treatments were randomly assigned to the wells of a 6-microwell plate (Nunc™, Thermo Fischer Scientific, 9.6 cm^2 per well). The wells were filled with 5 ml of the appropriate agar and the germinated seeds were placed in five wells on the solidified agar with one blank.



trial	treatment						
	Imp leaf material	2-MNQ	control	intra competition	Imp competition	Imp competition & AC	AC control
seedling bioassay	×	×	×				
seedling competition			×	×	×	×	×
juveniles		×	×	×	×		

legend: T target-plant C conspecific competitor I *I. glandulifera* as competitor AC activated charcoal

Fig 1. Treatments applied in the seedling bioassay, seedling competition and the juveniles trial. Target plants were grown solitarily (control) or in intraspecific competition with their conspecifics (intra competition) or with *I. glandulifera* (Imp competition). The treatments are named as in all other figures. If the target plant is *I. glandulifera* intraspecific competition and competition with *I. glandulifera* is notably one and the same. Coloration indicates a treatment with *I. glandulifera* leaf material (green), pure 2-MNQ (orange) or activated charcoal (AC, grey). In the seedling bioassay and seedling competition trials plants were grown on agar in microwell plates, juveniles were grown in soil in pots.

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We conducted the experiment with 20 replicates per species, except for *S. fragilis* where we were only able to obtain 11 replicates. The seedlings were grown in a climate chamber (25 ˚C, 70% humidity, 12/12 h light/dark cycle, light source Osram Lumilux HO 80W/840) for six days. After this the target seedlings were removed from the agar and their root length was measured to the nearest 0.1 mm with a digital caliper. In the case of branched roots, which was often observed in *I. glandulifera*, the length of the longest branch was measured. Then the entire seedling was dried for 24 h at 60 ˚C and weighed to the nearest 1 μg (Santorius micro weighing scale M 500 P). In 2015 the germination rate of *F. ulmaria* was unfortunately so low that the competition trial could not be conducted for this species. Therefore, it was performed in June to July 2017 with 13 replicates but using the seeds collected in 2015 for the juvenile trial (see below).

To test if 2-MNQ is responsible for an allelopathic impact of *I. glandulifera* a bioassay was conducted on agar (derived from [41]), treating seedlings of the target species with pure 2-MNQ and with leaf material of *I. glandulifera* seedlings (Fig 1). Leaf material of *I. glandulifera* seedlings was used as it was shown that it contains high concentrations of 2-MNQ and that its extracts inhibit seed germination [21]. *I. glandulifera* seedlings whose primary leaves were still shorter than the cotyledons (average length of the cotyledons 18 ± 3 mm, n = 20) were collected in the end of April 2015 at four sites in Bayreuth comprising of habitats such as forest, riparian forest and wet meadow. Cotyledons and primary leaves were dried for 24 h at 70 ˚C and ground with a pestle. This powder was added to fresh agar (60 ˚C; 0.5% w/v) at the concentrations of 0, 0.15, 0.30, 0.60, 1.20 and 2.40 g/l. In a second approach, 2-MNQ (Sigma-Aldrich) was used. As the solid 2-MNQ is not solvable in water it was solved in ethanol (2 mg 2-MNQ per 1 ml 80% ethanol) and the solvent was added to the agar to obtain the final concentrations of 0, 0.8, 1.6, 3.2, 6.4 and 12.8 mg 2-MNQ per liter agar. For the control without 2-MNQ, 6.4 μl 80% ethanol was added per 1 ml agar as this is the highest used amount of ethanol solution. The concentrations of *I. glandulifera* leaf material and 2-MNQ used were chosen according to the study of [21]. Leaf extracts are known to reduce seed germination and the low 2-MNQ concentrations are known to affect mycorrhiza growth while the high 2-MNQ concentrations were found in rainwater rinsed from *I. glandulifera* plants. In total there were 12 different treatments (5 concentrations of *I. glandulifera* leaf material plus control and 5 concentrations of 2-MNQ plus control). The treatments were randomly assigned to the wells of a 24-microwell plate (Nunc™, Thermo Fischer Scientific, 1.8 cm^2 per well), with two replicates per treatment resulting in a block design. Each well was filled with 1 ml appropriate agar. Finally, per well one germinated seed was put on the solidified agar. If fewer than 24 germinated seeds were available at once, only one replicate per treatment was realized within one particular plate. For *I. glandulifera*, *L. sativum*, *U. dioica*, *G. urbanum* and *S. fragilis* in total 12 replicates per treatment were performed. For *F. ulmaria* which germinated rather poorly, we had only seven replicates. The seedlings were grown at the same time and in the same climate chamber as those of the experiment on seedling competition. The positions of all plates within the climate chamber were changed randomly each day. Same as in the seedling competition experiment, the seedlings' root length and dry biomass was measured after 6 days of growth.

Juvenile trial

Competition and impact of 2-MNQ was studied for the first-year growth of *F. ulmaria*, *U. dioica*, *G. urbanum* and on *I. glandulifera*. Seeds were collected in 2015, stored and stratified as they were in 2014 for the seedling trials but *I. glandulifera* did not need stratification. Seeds were sown in the first and second week of April 2016 on potting compost in sowing shells which were placed in a greenhouse (17–27 ˚C). After 2 weeks the seedlings were pricked out to

pots with a volume of 230 cm^3 soil within QuickPot trays. Two weeks after pricking *I. glandulifera* plants were brought outdoors. Four weeks after pricking (third and fourth week of May) plants of medium and homogeneous size were used for the trial.

The individual plants as well as the processing order were randomly assigned to the 4 treatments, each in 10 repetitions. The target plants were potted in 20-liter pots according to the treatments, either solitarily, in intraspecific competition or in competition with *I. glandulifera* (Fig 1). If *I. glandulifera* is the target species intraspecific competition and competition with *I. glandulifera* is notably one and the same, resulting in three instead of four treatments overall. For the 2-MNQ treatment 1 liter of a 10 mg/l 2-MNQ solution was applied to a single target plant following regular watering. For this purpose, each time 2-MNQ (Sigma Aldrich) was dissolved in pure ethanol (2 mg/ml) and diluted with tap water. The potting soil contained 39% white peat, 11% black peat, 20% coconut fibre, 15% lava granules and 15% bark compost. Per 1 m^3 the substrate was fertilized with 3 kg slow-release fertilizer with macro-nutrients (Osmocote Exact Protect 14% N, 8% P_2O_5, 11% K_2O, 2% MgO, 8–9 month effect duration; EVERRIS) and 200 g slow-release fertilizer with micro-nutrients (Radigen 2% Fe, 1.5% Cu, 1% Mn, 0.8% Mo, 0.6% B, 0.5% Zn; TERRAFLOR) and 1 kg carbonic agricultural lime. At the time of potting target plants of *I. glandulifera* were 19 ± 4 cm (n = 30; ten repetitions per three treatments) in height, *U. dioica* 19 ± 6 cm, *G. urbanum* 7 ± 2 cm and *F. ulmaria* 7 ± 2 cm (each n = 40; ten repetitions per four treatments). Pots were placed within 5 blocks of 30 pots outdoors in the Ecological–Botanical Gardens of the University of Bayreuth, Germany. Each block contained two replicates of all treatments and all species randomly assigned to the positions in the blocks. The substrate was always kept moist by watering or natural precipitation. During the trial air temperature was 20 ˚C in average (min 7 ˚C, max 40 ˚C) and humidity 75% (min 21%, max 100%), both measured hourly using an iButton (DS1923, Maxim).

Ten weeks after potting (fourth week of July and first week of August) the growth of the target plants was quantified. Of the stem building species *I. glandulifera* and *U. dioica* height (from soil to the highest point of the plant) was measured with a folding ruler to the nearest 0.5 cm. For the rosette forming species *G. urbanum* and *F. ulmaria* the rosette's projection area was approximated, assuming the rosette to be an ellipse: we measured the widest expansion of the rosette and its orthogonal expansion with a folding ruler to the nearest 0.5 cm as axes for calculation of the area of ellipse. Of all species the above-ground biomass was harvested, dried at 90 ˚C for two days and weighed to the nearest 0.01 g with a weighing scale (Mettler PM 4600).

Statistical analyses

Data analyses were done using the software package R [42], RSTUDIO 99.9.9 and various additional packages: LME4 [43], GGPLOT2 [44], PLYR [45], MULTCOMP [46], COWPLOT [47], R COLORBREWER [48], BROOM [49] and RMISC [50]. Figures were arranged with INKSCAPE 0.92. In the seedling trials some of the germinated seeds died shortly after they were placed on the agar; there was no visible root elongation and the cotyledons did not emerge from the testa. In total there were 7 dead seedlings in the trial on competition and allelopathy, 6 in the bioassay with 2-MNQ and 17 in the bioassay with leaf material. The count did not depend on the treatment, except the bioassay with leaf material (chi-squared test χ^2 = 13.27, df = 5, p = 0.021). When mortality was analyzed per species this was not significant in any case. Thus, we consider death of seedlings to be a transplantat effect and excluded them from growth analyses. Seedlings were also excluded from analyses if they were conspicuously infested by fungi (30 of 474 seedlings in the trial on competition and allelopathy, 38 of 804 in the bioassays), or if, less than three competitor-seedlings had grown. This led to varying

sample sizes within a species. To analyze the growth of the target plants linear mixed effect models were used with the microwell-plate (seedlings) or block (juveniles) as random factor. The models were built with the lmer function of lme4-package with a random intercept error term. The full models were compared against null-models with likelihood ratio tests (anova function), resulting χ^2-values, degrees of freedom and p-values give the significance of the models and were reported.

First, with the log-transformed data it was tested whether the growth depended on plant species, treatment and their interaction. Separate *p*-values for the single predictors were calculated using the CAR-package [51]. In a second step differences in growth between treatments were tested for each species separately with a linear mixed effect model and a post-hoc Tukey's HSD test. Because of heteroscedasticity, biomass, rosette projection area and growth height of juveniles were log-transformed. In the seedling bioassay, it was tested whether growth declined exponentially with increasing concentration of 2-MNQ or *I. glandulifera* leaf material respectively. Therefore the regression equation $f(x) = \exp(ax + b)$ was fitted. To compare the impact of competition and *I. glandulifera* allelochemicals, between both developmental stages and the species *G. urbanum*, *F. ulmaria*, *U. dioica* and *I. glandulifera* a relative interaction index [30,52] was calculated as, comparing a certain treatment with the related control (mean(treatment)–mean(control) / mean(treatment)+mean(control)). The resulting values were visualized in a heatmap.

Results

Seedling competition and allelopathy via roots

In the seedling competition trial, we grew the target seedlings solitarily, in intraspecific competition and in competition with *I. glandulifera*. An overall linear mixed-effect model ($\chi^2 = 295.77$, df = 16, $N = 255$, $p < 0.001$) showed that the root length of the seedlings depended on the species ($\chi^2 = 1173.81$, df = 5, $p < 0.001$), the treatment ($\chi^2 = 9.87$, df = 2, $p = 0.007$) and the interaction between species and treatment ($\chi^2 = 17.32$, df = 9, $p = 0.044$). This means that species responded differently to the treatments. In the control treatments (Fig 2) median root length varied from 7.8 mm (*S. fragilis*) to 131 mm (*L. sativum*) and the biomass from 0.1 mg (*S fragilis*) to 12.4 mg (*I. glandulifera*). Competition affected the root length of *G. urbanum* ($\chi^2 = 6.22$, df = 2, $p = 0.045$), *U. dioica* ($\chi^2 = 18.09$, df = 2, $p < 0.001$), *L. sativum* ($\chi^2 = 9.16$, df = 2, $p = 0.010$) and *I. glandulifera* ($\chi^2 = 11.06$, df = 1, $p < 0.001$) as well as seedling biomass of *U. dioica* ($\chi^2 = 17.98$, df = 2, $p < 0.001$) and *L. sativum* ($\chi^2 = 10.87$, df = 2, $p = 0.004$). Compared to the control treatment (solitary seedlings), intraspecific competition (four conspecific seedlings per well) had no impact on the root length of the native target species and *L. sativum* but reduced the biomass of *U. dioica* and *L. sativum*. Also root length of *I. glandulifera* in competition with its conspecifics was reduced. Competition with *I. glandulifera* seedlings reduced the root length of *G. urbanum*, *U. dioica* and *L. sativum* as well as the biomass of *U. dioica* and *L. sativum* in comparison to the control treatment. The mean root length of the most affected native species, *U. dioica* was 32% and those of the least affected *G. urbanum* 13% shorter than in the controls. Interspecific competition with *I. glandulifera* had a stronger impact on the growth of seedlings in comparison to intraspecific competition as the root length and biomass of *U. dioica* and root length of *L. sativum* were reduced more strongly. To investigate whether *I. glandulifera* seedlings release allelopathic substances into the agar that are responsible for the growth reduction we added activated charcoal to the agar. In the control treatment it had no negative effect on the growth of a single target seedling. Seedling biomass of *G. urbanum* was even slightly enhanced ($\chi^2 = 5.35$, df = 1, $p = 0.021$, linear mixed effect model). However, in competition with *I. glandulifera* the addition of activated charcoal

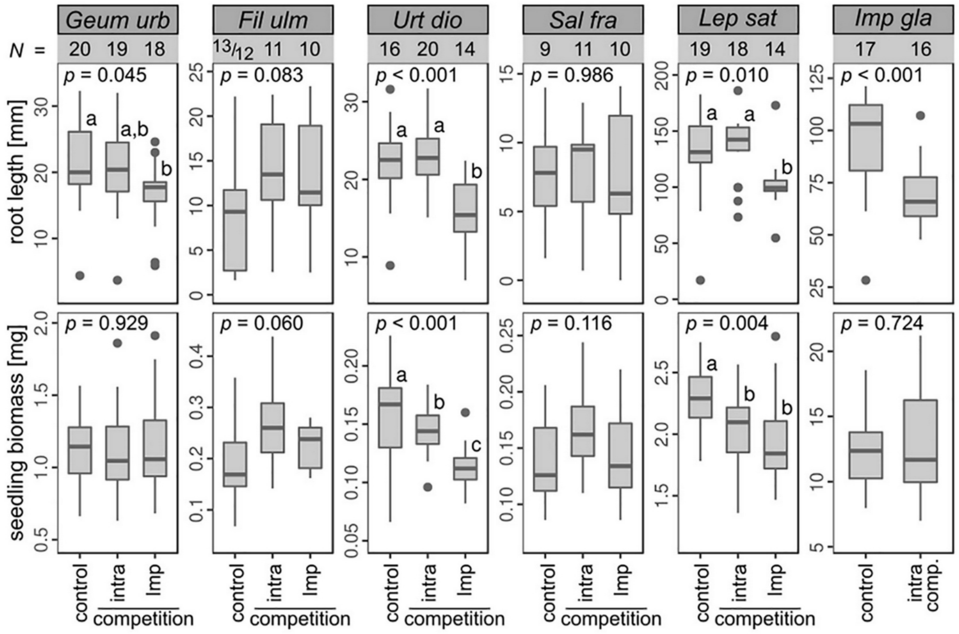

Fig 2. Effect of competition on root length and total dry biomass of seedlings. Seedlings of the target species *Geum urbanum* (*Geum urb*), *Filipendula ulmaria* (*Fil ulm*), *Urtica dioica* (*Urt dio*), *Salix fragilis* (*Sal fra*), *Lepidium sativum* (*Lep sat*) and *Impatiens glanduifera* (*Imp gla*) were grown solitarily (control), in intraspecific competition (intra) or in competition with *Impatiens glandulifera* seedlings (Imp). Note that the scale of the y-axis varies among species. Number of observations (*N*) are shown. It was tested if the growth depended on the treatments using a linear mixed effect model (microwell plate in which the seedlings were grown as random factor) (*p*-values are given); different letters mark significant differences among treatments (post-hoc Tukey's HSD test for $p < 0.050$). Boxes represent the first and third quartiles, bands inside the boxes the median. Whiskers are restricted to the 1.5 interquartile ranges. Datapoints not included in the whiskers are depicted as dots.

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did not improve seedling growth. Root length of *L. sativum* ($\chi^2 = 11.14$, df = 1, $p < 0.001$) and biomass of *U. dioica* ($\chi^2 = 5.01$, df = 1, $p = 0.025$) were even reduced in comparison to the *I. glandulifera* competition treatment without activated charcoal (linear mixed-effect models).

Impact of 2-MNQ and *I. glandulifera* leaf material on seedling growth

For the bioassay with 2-MNQ an overall linear mixed-effect model ($\chi^2 = 136.64$, df = 11, $N = 392$, $p < 0.001$) revealed that the root length depended on species ($\chi^2 = 687.49$, df = 5, $p < 0.001$) and concentration of 2-MNQ ($\chi^2 = 19.28$, df = 1, $p < 0.001$), but the interaction term of both was not significant ($\chi^2 = 7.11$, df = 5, $p = 0.213$). While *G. urbanum*, *F. ulmaria*, *S fragilis* and *I. glandulifera* were not affected by 2-MNQ, the root length of *U. dioica* and *L. sativum* declined exponentially with increasing concentration of 2-MNQ (Table 1, S1 Fig). However, the correlation coefficient *a* showed only a slight decline (Table 1) and the R^2 values of the corresponding linear models without random factor were very low (S1 Fig), showing a weak correlation. The seedling biomass was not affected by 2-MNQ at all.

For the bioassay with *I. glandulifera* leaf material an overall linear mixed-effect model ($\chi^2 = 179.62$, df = 11, $N = 374$, $p < 0.001$) revealed that the root length depended significantly on plant species ($\chi^2 = 125.12$, df = 5, $p < 0.001$), concentration of leaf material ($\chi^2 = 107.84$, df = 1, $p < 0.001$) and likewise their interaction term ($\chi^2 = 37.81$, df = 5, $p < 0.001$). Thus,

Table 1. Seedlings growth as a function of the concentration of 2-MNQ and *I. glandulifera* leaf material.

	species	*N*	root length				seedling biomass			
			χ^2 DF = 1	*p*-value	regression coefficients		χ^2 DF = 1	*p*-value	regression coefficients	
					a	*b*			*a*	*b*
2-MNQ	*Geum urb*	71	2.00	0.157			0.20	0.653		
	Fil ulm	42	0.52	0.470			0.01	0.926		
	Urt dio	72	12.36	< 0.001	-0.042	3.174	1.19	0.276		
	Sal fra	72	0.18	0.671			1.94	0.164		
	Lep sat	72	11.93	0.001	-0.043	4.923	1.52	0.217		
	Imp gla	63	3.33	0.068			0.27	0.605		
leaf material	*Geum urb*	71	28.50	< 0.001	-0.376	3.021	0.47	0.492		
	Fil ulm	30	3.37	0.066			0.19	0.661		
	Urt dio	66	54.72	< 0.001	-0.716	3.012	6.45	0.011	-0.102	-1.946
	Sal fra	71	26.25	< 0.001	-0.835	2.277	3.50	0.061		
	Lep sat	72	24.58	< 0.001	-0.652	4.730	3.20	0.074		
	Imp gla	64	0.05	0.821			0.06	0.801		

For each target species it was tested whether root length and total dry biomass declined exponentially with increasing concentration of 2-MNQ (0–12.8 mg/l) and amount of *I. glandulifera* leaf material (0–2.4 g/l) that was added to the agar. See S1 and S2 Figs for plots of the raw data. Using a linear mixed effect model (microwell plate in which the seedlings were grown as random factor) the regression equation $f(x) = \exp(ax + b)$ was fitted; χ^2-values, resulting *p*-values and, in the case of significance, the regression coefficients *a* and *b* are given. A negative sign of *a* implies a decline of the fitted curve, its absolute value the strength of the decline. The coefficient *b* gives the y-intercept, calculated as exp(b). target species are abbreviated as follows: *Geum urbanum* (*Geum urb*), *Filipendula ulmaria* (*Fil ulm*), *Urtica dioica* (*Urt dio*), *Salix fragilis* (*Sal fra*), *Lepidium sativum* (*Lep sat*) and *Impatiens glanduifera* (*Imp gla*).

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species responded differently to *I. glandulifera* leaf material. *I. glandulifera* leaf material had a higher impact on the seedling growth than 2-MNQ. It reduced the root length of *G. urbanum*, *U. dioica*, *S fragilis* and *L. sativum* (Table 1, S2 Fig). Seedling biomass of *U. dioica* slightly declined with increasing concentration of the leaf material (linear mixed-effect model $p = 0.011$, but linear model $R^2 = 0.08$; Table 1, S2 Fig). The regression coefficient was higher in the bioassay with *I. glandulifera* leaf material compared to the one in trials with 2-MNQ (Table 1), e.g. in *U. dioica* the regression coefficient of root length with leaf material was -0.716 (median declined from 26 to 5 mm) compared to -0.042 with 2-MNQ (median declined from 26 to 14 mm). *F. ulmaria* and *I. glandulifera* were not significantly affected at all, but *F. ulmaria* root length slightly declined with higher leaf material concentration and *I. glandulifera* root length with higher 2-MNQ concentration (Table 1).

Allelopathy and competition in juveniles

In the pot experiment with juveniles, target plants were grown solitarily, in intraspecific competition, in competition with *I. glandulifera* or they were treated with 2-MNQ (Fig 3). An overall linear mixed-effect model ($\chi^2 = 255.6$, df = 14, $N = 150$, $p < 0.001$) showed that the juveniles' biomass depended on species ($\chi^2 = 279.80$, df = 3, $p < 0.001$) and treatment ($\chi^2 = 217.92$, df = 3, $p < 0.001$). The species responded quite similar to the treatments (interaction species * treatment:$\chi^2 = 14.69$, df = 8, $p = 0.065$). On average the growth of all species was lower when they were watered with 2-MNQ than in the control, but only significant with respect to the biomass of *U. dioica* and *I. glandulifera* showing a growth reduction of 51% and 46%, respectively. All species except *F. ulmaria* competed intraspecifically, resulting in 66% less biomass in the most affected species *U. dioica*. The competition with *I. glandulifera* had an even stronger effect than the intraspecific competition, except on the height of *U. dioica*. In

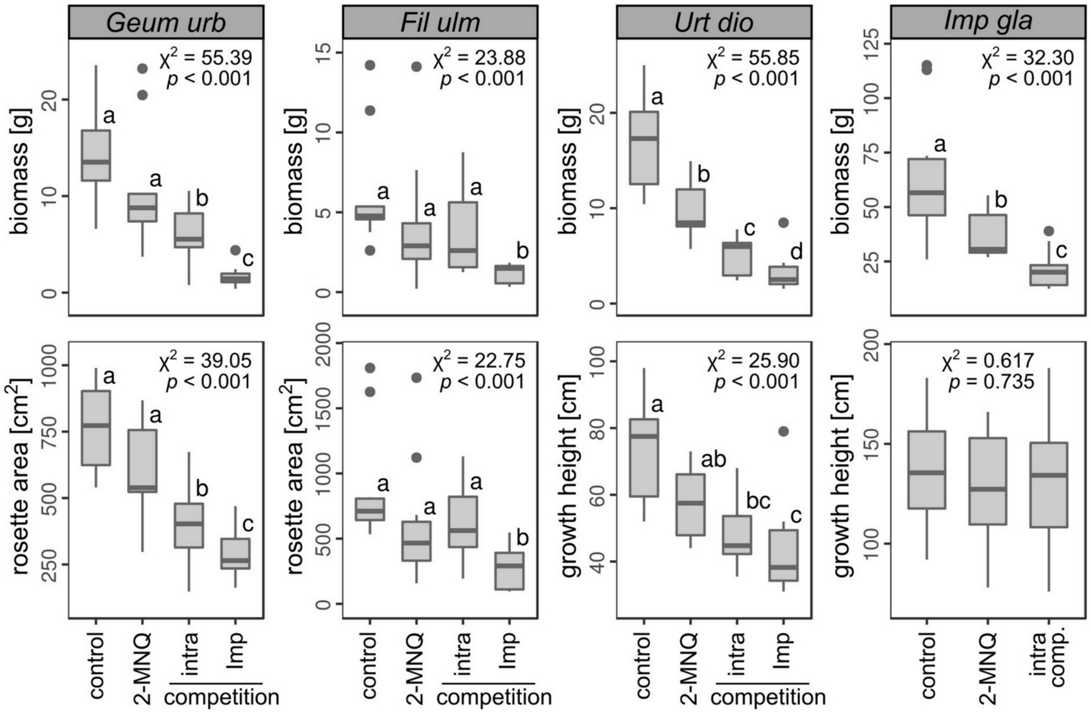

Fig 3. Effect of 2-MNQ and competition on the growth of juvenile target plants. For all target species the aboveground dry biomass after 10 weeks growth in pots is shown. For *G. urbanum* and *F. ulmaria* also the projection area of the rosettes and for *U. dioica* and *I. glandulifera* the plant height is shown. The dependence of the growth on the treatments was tested with a linear mixed effect model ($N = 10$ per treatment; block in which the pots were arranged as random factor) using log-transfomed data; χ^2-values (DF = 2 for *I. glandulifera* or DF = 3 for all other species) and resulting *p*-values are given. Different letters resulting from a post-hoc Tukey's HSD test mark significant different groups for $p < 0.050$. Note that in the boxplots the untransformed data are presented. Boxes represent the first and third quartiles, bands inside the boxes the median. Whiskers are restricted to the 1.5 interquartile ranges. Datapoints not included in the whiskers are depicted as dots. target species are abbreviated as follows: *Geum urbanum* (*Geum urb*), *Filipendula ulmaria* (*Fil ulm*), *Urtica dioica* (*Urt dio*), *Salix fragilis* (*Sal fra*), *Lepidium sativum* (*Lep sat*) and *Impatiens glanduifera* (*Imp gla*).

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competition with *I. glandulifera* biomass of *U. dioica* was reduced by 85% compared to the control; in the most affected species *G. urbanum* biomass was reduced by 89%. In *I. glandulifera* the biomass of the target plant was reduced by 65% in competition with its conspecifics, whereas the height was not affected.

Comparison of the impact of *I. glandulifera* in all trials

Negative relative interaction indices, as an indicator of the intensity of effects, showed that *I. glandulifera* allelochemicals and competition reduced the growth of the target species in all trials (Fig 4). The intensity of the impact depended on the species. *U. dioica* was most affected, considering the relative interaction indices as well as statistical differences between treatments and controls. In all cases, the growth of *U. dioica* was significantly reduced by *I. glandulifera*. *F. ulmaria* was the least affected as only the growth of juveniles in competition with *I. glandulifera* was significantly reduced. Furthermore, the impact depended on the developmental stage, with the juveniles being more affected than the seedlings, both by allelochemicals and competition. Hence, the relative interaction indices of intraspecific competition were lower in seedlings (up to -0.16 in *I. glandulifera*) than in the juveniles (up to -0.54 in *U. dioica*). Likewise,

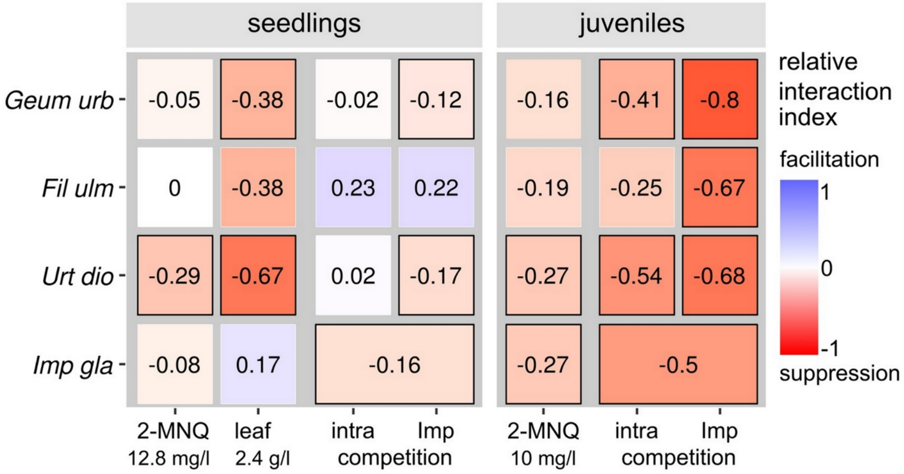

Fig 4. Intensity of the impact of competition and allelopathy by *I. glandulifera*. The intensity is expressed as relative interaction index among the different treatments and the appropriate control, calculated as (mean(treatment)-mean(control) / mean(treatment)+mean(control)). The relative interaction indices for all groups are given and represented by the colors of the heatmap. The more reddish the higher is a negative impact. Underlying growth parameters are root length of seedlings and aboveground dry biomass of juveniles. To visualize the impact of 2-MNQ and *I. glandulifera* leaf material (leaf) on seedlings the treatments with the highest concentrations were chosen. Black edged squares indicate that the growth of the target plants in the given treatment is significantly different from the related control. For the seedlings treated with 2-MNQ or *I. glandulifera* leaf material respectively, the black edged squares indicate an exponential decline of the root length in the bioassays. target species are abbreviated as follows: *Geum urbanum* (*Geum urb*), *Filipendula ulmaria* (*Fil ulm*), *Urtica dioica* (*Urt dio*), *Salix fragilis* (*Sal fra*), *Lepidium sativum* (*Lep sat*) and *Impatiens glanduifera* (*Imp gla*).

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the competitive effect of *I. glandulifera* on seedlings was only expressed as a relative interaction index up to -0.17, whereas it was more than 4 times stronger on juveniles (relative interaction index ranging from -0.68 to -0.8). The effect of 2-MNQ was rather low as in the seedling trial it was lower than the effect of *I. glandulifera* leaf material. Similarly, in the experiment with juvenile plants it had a smaller impact than the competition with *I. glandulifera*. *I. glandulifera* seedlings were tolerant to 2-MNQ and *I. glandulifera* leaf material but juveniles were not (relative interaction index -0.27). Seedlings and juveniles of *I. glandulifera* competed intraspecifically, but the impact of *I. glandulifera* juveniles on their conspecifics was lower than on the native target species.

Discussion

In the present study we compared impacts of *I. glandulifera* on different native plant species among seedlings and juvenile plants, in order to detect species-specific and developmental stage-specific effects. We found a competitive and allelopathic effect of *I. glandulifera* on target plants depending on species and developmental stage. Considering all trials *F. ulmaria* was the least and *U. dioica* the most affected species and in general the juveniles were more affected than the seedlings of all species.

Dependency of competition and allelopathy on plant species and developmental stage

Species- and developmental stage-specific response to *I. glanduifera*, as we found, may be based on specific traits. In later developmental stages the studied target species change in their

architecture. As juveniles *U. dioica*, *F. ulmaria* and *G. urbanum* start to build a rhizome from which they sprout in the following years. This could enable a fast growth in spring and give them an advantage in competition with *I. glandulifera* compared to plants developing from seeds. *U. dioica* however, seems to be sensitive to competition with *I. glandulifera* also when sprouting from rhizomes [5,53]. Furthermore, *F. ulmaria* initially forming a rosette can develop a flowering shoot from the second year onwards [54]. *F. ulmaria* may then reach a height of up to 2 m [36], which is comparable to *I. glandulifera* and could influence the outcome of their competition. Also comparing the species rosettes may be more shaded than tall growing plants, and hence affected by competition for light. In juveniles however we found no obvious difference among the response of the rosette forming species *F. ulmaria* and *G. urbanum* and stem building *U. dioica*. Nitrophilous species such as *U. dioica* may be more affected by competition for nutrients than competition for light. *I. glandulifera* can be considered as strong competitor due to its architecture. Tall plant growth is generally connected to a strong competitive effect, because tall plants shade co-occurring plants and remove other resources such as nutrients, water and space [55,56].

Disentangling allelopathy from competition and the role of 2-MNQ

Effects of allelopathy and competition for resources are difficult to disentangle, because they interact with each other [57]. A possible method to detect allelopathy is to add activated charcoal to the plant substrate that absorbs allelopathic substances. Using this method [30] detected a rather large allelopathic impact of *I. glandulifera* on juvenile *U. dioica* in addition to competition. We found a negative effect of *I. glandulifera* among seedlings but adding activated charcoal did not reduce this effect, suggesting only a competitive effect. 2-MNQ is assumed to be the major allelopathic substance of *I. glandulifera* [21]. We found a negative but overall small effect of 2-MNQ on the growth of native plants. In juvenile plants, the effect of competition with *I. glandulifera* was much higher than the effect of 2-MNQ. When they are grown together with *I. glandulifera* the negative effects can be mediated by both competition and allelopathy as *I. glandulifera* should consume resources but may also secrete allelopathic substances. An interaction of competition and allelopathy may amplify their single effects.

In our study 2-MNQ had a lower impact on seedling growth than *I. glandulifera* leaf material. High impact of leaf material may also be intensified by a changed osmotic potential of the agar. Nevertheless, the lower impact of 2-MNQ indicates that 2-MNQ may not be the only substance responsible for the allelopathic effect of *I. glandulifera*. Likewise, [58] found no correlation between the allelopathic effect of senescent *I. glandulifera* leaves and their 2-MNQ content. However, the 2-MNQ content in their study was very low compared to the study of [21] who showed a negative effect of *I. glandulifera* shoot extracts on seed germination with higher concentrations of 2-MNQ. Several other substances were detected in *I. glandulifera* such as the naphtoquinone 2-hydroxy-naphtoquinone, other phenolic compounds, steroids, several flavonoids, or essential oils [22,24,25,59–62], could also be allelochemicals. For example the steroid glanduliferins A and B were shown to have an in vitro cytostatic effect [59]. In addition, 2-MNQ may have other effects, indirectly favoring the invasiveness of *I. glandulifera*. It can for example suppress the growth of mycorrhizal fungi [21] or reduce mycorrhiza colonization of some native species in soils invaded by *I. glandulifera* [28,29,63]. Furthermore, there might be a link between allelopathy and herbivore resistance. Pure 2-MNQ might have the potential to inhibit the reproduction of insects [64]. [58] in fact found no correlation between herbivore leaf damage and 2-MNQ concentration in senescent *I. glandulifera* leaves but a negative correlation with the concentration of the glycoside form of 2-MNQ.

Effect of *I. glandulifera* on conspecifics

I. glandulifera plants were not fully tolerant to their conspecifics. We suggest that the tolerance of *I. glandulifera* seedlings to their own chemicals could enable massive seedling recruitment. In the seedling stage *I. glandulifera* produces a huge amount of allelochemicals [21] that can suppress other plant species. Due to tolerance towards their own chemicals *I. glandulifera* can form a dense and monospecific carpet of seedlings (own observations). During further development intraspecific competition becomes stronger and *I. glandulifera* plants become intolerant to their own allelochemicals as we observed in our trial with *I. glandulifera* juveniles. Such an allelopathic self-inhibition ("autotoxicity") seems to be paradox but is often observed [65,66]. Self-inhibition may just be a side-effect outweighed by the benefit of inhibition of other species, but it is also thought to play a role in population dynamics [65–67]. It may intensify density-dependent mortality ("self-thinning"), and thus lead to spacing between individuals and reduce intraspecific resource competition among the remaining individuals. Autotoxicity should anyway not be a problem for species whose populations do not persist for long time on a specific site. These are, for example, species populations that are regularly replaced by succession [66]. It is known that crop plants can release allelopathic substances into the soil that impair the growth of their conspecifics in the following years [65]. Maybe autotoxicity can even induce the decline of a population. In the case of *I. glandulifera*, we suggest that autotoxicity of juveniles could intensify density-dependent mortality of individuals in *I. glandulifera* populations and play a role in the observed population fluctuations of this species [68]. Due to its high dispersal potential [5] *I. glandulifera* could compensate the collapse of a population by colonizing new sites rapidly.

Consequences of *I. glandulifera* allelopathy and competition for native plant communities

In our study *I. glandulifera* overall suppressed the growth of the target species investigated. Therefore, we expect such a growth reduction also in the field. The response of our target species on *I. glandulifera* should be crucial for the native vegetation. Dominant species such as our target species are considered to make up a large portion of the community biomass and thereby determine the community structure [69]. For example, *F. ulmaria* plays a major role in succession dynamics. By suppressing other species it rapidly colonizes abandoned fields until it becomes senescent after several years and forest species are able to invade the area [54]. Here, *F. ulmaria* was the species least affected by *I. glandulifera* suggesting only a minor impact of *I. glandulifera* in associations dominated by *F. ulmaria*. Also *S. fragilis* that can form shrubs and start succession of woodlands after disturbances as flooding, was affected moderately. Suppression of *S. fragilis* by *I. glandulifera* may increase erosion as *S. fragilis* can protect riverside soil from erosion, whilst *I. glandulifera* is thought to favor erosion by not fixing the soil.

The fact that seedlings and juveniles as recruitment stages were affected should give *I. glandulifera* an advantage in cases where plant recruitment is crucial, i. e. when a plant colonizes new sites. Generally it can have important consequences on plant communities as early processes in plant development can determine community assembly [70]. So plant invasions can be enhanced by early superiority over native species (priority effect; [71,72]). The earlier a species is suppressed the more likely it should disappear from a community. *I. glandulifera* extracts and litter can reduce seed germination, the earliest step of plant recruitment, species-specifically [21,26,27]. This may have a more severe impact on the further development than the growth reduction of juvenile plants, as we have observed. All of our juvenile plants survived, hence they should also be able to establish. In established vegetation not only the competition ability of the plants, may be different compared to the early developmental stages, but

also the importance of the components of competition may change. In the early stage of an invasion the ability of an invader to suppress natives is important. For the long-term success of an invasion in an established vegetation however, the ability of the invader to withstand competition by natives becomes more important (competitive-effect versus -response; [30,73]).

Species-specific sensitivity to *I. glandulifera* may lead to an altered community composition in the field with some species being more suppressed than others. Nevertheless, several field studies revealed only an overall weak effect of *I. glandulifera* on mostly riparian [18,19,74] and forest plant community composition and diversity [10]. As [18] discuss, this may be due to the fact that *I. glandulifera* just takes over the role of native dominant species and reduces their growth while species in the undergrowth remain unaffected. Likewise, we found that the competitive effect of *I. glandulifera* was in a comparable order of magnitude as the competitive effect of the natives on their conspecifics (intraspecific competition). In contrast to the aforementioned field studies [16,17] found a rather negative impact of *I. glandulifera* on riparian vegetation. Such ambiguities may be explained by different study conditions leading to different results due to additional context-dependencies. The consequence of competition between two species for a plant community is very complex and depends on several factors such as abiotic stress or the indirect reactions of other species [35]. Therefore, the impact of an invasive species on native communities should depend strongly on environment and ecosystem conditions such as climate, abiotic factors and the resident community [4].

Conclusion

We conclude that the strong competitive effect of juvenile *I. glandulifera* should be caused by a combination of resource competition and allelopathic substances released by *I. glandulifera*. The low effect of 2-MNQ compared to *I. glandulifera* leaf material indicates that there could be allelopathic substances in addition to 2-MNQ. *I. glandulifera* was not fully tolerant to its conspecifics which may be connected to dynamics of *I. glandulifera* populations. Autotoxicity may intensify density-dependent mortality and eventually cause the known population fluctuations. We suggest that *I. glandulifera* reduces the growth of the native vegetation in the field. Species-specific growth reduction alters community composition with some species suppressed and others not. The succession of native plants might be delayed or changed but not fully hindered by *I. glandulifera*.

Supporting information

S1 Fig. Dependence of seedlings growth on the concentration of 2-MNQ. For each target species the root length, total dry biomass of the seedlings as well as number of seedlings that died shortly after placing the germinated seeds on the agar (no further growth observed) are shown. Using a linear model the regression equation $f(x) = \exp(ax + b)$ was fitted to test the dependency of root length and seedling biomass of the leaf material concentration; resulting *p*-values and coefficients *a* and *b* are given. Note that in contrast to Tab. 1 in results a linear model instead of a linear mixed effect model was used because the effect of random factor can not be visualized correctly with a regression line. target species are abbreviated as follows: *Geum urbanum* (*Geum urb*), *Filipendula ulmaria* (*Fil ulm*), *Urtica dioica* (*Urt dio*), *Salix fragilis* (*Sal fra*), *Lepidium sativum* (*Lep sat*) and *Impatiens glanduifera* (*Imp gla*).
(PDF)

S2 Fig. Dependence of seedlings growth on the amount of *I. glandulifera* leaf material. For each target species the root length, total dry biomass of the seedlings as well as number of seedlings that died shortly after placing the germinated seeds on the agar (no further growth

observed) are shown. Using a linear model the regression equation f(x) = exp(*a*x + *b*) was fitted to test the dependency of root length and seedling biomass on the amount of leaf material; resulting *p*-values and coefficients *a* and *b* are given. Note that in contrast to Tab. 1 in results a linear model instead of a linear mixed effect model was used because the effect of random factor can not be visualized correctly with a regression line. target species are abbreviated as follows: *Geum urbanum* (*Geum urb*), *Filipendula ulmaria* (*Fil ulm*), *Urtica dioica* (*Urt dio*), *Salix fragilis* (*Sal fra*), *Lepidium sativum* (*Lep sat*) and *Impatiens glanduifera* (*Imp gla*).
(PDF)

S1 Data. Dataset of the seedling competition trial and allelopathy via roots. Seedlings of six target species were grown in five treatments testing competition and allelopathy of *I. glandulifera*. This dataset contains measured radicle length and biomass of the target seedlings dependent on the treatments. A description of all columns and factor levels is included in the document.
(TXT)

S2 Data. Dataset of the seedling bioassay. Seedlings of six target species were treated with *I. glandulifera* leaf material or 2-MNQ to test the allelopathic effect of this substances. This dataset contains measured radicle length and biomass of the target seedlings dependent on the treatments. A description of all columns and factor levels is included in the document.
(TXT)

S3 Data. Dataset of the juvenile trial. Juvenile plants of four target species were grown in four treatments testing competition and allelopathy of *I. glandulifera*. This dataset contains measured rosette projection area and biomass of the target plants dependent on the treatments. A description of all columns and factor levels is included in the document.
(TXT)

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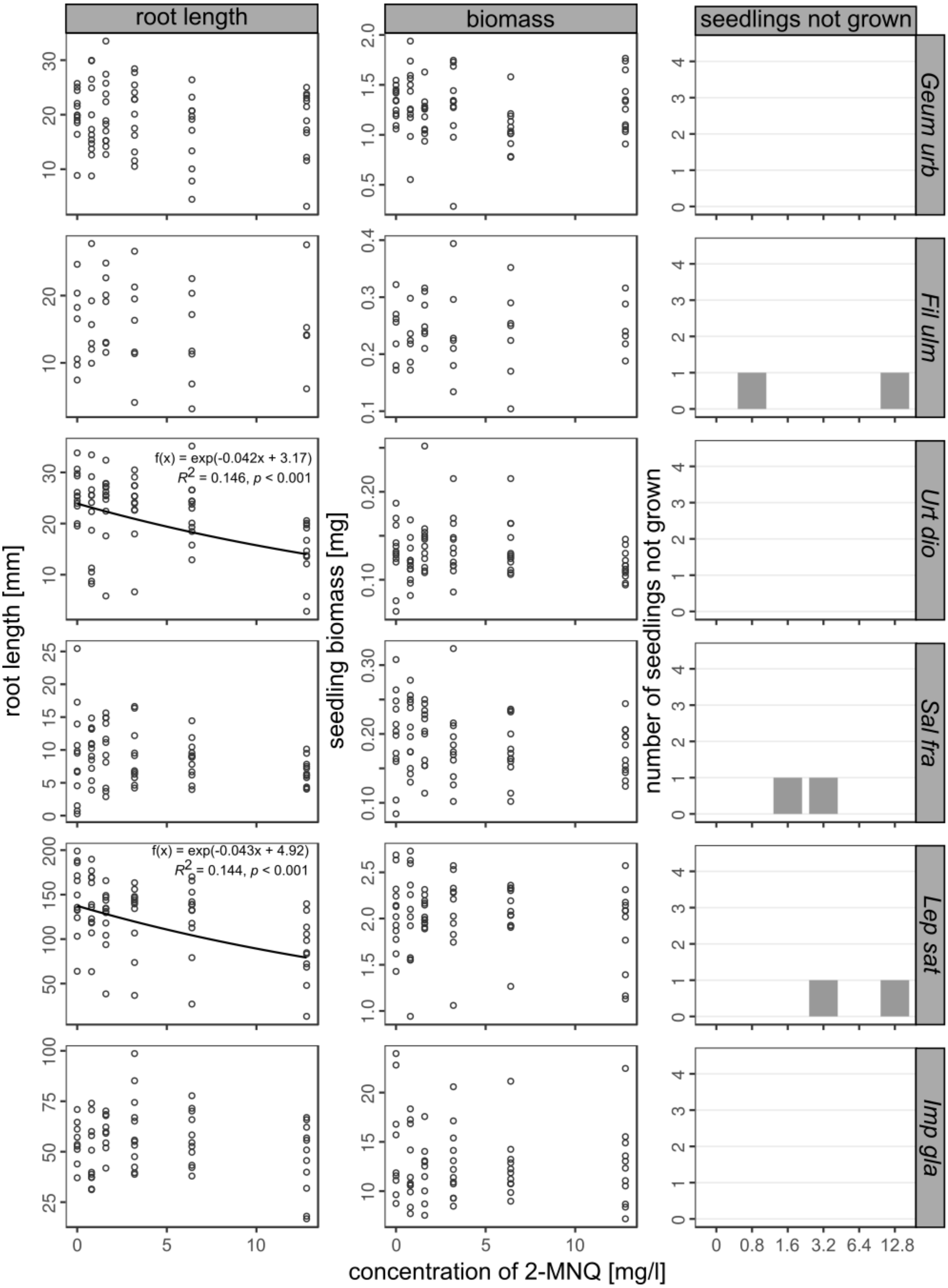
Supporting information

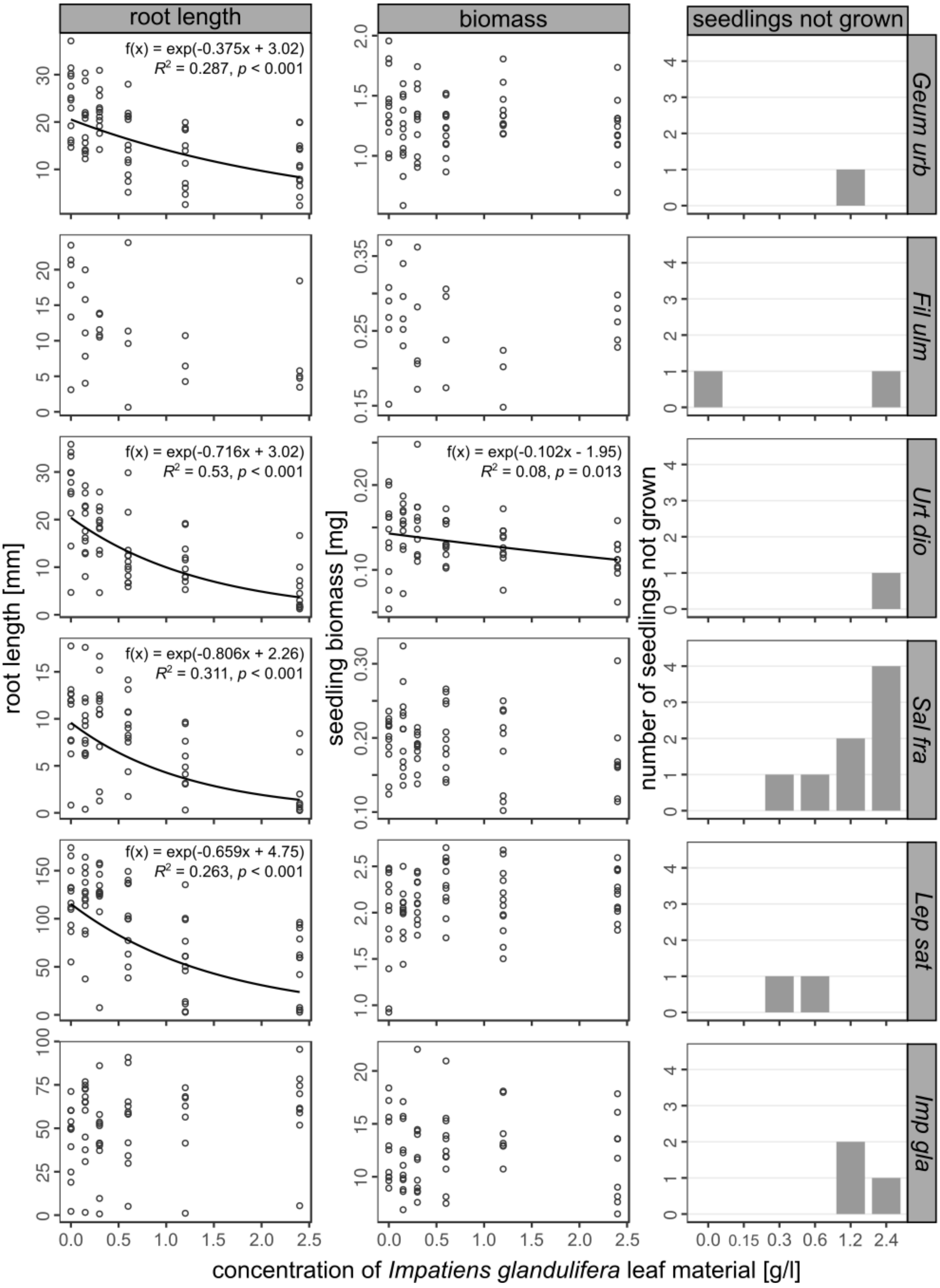
S1 Fig. Dependence of seedlings growth on the concentration of 2-MNQ.

For each target species the root length, total dry biomass of the seedlings as well as number of seedlings that died shortly after placing the germinated seeds on the agar (no further growth observed) are shown. Using a linear model the regression equation $f(x) = \exp(ax + b)$ was fitted to test the dependency of root length and seedling biomass of the leaf material concentration; resulting p-values and coefficients a and b are given. Note that in contrast to Tab. 1 in results a linear model instead of a linear mixed effect model was used because the effect of random factor can not be visualized correctly with a regression line. target species are abbreviated as follows: *Geum urbanum* (Geum urb), *Filipendula ulmaria* (Fil ulm), *Urtica dioica* (Urt dio), *Salix fragilis* (Sal fra), *Lepidium sativum* (Lep sat) and *Impatiens glandulifera* (Imp gla).


root length
biomass
seedlings not grown
Geum urb
Fil ulm
Urt dio
Sal fra
Lep sat
Imp gla
f(x) = exp(-0.042x + 3.17)
R^2 = 0.146, p < 0.001
f(x) = exp(-0.043x + 4.92)
R^2 = 0.144, p < 0.001
root length [mm]
seedling biomass [mg]
number of seedlings not grown
concentration of 2-MNQ [mg/l]
0
5
10
0
0.8
1.6
3.2
6.4
12.8

S2 Fig. Dependence of seedlings growth on the amount of I. glandulifera leaf material.

For each target species the root length, total dry biomass of the seedlings as well as number of seedlings that died shortly after placing the germinated seeds on the agar (no further growth observed) are shown. Using a linear model the regression equation $f(x) = \exp(ax + b)$ was fitted to test the dependency of root length and seedling biomass on the amount of leaf material; resulting p-values and coefficients a and b are given. Note that in contrast to Tab. 1 in results a linear model instead of a linear mixed effect model was used because the effect of random factor can not be visualized correctly with a regression line. target species are abbreviated as follows: Geum urbanum (Geum urb), Filipendula ulmaria (Fil ulm), Urtica dioica (Urt dio), Salix fragilis (Sal fra), Lepidium sativum (Lep sat) and Impatiens glanduifera (Imp gla).


root length
biomass
seedlings not grown
Geum urb
Fil ulm
Urt dio
Sal fra
Lep sat
Imp gla
f(x) = exp(-0.375x + 3.02)
R^2 = 0.287, p < 0.001
f(x) = exp(-0.716x + 3.02)
R^2 = 0.53, p < 0.001
f(x) = exp(-0.102x - 1.95)
R^2 = 0.08, p = 0.013
f(x) = exp(-0.806x + 2.26)
R^2 = 0.311, p < 0.001
f(x) = exp(-0.659x + 4.75)
R^2 = 0.263, p < 0.001
root length [mm]
seedling biomass [mg]
number of seedlings not grown
0.0 0.5 1.0 1.5 2.0 2.5
0.0 0.15 0.3 0.6 1.2 2.4
concentration of *Impatiens glandulifera* leaf material [g/l]

The datasets are to long for printing. They are online available.

S1 Data. Dataset of the seedling competition trial and allelopathy via roots.

Seedlings of six target species were grown in five treatments testing competition and allelopathy of *I. glandulifera*. This dataset contains measured radicle length and biomass of the target seedlings dependent on the treatments. A description of all columns and factor levels is included in the document.

https://doi.org/10.1371/journal.pone.0205843.s003

S2 Data. Dataset of the seedling bioassay.

Seedlings of six target species were treated with *I. glandulifera* leaf material or 2-MNQ to test the allelopathic effect of this substances. This dataset contains measured radicle length and biomass of the target seedlings dependent on the treatments. A description of all columns and factor levels is included in the document.

https://doi.org/10.1371/journal.pone.0205843.s004

S3 Data. Dataset of the juvenile trial.

Juvenile plants of four target species were grown in four treatments testing competition and allelopathy of *I. glandulifera*. This dataset contains measured rosette projection area and biomass of the target plants dependent on the treatments. A description of all columns and factor levels is included in the document.

https://doi.org/10.1371/journal.pone.0205843.s005

5.2 Manuscript 2

Micro-habitat and season dependent impact of the invasive *Impatiens glandulifera* on native vegetation

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

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Authors contributions: JB, HF, and ML had the idea and developed the study design. JB did the field work collecting the data (with support in plant species determination by Alfred Bolze, see acknowledgment). JB curated and analyzed the data, prepared the figures and first manuscript draft. JB, HF, and ML reviewed and edited the manuscript. HF and ML supervised the study.

Author contributions adopted literally from the manuscript webpage:
JB: research idea, study design, data collection, statistical analysis, figures, manuscript writing
HF: research idea, study design, manuscript writing, supervision
ML: research idea, study design, manuscript writing, supervision

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Micro-habitat and season dependent impact of the invasive *Impatiens glandulifera* on native vegetation

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Abstract

The impact of invasive species is often difficult to assess due to species × ecosystem interactions. *Impatiens glandulifera* heavily invaded several habitat types in Central Europe but its impact on native plant communities is rated ambiguously. One reason could be that the impact differs between habitat types or even between environmentally heterogeneous patches (micro-habitats) within one habitat type. In the present study a vegetation survey was performed within heterogeneous riverside habitats in Germany investigating the impact of *I. glandulifera* on native vegetation in dependence of environmental conditions. The vegetation was recorded in summer and spring because of seasonal species turnover and thus potentially different impact of the invasive plant. We found that the cover of *I. glandulifera* depended on environmental conditions resulting in a patchy occurrence. *I. glandulifera* did not have any impact on plant alpha-diversity but reduced the cover of the native vegetation, especially of the dominant species. This effect depended on micro-habitat and season. The native vegetation was most affected in bright micro-habitats, especially those with a high soil moisture. Not distinguishing between micro-habitats, plant species composition was not affected in summer but in spring. However, environmental conditions had a higher impact on the native vegetation than *I. glandulifera*. We conclude that within riparian habitats the threat of *I. glandulifera* to the native vegetation can be rated low since native species were reduced in cover but not excluded from the communities. This might be due to patchy occurrence and year-to-year changes in cover of *I. glandulifera*. The context-dependency in terms of micro-habitat and season requires specific risk assessments which is also an opportunity for nature conservation to develop management plans specific to the different habitats. Particular attention should be given to habitats that are bright and very wet since the effect of *I. glandulifera* was strongest in these habitats.

Keywords
context-dependency, early-flowering spring vegetation, environment, plant community, plant invasion, riverside vegetation

Introduction

Biological invasions are one aspect of anthropogenic global change. Invasive species can alter ecosystems processes, change native community structure and reduce diversity (Ehrenfeld 2010, Vilà et al. 2011). The success of an invader depends, among other things, on its ability to occupy various habitats. A broad tolerance to abiotic site factors can thus facilitate the establishment in different communities. Alternatively, superior fitness within a particular niche can lead to success in particular communities (MacDougall et al. 2009). Ecosystems in turn affect invasion processes (Kueffer et al. 2013) as site specific conditions can modify the performance of the invader and its interaction with other organisms. Since such species × ecosystem interactions (Kueffer et al. 2013) make it difficult to generalize the impact of an invasive species on native ecosystems it is important to understand such context-dependencies. Knowledge of species × ecosystem interactions helps to understand species invasions and allows nature conservation authorities to develop more targeted management plans, prioritizing those habitats where an invasive species should have highest impact.

A good model system to study plant species × ecosystem interactions is *Impatiens glandulifera*. Originating from the Himalayan Mountain ranges, it now occurs all over Europe over a broad range of elevation, geographical latitude, and ecosystem types (Pyšek and Prach 1995, Larsson and Martinsson 1998, Kollmann and Bañuelos 2004, Pacanoski and Saliji 2014, Laube et al. 2015). After introduction to Europe in the 19th century it spread mainly along riverbanks and into wet habitats such as fens, mesotrophic grasslands, and woodland, but also forests out of the riparian zone, and into ruderal vegetation (Beerling and Perrins 1993, Pyšek and Prach 1993, 1995, Čuda et al. 2017). The invasion success of *I. glandulifera* is, among other factors, favored by a strong competitive and allelopathic effect, reducing the growth of native plants as seen in experimental studies (Vrchotová et al. 2011, Gruntman et al. 2014, Ruckli et al. 2014a, Loydi et al. 2015, Bieberich et al. 2018). However, field studies showed ambiguous results. In riparian habitats Cockel et al. (2014) and Hulme and Bremner (2006) found a strong negative impact of *I. glandulifera* on the native vegetation, while others found a weak impact in riparian habitats (Hejda and Pyšek 2006, Hejda et al. 2009, Diekmann et al. 2016) and in forests (Čuda et al. 2017). Sometimes the weak effect of *I. glandulifera* is thought to be due to high fluctuations in its population size (Kasperek 2004, Diekmann et al. 2016).

The impact of an invasive species can also depend on environmental conditions because its competitive ability depends on environmental conditions (Amarasekare 2003). Previous studies indicate that high soil nutrient availability and medium light is beneficial for *I. glandulifera* growth (Andrews et al. 2005, Čuda et al. 2014). In a heterogeneous habitat the competitive environment for *I. glandulifera* and the residents can change from patch to patch determining which of the species becomes dominant and leading to a mosaic of the different species (Amarasekare 2003). Such a patchy occurrence of invasive and native species could facilitate spatial co-existence (Amarasekare 2003) and could be a reason for the overall low impact of the invader as found in some studies (Hejda and Pyšek 2006, Hejda et al. 2009, Diekmann et al. 2016, Čuda et al. 2017). Another possibility for species co-existence is temporal niche partitioning. In riparian habitats, especially forests, in the temperate region the plant community in spring often differs compared to summer due to seasonal species turnover with spring communities often being characterized by early flowering geophytes (Ellenberg and Leuschner 2010, Czapiewska et al. 2019).

We hypothesize that within heterogeneous riparian habitats, the impact of *I. glandulifera* on the resident vegetation depends on the environmental conditions at a particular patch (subsequently named micro-habitat) because the growth of *I. glandulifera* also depends on this. Regarding seasonal effects we hypothesize a lower impact of *I. glandulifera* in spring compared to summer because of species turnover, and in particular differences in *I. glandulifera* plant size and cover, thus competition for resources (Grime 1977, Goldberg 1990). In order to test our hypotheses we conducted a field study in Germany within riparian habitats in spring and summer. This is the first study on the impact on spring vegetation and on seasonal differences in the impact of *I. glandulifera* on native vegetation. Here we especially directly link the impact of *I. glandulifera* with environmental conditions.

Materials and methods

Study sites and plot design

Within five riparian field sites ranging from alder woods to abandoned meadows we systematically sampled (Table 1, Fig. 1) the environmental conditions and the vegetation. Each site comprises patches of *Impatiens glandulifera* and heterogeneous micro-habitats regarding tree cover and soil moisture. All sites are located in the region around Bayreuth, Germany at an elevation between 345 m a.s.l. and 426 m a.s.l.. Within each site, plots were arranged on a grid of 20 m × 20 m. Every grid intersection point was used as position for a plot of 2 m × 2 m, independently of environmental condition, *I. glandulifera* or native vegetation cover (Fig. 1). This systematic design allowed us a representative sampling over the whole gradient of environmental conditions and *I. glandulifera* cover and regression analysis instead of comparison between invaded and uninvaded plots only. Across the five sites 114 plots of 2 m × 2 m were established in total (Table 1). In spring two plots were not accessible because of a very high soil water content and one plot was hit by a fallen tree, decreasing the number of replicates to 111 in spring.

Table 1. Field sites used for this study. For each site the main habitat type, the name of the next locality and the adjacent river is given as well as the GPS-location, approximate area and number of established plots.

Main habitat	alder forest	alder swamp forest	abandoned meadow	abandoned meadow	abandoned meadow
Next town	Ludwigschorgast	Neunkirchen	Weidenberg	Pegnitz	Waischenfeld
GPS-location	50°6.66'N 11°35.20'E	49°55.20'N 11°38.05'E	49°56.95'N 11°42.15'E	49°46.84'N 11°32.80'E	49°49.98'N 11°20.17'E
Area	20000 m^2	7000 m^2	16000 m^2	4000 m^2	9000 m^2
n plots summer	44	17	27	11	15
n plots spring	44	15	27	11	14

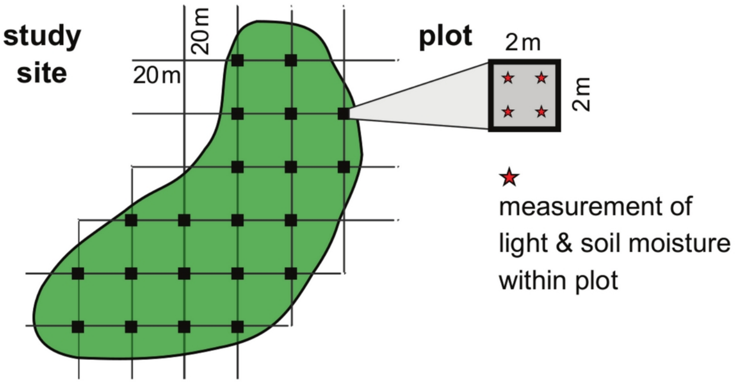


Figure 1. Plot design used for this study. Plots were arranged on a grid laid over the study site. Positions for light and soil moisture measurements within each plot are marked.

Data collection

The herb layer vegetation was surveyed in summer while *I. glandulifera* was flowering (2016-07-12/08-17), and in spring while the spring geophytes were flowering (2017-04-20/05-04). All vascular plant species were determined using standard literature (Schmeil et al. 2011, Eggenberg and Möhl 2013, Jäger et al. 2013, Aas 2017, Jäger 2017), and their cover was estimated according to extended Braun-Blanquet scale (Braun-Blanquet 1964, Reichelt and Wilmanns 1973). Additionally the maximum height of the vegetation, and in summer 2017 the cover of *I. glandulifera* was measured as described in Suppl. materials 1, 2. The environmental variables volumetric soil water content, light (relative photosynthetically active radiation), tree layer species composition and cover, and Ellenberg indicator values were gathered once in each plot in summer. The volumetric soil water content (named soil water content hereafter) was measured on 2017-05-23/05-28 in the uppermost soil layer with a SM-150 sensor (Delta-T Devices). Recordings were taken at four positions per plot and their median was calculated (Fig. 1). Relative photosynthetically active radiation (PAR, Parent and Messier 1996, Gendron et al. 1998) was measured with Quantum sensors (LICOR) when trees were fully foliate (2016-08-03/10-03). In the plot four single point records were taken just above the herb layer (Fig. 1). Simultaneously a reference value was taken at a totally unshaded site nearby using a second Quantum sensor. This sensor was connected to a BayEOS logger (BayCEER, University of Bayreuth) taking records every 30 s and saving them as means over 5 minutes. Relative PAR was calculated with the median of the point records within the plots divided by the particular logged reference matching in time. All light measurements were taken under a homogeneous overcast sky with the sun invisible and no rain, and always between 11:00 and 17:00. The tree layer was characterized estimating the cover of each tree species separately (2017-08-17/09-07) according to extended Braun-Blanquet scale (Braun-Blanquet 1964, Reichelt and Wilmanns 1973). Mean Ellenberg indicator values for light L, soil moisture F, soil nutrients N, and soil reaction R were calculated per plot based on the summer vegetation. Based on additional information included in the F-value, the percentage of plants preferring either periodically wet soils or constantly wet soils was calculated. Hereafter, these parameters are named index of periodically wet soil and index of constantly wet soil.

Statistical analysis

All statistical analyses were done with the software package R 3.5.2 (R Core Team 2018). To find the polynomial model best describing the dependence of cover of *I. glandulifera* on light and soil water content a multiple regression analysis was performed. To identify environmental variables affecting the cover of *I. glandulifera*, we performed an automated model selection (Bartoń 2018) separately for summer and spring vegetation. First of all a global model was built with the cover of *I. glandulifera* as response variable and 13 predictor variables that were expected to affect the cover of *I. glandulifera*: relative PAR (squared because of hump-shaped relationship), soil water content (squared), number of tree species, cover of these tree species occurring at least in 20 plots (*Alnus glutinosa*, *Salix fragilis*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Betula pendula*), Ellenberg values N, R, and indices for periodically or constantly wet soils. Ellenberg values L, and F were excluded because they correlated with relative PAR and soil water content, (Pearson correlation coefficient 0.549 and 0.544 respectively). All variables were standardized to zero mean and unit variance (VEGAN, (Oksanen et al. 2018)). For analysis of spring vegetation, the cover of *I. glandulifera* was log-transformed to counter heteroscedasticity of the model. The study site was considered as a random factor (NLME, (Pinheiro et al. 2018)). Next a set of models with combinations of all parameters was generated from the global model and the models were weighted by their AICc (MuMIn, (Bartoń 2018)). Models with ΔAICc > 2 were used to calculate the relative importance of each variable as the sum of AICc weights of all models including the variable.

Using the variables resulting from the model selection, we performed a piecewise structural equation model (piecewiseSEM, (Lefcheck 2016)) to test the effects of the environmental variables on *I. glandulifera*, and how in turn *I. glandulifera* affects the resident vegetation (all species except *I. glandulifera*). This also allowed us to infer whether the resident vegetation is more affected by *I. glandulifera* or by the environment based on the regression coefficients of the SEM. The resident vegetation was represented by species number, total cover (sum of the cover of all resident species in a plot) and the cover of those herbaceous species occurring in more than 20 plots. The construction of the initial models is visualized in Suppl. material 3, Fig. 1. The SEMs were fitted separately for summer and spring vegetation, and within the models the study site was considered as a random factor. For each path in the piecewise structural equation model, a standardized regression coefficient (β) and its significance were calculated as well as conditional R^2-values for all response variables.

To analyze plant community composition in summer, or respectively spring, we performed a Detrended Correspondence Analysis of the cover of the resident plant species with downweighting of rare species (DCA, package VEGAN (Oksanen et al. 2018)). DCA was confirmed to be appropriate because the DCA-axis gradient length was more than four times the standard deviation. Cover of *I. glandulifera*, as well as environmental parameters, were post-hoc fitted into the DCA result. Additionally, a Constrained Correspondence Analysis (CCA, VEGAN) was performed with the same data constraining the resident community with *I. glandulifera* cover. With an ANOVA-like permutation test (VEGAN) significance of the constraints was tested.

With the summer dataset of the year 2016, we analyzed whether the impact of *I. glandulifera* on the resident vegetation differed between micro-habitat groups. The groups were created by dividing the dataset according to the median of light (23.9 % PAR) and soil water content (51.5 %). Subsequently, they are named moist–bright (n = 30), wet–bright (n = 28), moist–dark (n = 27) and wet–dark (n = 29). For each of this groups separately and for the complete dataset impact of *I. glandulifera* on various variables representing the resident vegetation was analyzed: Impact on species number, Shannon-index and total plant cover was tested with linear models. Some parameters in the wet–dark group were log-transformed to counter heteroscedasticity of the models. Impact on cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica* was tested with a quantile regression (R package QUANTREG (Koenker 2018)) because data were not homogenous in variance hence linear regression was not the appropriate test (Cade and Noon 2003). We took the 0.50, 0.75, 0.85 and 0.95 quantiles emphasizing the upper quantiles because after visual inspection of the data we expected *I. glandulifera* to especially restrict maximum cover of other plants. For each quantile regression, standard errors and *p*-values were calculated by bootstrap analysis. Impact of *I. glandulifera* on community composition was tested with a DCA (with downweighting of rare species) and with CCA (VEGAN).

Results

Vegetation characteristics

I. glandulifera occurred in about 80 % of all plots in summer (87 of 114) and in spring (91 of 111, Fig. 2). Especially in spring the cover of *I. glandulifera* was often very low and rarely above 25 %. In summer *I. glandulifera* reached more than 50 % cover in 28 plots. By summer 2017 the cover of *I. glandulifera* changed largely in few plots (Suppl.

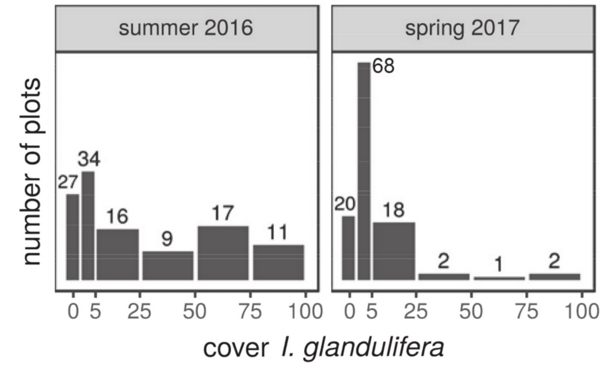


Figure 2. Distribution of cover of *Impatiens glandulifera* in summer 2016 and spring 2017. Shown categories correspond to the Braun-Blanquet scale.

material 1). In summer, *I. glandulifera* plants were higher than the resident vegetation if they reached more than 20 % cover, while in spring *I. glandulifera* was always lower than the resident vegetation (Suppl. material 2). The resident vegetation consisted of in total 128 plant species in summer 2016 and 109 in spring 2017 ranging from 2 to 20 species per plot. None of these plant species was an endangered one. Besides *I. glandulifera* further alien species were recorded: *Lamium argentatum* occurred in 14 plots, sometimes reaching more than 75 % cover. *Fallopia japonica*, *Lysimachia punctata*, *Bidens frondosa* and *Epilobium ciliatum* each occurred in only one plot with always less than 5 % cover. Most frequent native species were typical ones of tall herbaceous vegetation at riparian sites (Fig. 4A, B). Especially *Urtica dioica*, *Filipendula ulmaria*, and *Phalaris arundinacea* in summer, and additionally the geophytes *Ranunculus ficaria* and *Anemone nemorosa* in spring could reach cover of more than 50 %. In spring further early flowering species such as *Corydalis cava*, *Caltha palustris*, *Polygonum bistorta*, *Cardamine amara* and *Alliaria petiolata* occurred.

Relationship between environmental variables, cover of *Impatiens glandulifera* and the resident vegetation

Light (relative PAR) and soil water content spanned nearly the whole gradient from 0–100 %. However, Ellenberg values that correlated with light and soil moisture showed rather smaller gradients (L-value for light 4–7.5, F-value for soil moisture 5.5–9.3) indicating that there were medium light conditions and no sites with dry soils. *I. glandulifera* occurred over the whole range of light and soil water content measured in this study, but in summer it reached high cover mainly at 50–70 % light and 30–40 % soil water content (Fig. 3). The relationship between *I. glandulifera* and light and soil water content was hump-shaped being a typical species reaction on a long environmental gradient (light: linear model, $f(x) = x + x^2 + x^3$, $F_{(3,110)} = 7.221$, $R^2 = 0.142$, $p < 0.001$).

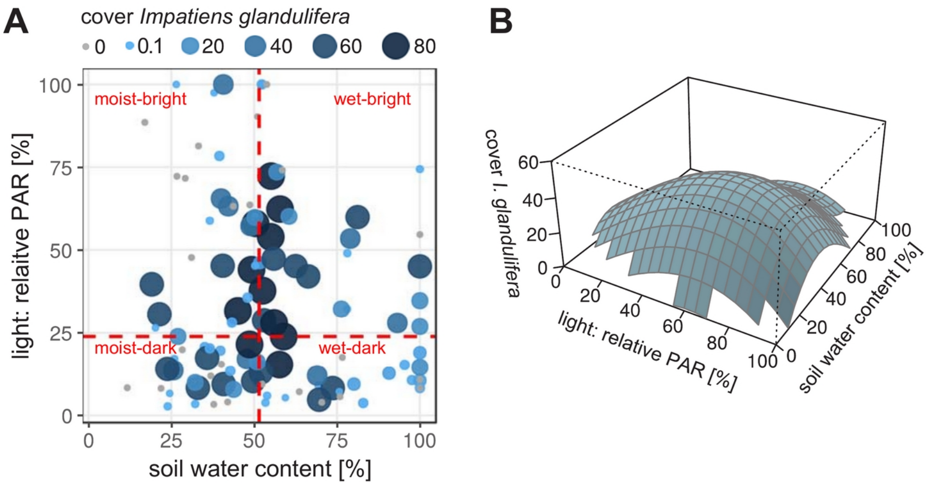


Figure 3. Cover of *Impatiens glandulifera* in summer 2016 in dependence of light and volumetric soil water content. **A** Cover of *I. glandulifera* is represented by point size and color as given in the legend. Grouping the plots into the micro-habitats moist–bright, wet–bright, moist–dark and wet–dark is based on the medians of light and soil water content. **B** Fitted function of the same data shown in 3d-space. f(cover) = light + light^2 + light^3 + water content + water content^3. Linear model, $R^2 = 0.208$, $F_{(5,108)} = 6.928$, $p < 0.001$, n = 114.

Notably soil water content on its own had only low explanatory power (linear model, $f(x) = x + x^3$, $F_{(2,111)} = 4.88$, $R^2 = 0.064$, $p = 0.009$) but in combination with light the R^2 increased to 0.208 (Fig. 3A, B).

The piecewise SEM revealed that in summer 39 % of the variation in the cover of *I. glandulifera* was explained by the environmental variables identified as important by the model selection ($R^2 = 0.39$, Fig. 4A, Suppl. material 4: Table S1). The reaction of *I. glandulifera* to light was unimodal hence the cover was highest at moderate light ($\beta = -0.294$). The cover of *I. glandulifera* was enhanced by a high Ellenberg value N for nutrients and by periodically wet soils (Fig. 4A). In contrast it was reduced by constantly wet soil and cover of the specific tree species *Acer pseudoplatanus*, *Fraxinus excelsior*, and *Alnus glutinosa*. In turn, *I. glandulifera* had no impact on the number of plant species but on plant cover. It strongly reduced the cover of *U. dioica* ($\beta = -0.387$), slightly that of *F. ulmaria* (not significant, $p = 0.073$) and the total cover of the resident vegetation. Besides the effect of *I. glandulifera* the parameters representing the resident vegetation were mainly directly affected by the environmental variables. For example, the number of plant species increased with the number of tree species and strongly decreased with increasing Ellenberg value N. Cover of *U. dioica* was determined by Ellenberg value N, index of constant wet soil and by cover of *A. glutinosa* similarly to *I. glandulifera*.

The piecewise SEM on spring vegetation showed that 30 % of the variation of the *I. glandulifera* cover was explained by the environmental variables identified as important by the model selection (Fig. 4B, Suppl. material 4: Table S1). As in sum-

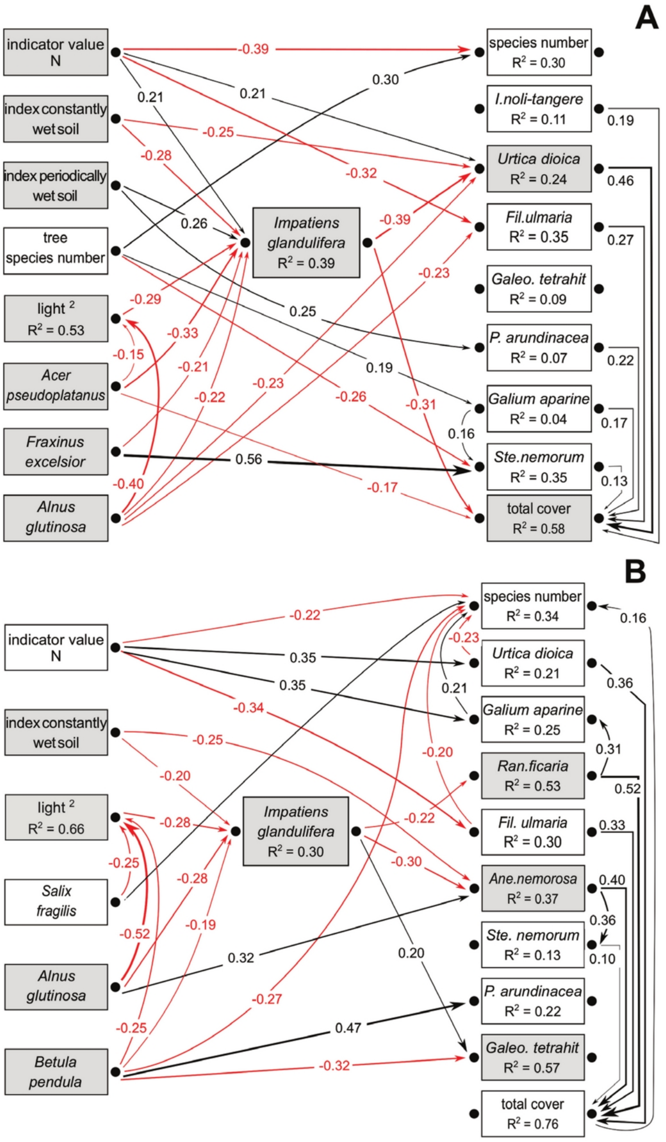


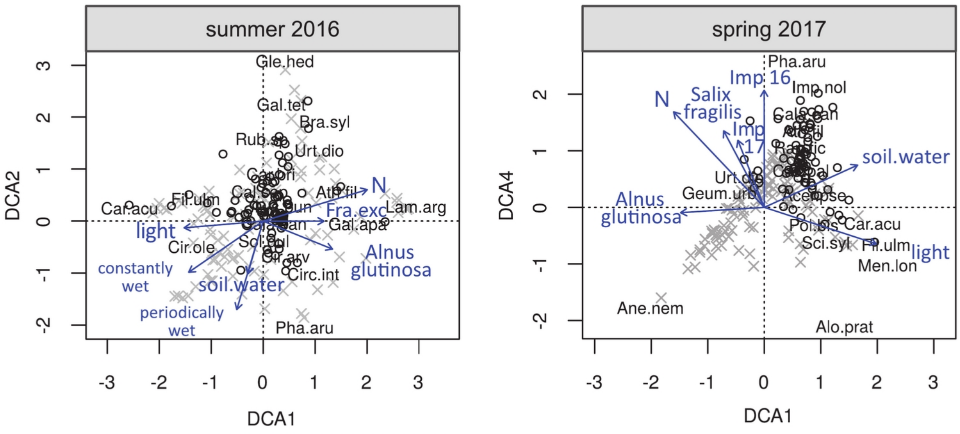
Figure 4. Results of the piecewise structural equation modeling for summer (**A**) and spring (**B**). Arrows show significant correlations between the environmental variables shown to be important by the model selection (Suppl. material 4, Table 1), cover of *Impatiens glandulifera* and resident vegetation parameters. Included resident species are the most frequent ones: *Ranunculus ficaria* (*Ran.ficaria*), *Urtica dioica*, *Filipendula ulmaria* (*Fil.ulmaria*), *Galium aparine*, *Anemone nemorosa* (*Ane.nemorosa*), *Phalaris arundinacea* (*P.arundinacea*), *Galeopsis tetrahit* (*Galeo.tetrahit*), *Stellaria nemorum* (*Ste.nemorum*) and *Impatiens noli-tangere* (*I.noli-tangere*). Arrows show significant correlations, red arrows negative ones, black arrows positive ones. The thicker the arrows, the higher are the standardized regression coefficients (β), which are stated next to the arrows. R^2 values for the component models are given within the boxes of all response variables. Variables that are directly connected to *I. glandulifera* are highlighted by gray colored boxes. For the spring model cover of *I. glandulifera* was log-transformed. n = 114 plots for summer, n = 111 for spring.

mer, constantly wet soils and cover of the tree species *A. glutinosa* and *Betula pendula* reduced the cover of *I. glandulifera*, and reaction to light was unimodal (Fig. 4B). In contrast to summer, periodically wet soils were not found to be important (model selection, Suppl. material 4: Table S1), and the increase of *I. glandulifera* cover with increasing Ellenberg value N was not significant (SEM, Fig. 4B). Also *I. glandulifera* did not affect *U. dioica* and total plant cover, and the cover of *Galeopsis tetrahit* was even slightly increased. However, the cover of *R. ficaria* and *A. nemorosa* were reduced by *I. glandulifera*. The resident vegetation was mainly directly affected by the environmental variables and by interactions between the resident species. For example, the cover of *R. ficaria* and *G. aparine* were positively correlated and the cover of *U. dioica* and *R. ficaria* reduced the species number.

In summer *I. glandulifera* had no impact on plant community composition: The cover of *I. glandulifera* did not correlate with the axes of a DCA of the resident community (p = 0.222, Fig. 5) and was not able to constrain resident community in a CCA (p = 0.116, without figure). In contrast the resident plant community in spring was strongly affected by the cover of *I. glandulifera* of the previous summer 2016 (p < 0.001, DCA; p = 0.052, CCA; Fig. 5), and slightly by current cover in spring 2017 (p = 0.048, DCA; p = 0.551, CCA). In summer and in spring the resident plant community was also shaped by most of those environmental variables important for the cover of *I. glandulifera* (Fig. 5).

Micro-habitat specific impact of *Impatiens glandulifera* on the resident vegetation in summer

With the summer dataset four micro-habitat groups were created reflecting different conditions of light and soil water content (Fig. 3). These groups differed in their plant community composition (DCA p = 0.008, CCA p = 0.001). In each group the cover of *I. glandulifera* ranged from 0 to at least 80 % but its mean differed between groups, being highest in the wet–bright group (Table 2). The impact of *I. glandulifera* on plant cover was different between micro-habitat groups (Table 2, Suppl. material 6: Fig. S2). The cover of *I. glandulifera* reduced the total plant cover in all micro-habitat except for the wet–dark group. The cover of *U. dioica* was reduced in the moist–bright and wet–dark groups, as well as the cover of *F. ulmaria* in the two bright micro-habitats. These were exactly those micro-habitats where the highest average cover of these species was observed (Table 2, Suppl. material 6: Fig. S2). In contrast, the cover of *Phalaris arundinacea* was not negatively affected at all, but its cover slightly increased with the cover of *I. glandulifera* under low light conditions. *I. glandulifera* had no impact on plant species number and Shannon-index in any micro-habitat group. In contrast plant species composition was changed under bright conditions especially with high soil water content. Within the wet–bright micro-habitat for example *Calystegia*



not significant: Imp 16, tree species number, *Acer pseudoplatanus*. **Eigenvalues:** DCA1 0.898, DCA2 0.744, DCA3 0.6436, DCA4 0.7213

not significant: constantly wet, *Betula pendula* **Eigenvalues:** DCA1 0.484, DCA2 0.298, DCA3 0.173, DCA4 0.322

Figure 5. Ordination (DCA) of the resident plant community in summer 2016 and spring 2017. Cover of *I. glandulifera* in summer 2016 (Imp 16) and in spring 2017 (Imp 17) and important environmental variables (Suppl. material 4, Table 1) as well as volumetric soil water content (soil.water) were post-hoc fitted onto the DCA. Significant variables are shown as arrows. Plots are indicated as crosses, species as open circles. Most abundant species are labeled. Not significant environmental variables and Eigenvalues of DCA axes are given in boxes below the plots. n = 114 plots for summer, n = 111 for spring. For abbreviations of the species names see Suppl. material 5: Table S2.

sepium, *Glechoma hederacea*, and *Polygonum bistorta* tended to occur at high cover of *I. glandulifera* (CCA). In contrast *Carex acutiformis*, *Geranium palustre* and also some species of very wet plots as *Galium elongatum* and *Equisetum fluviatile* occurred at low cover of *I. glandulifera* (Suppl. material 7: Fig. S3). Considering all parameters representing the native vegetation *I. glandulifera* had the lowest impact in the wet–dark micro-habitat where also the cover of *I. glandulifera* was lowest.

Discussion

In this field study, we examined the impact of *Impatiens glandulifera* on native vegetation in riparian habitats depending on micro-site conditions and season. We found that the cover of *I. glandulifera* depended on environmental conditions. *I. glandulifera* did not affect resident plant species alpha-diversity at all. Plant cover in contrast was reduced and species composition changed depending on micro-habitat and season. However, the resident vegetation was more strongly shaped by environmental conditions than by the cover of *I. glandulifera*.

Table 2. Micro-habitat specific impact of *I. glandulifera* on the resident vegetation. With the complete dataset and four subsets representing different micro-habitats regarding light (relative PAR) and soil water content (see also Fig. 3) it was tested whether vegetation parameters depend on cover of *I. glandulifera*. Resulting p-values from linear models (total cover, species number, Shannon index), DCA and CCA (species composition) are given. Log-transformations of data are indicated: (log-log) means predictor and response variable transformed, (log) means response variable transformed. For quantile regression (cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica*) 0.50, 0.75, 0.85 and 0.95 quantiles were used (τ). Quantile regressions with ($p < 0.1$) are reported including their regression equation. Bold letters indicate $R^2 > 0.1$ and $p < 0.001$. Number of plots and mean cover of *I. glandulifera* ($\bar{x}_{Imp}$) are given per group. Different letters indicate whether there are differences in the $\bar{x}_{Imp}$ between groups (Kruskal-Wallis Anova, $\chi^2 = 10.6$, df = 3, $p = 0.014$). See Suppl. material 6, 7: Fig. S2 and S3 for plots of the raw data.

parameter	**quantile**	**complete dataset**	**moist–bright**	**wet–bright**	**moist–dark**	**wet–dark**
		n = 114	n = 30	n = 28	n = 27	n = 29
		$\bar{x}_{Imp}$ = 23%	$\bar{x}_{Imp}$ = 22% (ab)	$\bar{x}_{Imp}$ = 39% (a)	$\bar{x}_{Imp}$ = 20% (ab)	$\bar{x}_{Imp}$ = 13% (b)
total cover		$F_{(1,112)} = 27.3$, **$p < 0.001$**, **$R^2 = 0.189$**	$F_{(1,28)} = 28.44$, **$p < 0.001$,** **$R^2 = 0.486$**	$F_{(1,26)} = 9.59$, **$p = 0.005$,** **$R^2 = 0.241$**	$F_{(1,25)} = 8.12$, **$p = 0.009$,** **$R^2 = 0.215$** (log)	$F_{(1,27)} = 3.62$, $p = 0.068$, $R^{2=}0.086$ (log)
cover *Urtica dioica*	τ 0.50					
	τ 0.75		**$p = 0.023$**, f(x) = 63–0.67x			
	τ 0.85	**$p = 0.003$**, f(x) = 63–0.61x	**$p < 0.001$**, f(x) = 87.5–0.90x			
	τ 0.95	$p = 0.052$, f(x) = 87.5–0.67x	**$p < 0.001$**, f(x) = 87.8–0.68x			**$p = 0.022$**, f(x) = 63–0.69x
cover *Filipendula ulmaria*	τ 0.50			$p = 0.056$, f(x) = 21–0.21x		
	τ 0.75	$p = 0.057$, f(x) = 21–0.14x	$p = 0.094$, f(x) = 36–0.41x			
	τ 0.85		**$p = 0.046$**, f(x) = 49–0.56x	**$p = 0.050$,** f(x) = 63–0.62x		
	τ 0.95	**$p = 0.030$**, f(x) = 63 – 0.6x	**$p < 0.001$**, f(x) = 88–1.0x	**$p = 0.032$**, f(x) = 88–0.81x		
cover Phalaris arundi-nacea	τ 0.50	**$p = 0.039$**, f(x) = 0+0.03x			$p = 0.053$, f(x) = 0+0.03x	
	τ 0.75					**$p = 0.013$**, f(x) = 2+0.57x
	τ 0.85					$p = 0.052$, f(x) = 3+0.56x
	τ 0.95	$p = 0.093$, f(x) = 37.5+0.8x				
species number		$F_{(1,112)} = 2.16$, $p = 0.145$, $R^2 = 0.010$	$F_{(1,28)} = 2.54$, $p = 0.122$, $R^2 = 0.051$	$F_{(1,26)} = 2.76$, $p = 0.109$, $R^2 = 0.061$	$F_{(1,25)} = 1.80$, $p = 0.191$, $R^2 = 0.030$	$F_{(1,27)} = 0.04$, $p = 0.846$; $R^2 = -0.036$ (log–log)
Shannon index		$F_{(1,112)} = 0.52$, $p = 0.472$, $R^2 = -0.004$	$F_{(1,28)} = 0.12$, $p = 0.728$, $R^2 = -0.031$	$F_{(1,26)} = 0.05$, $p = 0.833$, $R^2 = -0.037$	$F_{(1,25)} = 2.86$, $p = 0.103$, $R^2 = 0.067$	$F_{(1,27)} = 0.37$, $p = 0.547$, $\mathrm{R}^2 = 0.023$ (log–log)
species composition: DCA		$p = 0.222$	$p = 0.099$	**$p = 0.032$**	$p = 0.715$	$p = 0.401$
CCA		$p = 0.116$	**$p = 0.016$**	**$p = 0.001$**	$p = 0.891$	$p = 0.823$

Patchiness of *Impatiens glandulifera* is associated with environmental conditions

Within our study sites, *I. glandulifera* occurred over a broad range of environmental conditions but it was unevenly distributed within the sites forming invaded and uninvaded patches. Its cover correlated with environmental variables. A positive effect of nutrients and moderate light as well as low importance of soil water content (measured at one point in time), is consistent with literature (Andrews et al. 2005, Čuda et al. 2014). However, we showed that soil water content in combination with light was a good predictor for the cover of *I. glandulifera*, with the cover being highest at moderate light and moderate soil water content. Ellenberg values indicated moreover that constantly high soil moisture had a negative effect on the cover but in summer periodically wet soils were favorable. A high N-supply is also more important in summer than for early establishment in spring. Considering a larger spatial scale, such a patchy occurrence can enable the co-existence of species that would outcompete each other within one patch (Amarasekare 2003). For example, in our study *I. glandulifera* and *U. dioica* coexisted within one study site forming a patchy mosaic.

Impatiens glandulifera had no impact on plant diversity but on plant cover

We found that *I. glandulifera* reduced the cover of the resident vegetation but it had no impact on species composition in summer or on plant species alpha-diversity at all. Thus the resident plant species seem to be able to coexist within *I. glandulifera* stands, albeit reaching only lower cover. Changes in *I. glandulifera* cover from year-to-year as they are reported in literature (Kasperek 2004) and which were also observed in our study, should then enable the resident plants to recover when *I. glandulifera* declines leading to co-existence at a larger time-scale (Stouffer et al. 2018).

I. glandulifera especially reduced the cover of the most dominant native species. Species were most affected in those micro-habitats where their average cover was highest and in each season those species with the highest cover were the most affected ones. These were *Urtica dioica* and *Filipendula ulmaria* in summer, and *Ranunculus ficaria* and *Anemone nemorosa* in spring. We suggest that this is due to competition for space and resources strengthening at high cover. Still, it cannot be ruled out that also less frequent species with lower cover are affected by *I. glandulifera*. Rare occurrence and thus small sample size of a species as well as huge variability result in low statistical power and may lead to an underestimation of the effect of the invader (Davidson and Hewitt 2014).

Similar to other studies comparing plots with and plots without *I. glandulifera*, we are not able to show a causal impact of *I. glandulifera* on native vegetation but only correlations (Hejda and Pyšek 2006). However, in our study the link to environmental conditions can help to disentangle negative correlation because of different spatial niches from negative correlation because of suppression within one spatial niche.

A. nemorosa and *I. glandulifera* could be an example for different spatial niches, because *A. nemorosa* was enhanced by a high cover of *Alnus glutinosa* which in contrast reduced the cover of *I. glandulifera*. *U. dioica* however, seems causally suppressed by *I. glandulifera*. The cover of both species correlated negatively, and according to the SEM they were favored by the same environmental conditions. Experimental studies confirm that *U. dioica* is negatively affected by *I. glandulifera* and that this effect is larger than vice versa (Tickner et al. 2001, Gruntman et al. 2014, Bieberich et al. 2018).

The impact of *Impatiens glandulifera* depended on the micro-habitat

The habitat depending impact of *I. glandulifera* indicates that the impact gets stronger with increasing cover of *I. glandulifera*. This is also indicated by Cockel et al. (2014). In our study the wet–dark micro-habitat with the lowest cover of *I. glandulifera*, was the least affected. The plant species composition was most affected in the wet–bright micro-habitat which had also a strong gradient and highest average cover of *I. glandulifera*. Species that tended to occur only in plots without *I. glandulifera* generally occurred less frequently (for example *Equisetum fluviatile*) while those that tended to occur at high cover of *I. glandulifera* (for example *Glechoma hederacea*) were very common ones.

Micro-habitat specific interactions between native species and an invader can also be due to micro-habitat specific performance of the plant species. If two C-strategists compete for resources, which should be the case with our dominant species, the magnitude of competition is highest under most favorable as well as under most unfavorable environmental conditions (stress-gradient hypothesis, Maestre et al. 2009). In the strongly competitive situation inferiority of the natives in fitness leads to suppression by the invader (MacDougall et al. 2009). We suggest that this can explain the micro-habitat depending impact of *I. glandulifera* on *U. dioica* and *F. ulmaria*. Both natives were most reduced by *I. glandulifera* when they grew under environmental conditions that were, according to the SEM, most favorable for them (*U. dioica* in the moist–bright group and *F. ulmaria* in bright micro-habitats). *U. dioica* was additionally negatively affected by *I. glandulifera* in the wet–dark micro-habitat which was shown by the SEM to be unfavorable for *U. dioica*.

Plant communities in summer and spring were affected differently

Plant species composition in summer was not affected by *I. glandulifera* but in spring it was, despite the fact that *I. glandulifera* plants were smaller than the resident vegetation in spring. The reason could be a seasonally varying allelopathic effect of *I. glandulifera* because it is known, that in spring *I. glandulifera* has a higher content of the allelopathic compound 2-MNQ compared to summer (Ruckli et al. 2014a). In a previous experimental study we showed that *I. glandulifera* has a species-specific allelopathic and competitive impact on native plants especially in the seedlings- and juvenile-stage (Bieberich et al. 2018). Furthermore, cover of *I. glandulifera* from the previous summer 2016 affected species composition in spring while it did not affect the resident community in summer 2016 itself. Allelopathic legacy effects (Grove et al. 2012) may explain this: 2-MNQ could persist in the soil (Ruckli et al. 2014b) and affect early growing plants even before *I. glandulifera* germinates.

Assessment of the invasiveness of *Impatiens glandulifera*

Negative impact on biodiversity and ecosystem functions, processes and services are the criteria to grade an alien species as invasive (Ehrenfeld 2010, Hulme et al. 2013, Barney et al. 2013). German and European Union nature conservation authorities emphasize the impact on diversity and threat to other species (European Union 2014, Nehring et al. 2015). Taking this study and all available ones into account, the impact of *I. glandulifera* on plant species diversity can be rated to be relatively low (Hejda and Pyšek 2006, Hejda et al. 2009, Diekmann et al. 2016, Čuda et al. 2017) even if some studies showed stronger effects (Hulme and Bremner 2006, Cockel et al. 2014, Kiełtyk and Delimat 2019). Indeed, we found a negative impact on the dominant natives, *U. dioica* and *F. ulmaria*, but they are in general very common and widespread in Central Europe and thus not expected to be threatened (Schreiber 1958, Weber 1995). However, suppression of abundant dominant plant species could lead to changes in ecosystem processes as they account for functions such as primary production and nutrient cycles (Grime 1998).

The micro-habitat and season dependent impact of *I. glandulifera* requires that its invasion risk has to be assessed separately for different habitats. We found the lowest impact in the wet–dark micro-habitat which corresponds to alder swamp-forests. The impact was highest at bright conditions, as abandoned meadows, but especially under high soil moisture as found in marshes or open patches of swamp-forests. Special attention should be given to habitats with rare or specialized communities or with distinct spring communities. For nature conservation this is a great opportunity to develop more targeted management strategies of *I. glandulifera* and invasive species in general with vigorous efforts only in selected habitats.

Conclusion

I. glandulifera can reduce the cover of native plants and especially dominant species depending on micro-habitat and season. Against our expectations, we did not find that the vegetation in spring was less affected than in summer. A threat to the native vegetation is unlikely since the impact on plant alpha-diversity was low, which may be due to the patchy occurrence and year-to-year changes in the cover of *I. glandulifera*. However it has to be kept in mind that a reduction of dominant and frequent native plant species could change ecosystem processes. We suggest that the documented small-scale habitat-dependency is also relevant on larger spatial scales. Wet–dark habitats like swamp-forests should be generally least affected by *I. glandulifera* while wet–bright ones like marshes are most affected.

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Supplementary material 1

Year-to-year changes in cover of *Impatiens glandulifera*

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file describing additional data collection, analysis and results

Link: https://doi.org/10.3897/neobiota.57.51331.suppl1

Supplementary material 2

Maximum vegetation height in summer and spring

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file describing additional data collection, analysis and results

Link: https://doi.org/10.3897/neobiota.57.51331.suppl2

Supplementary material 3

Figure S1. Initial model of the piecewise structural equation modeling (SEM) for summer (A) and spring (B)

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file

Explanation note: Arrows show the hypothesized connections between variables the SEM was started with. Within the SEM all additional significant correlations between variables were then identified and the significance of each path was calculated. The results are shown in Figure 4A, B.

Link: https://doi.org/10.3897/neobiota.57.51331.suppl3

Supplementary material 4

Table S1. Result of the automated model selection approach identifying environmental variables that affected the cover of Impatiens glandulifera in summer 2016 and spring 2017

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file containing a table with results

Link: https://doi.org/10.3897/neobiota.57.51331.suppl4

Supplementary material 5

Table S2. Abbreviations of species names as shown in Figure 5

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: xls-table

Link: https://doi.org/10.3897/neobiota.57.51331.suppl5

Supplementary material 6

Figure S2. Micro-habitat specific impact of *I. glandulifera* on the resident vegetation

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file

Explanation note: With the complete dataset and four subsets representing different micro-habitats regarding light (relative PAR) and soil water content (see also Fig. 3) it was tested whether vegetation parameters depend on cover of *I. glandulifera*. Results of all statistical tests are given in Table 2. For total cover, species number, and Shannon index linear models were used. Resulting regression lines are shown if $p < 0.001$. For cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica* quantile regressions were applied using the 0.50, 0.75, 0.85 and 0.95 quantiles. Quantile regression lines are shown in blue color when $R^2 > 0.1$ and $p < 0.001$ or in grey color when $R^2 < 0.1$ and $p > 0.001$.

Link: https://doi.org/10.3897/neobiota.57.51331.suppl6

Supplementary material 7

Figure S3. Micro-habitat specific impact of I. glandulifera on the resident plant species composition

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file

Explanation note: With four data subsets representing different micro-habitats regarding light (relative PAR) and volumetric soil water content (see also Fig. 3) it was tested with DCA and CCA analyses whether the resident species composition changed depending on cover of *I. glandulifera*. In the case of significance cover of *I. glandulifera* is shown as arrow. All statistical results are given in Table 2.

Link: https://doi.org/10.3897/neobiota.57.51331.suppl7

Supplementary material 8

Additional information: information on the published datasets
Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer
Data type: table

Link: https://doi.org/10.3897/neobiota.57.51331.suppl8

Supplementary material 9

Dataset plant cover
Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer
Data type: table

Link: https://doi.org/10.3897/neobiota.57.51331.suppl9

Supplementary material 10

Dataset environment and vegetation characteristics

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer
Data type: table

Link: https://doi.org/10.3897/neobiota.57.51331.suppl10

Supplementary file 1, additional information: Year-to-year changes in cover of *Impatiens glandulifera*

Methods

In summer 2017 (2017-08-17/09-07) the cover of *I. glandulifera* was estimated in all plots according to extended Braun-Blanquet scale. With a linear model it was tested whether the cover of *I. glandulifera* in summer 2017 depended on the cover in summer 2016 (see Materials and Methods section of the manuscript) and between-year changes in cover of *I. glandulifera* were visualized.

Results

Cover of *I. glandulifera* in summer 2017 highly depended on its cover in summer 2016 ($R^2 = 0.698$, $F_{(1,112)} = 262.6$, $p < 0.001$, see figure). In 65 % of the plots cover of *I. glandulifera* changed less than ±10 % from year to year but in 10 % of the plots there was a change larger than 30 %. For example, in one plot cover of *I. glandulifera* declined from 87 % in summer 2016 to 0 % in summer 2017. Overall increase in cover >10 % of *I. glandulifera* occurred more often (24% plots) than decrease < -10 % (12% plots).

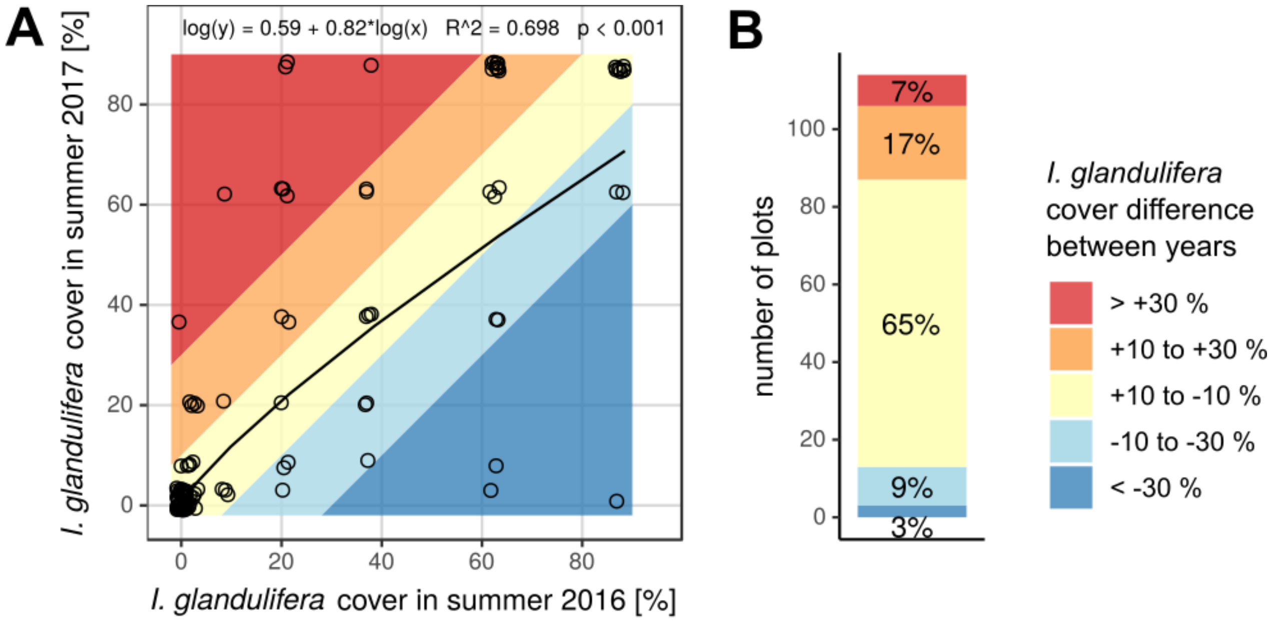


Figure legend. Year-to-year change in cover of *I. glandulifera*. **A** Cover of *I. glandulifera* in summer 2017 versus its cover in summer 2016. Regression was tested with a linear model log-transforming both, predictor and response variable (n = 114). Resulting regression equation, p-value and R^2 are given. To avoid overplotting of points 1 % random noise was added to the data. Color shading indicates difference in the cover of *I. glandulifera* between the two years as given in the legend. The colored areas in the plot are bound by straight lines with slope 1 and y-intercepts 30, 10, -10 and -30 respectively. **B** Number of plots depending on the difference in *I. glandulifera* cover between summer 2017 and summer 2016.

Supplementary file 2, additional information: Maximum vegetation height in summer and spring

Data collection

Maximum height of the resident vegetation and of *I. glandulifera* was recorded per plot within the vegetation surveys (2016-07-12/08-17 in summer, 2017-04-20/05-04 in spring, see Materials and Methods section of the manuscript). The five tallest plant individuals per plot were chosen regardless of the plant species, their height was measured with a folding ruler to the next cm and the mean was calculated. Because in seven plots the plants were pressed to the ground due to rainfall or wind we could not measure vegetation height in these plots and number of replicates decreased to 107 for vegetation height in summer.

Results

In summer *I. glandulifera* plants had a maximum height of 33 - 295 cm, significantly increasing with its own cover. From a cover larger than 20 % *I. glandulifera* plants were higher than the resident vegetation and this difference increased with increasing cover of *I. glandulifera* because the height of resident vegetation was quite constant and independent of *I. glandulifera* cover. In spring maximum height of *I. glandulifera* was 2-16 cm, which was, with one exception, always lower than the resident vegetation. Neither height of *I. glandulifera* nor height of the resident vegetation depended on the cover of *I. glandulifera*.

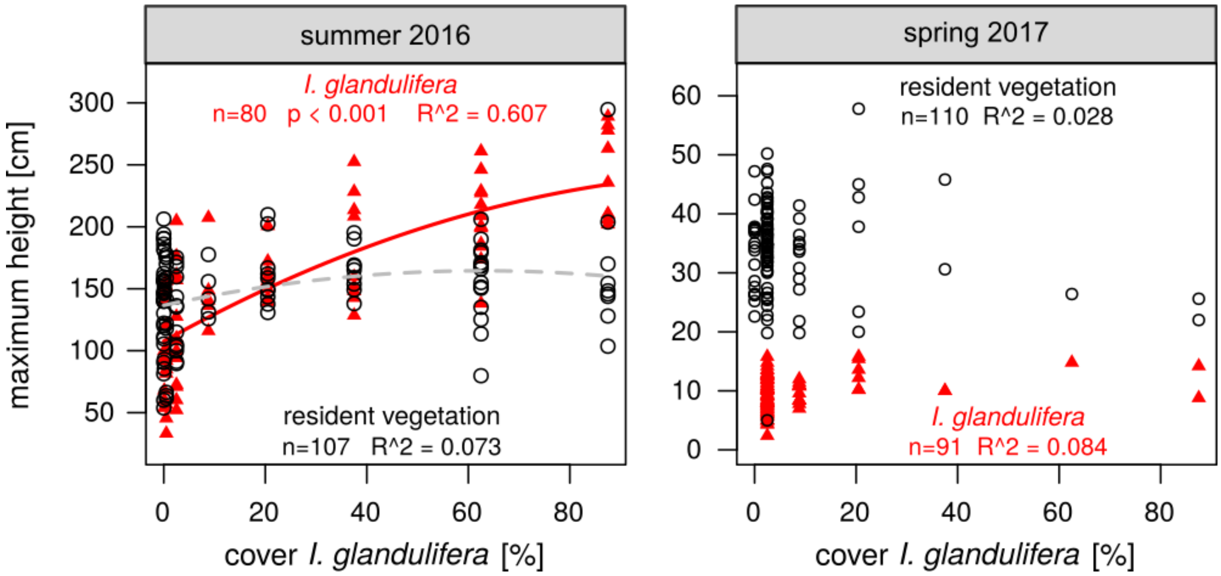
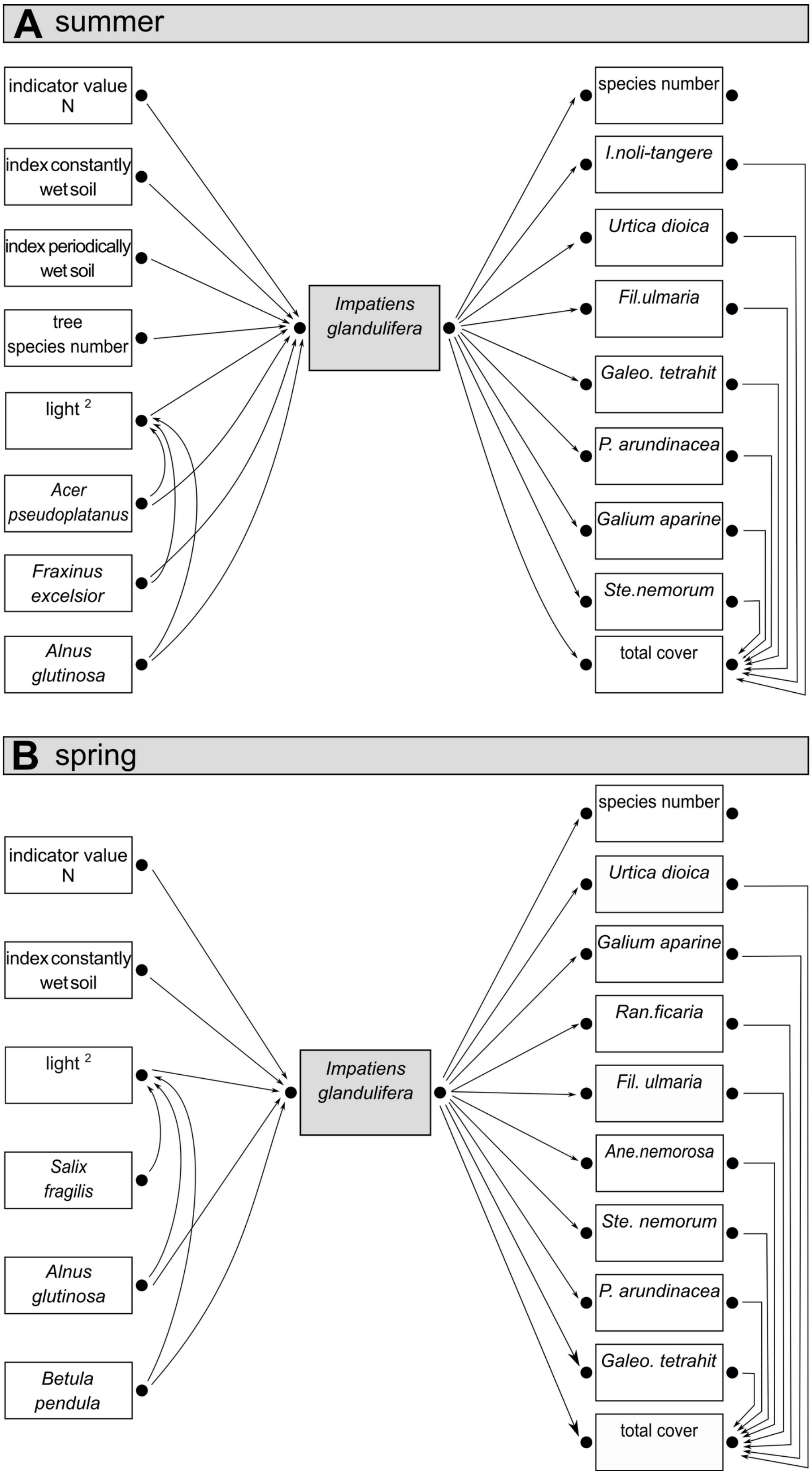


Figure legend. Maximum height of resident vegetation and of *Impatiens glandulifera* in summer 2016 and spring 2017. Dependence of the maximum plant height on cover of *I. glandulifera* was tested with a linear model according the formula $f(x) = ax^2+bx+c$. Number of samples, R^2-values and if $R^2 > 0.1$ p-values are also reported. F-statistic *I. glandulifera* in summer: $F_{2,77} = 61.88$.

Supplementary material 3, Figure S1.

Initial model of the piecewise structural equation modeling (SEM) for summer (A) and spring (B). Arrows show the hypothesized connections between variables the SEM was started with. Within the SEM all additional significant correlations between variables were then identified and the significance of each path was calculated. The results are shown in Figure 4A, B.

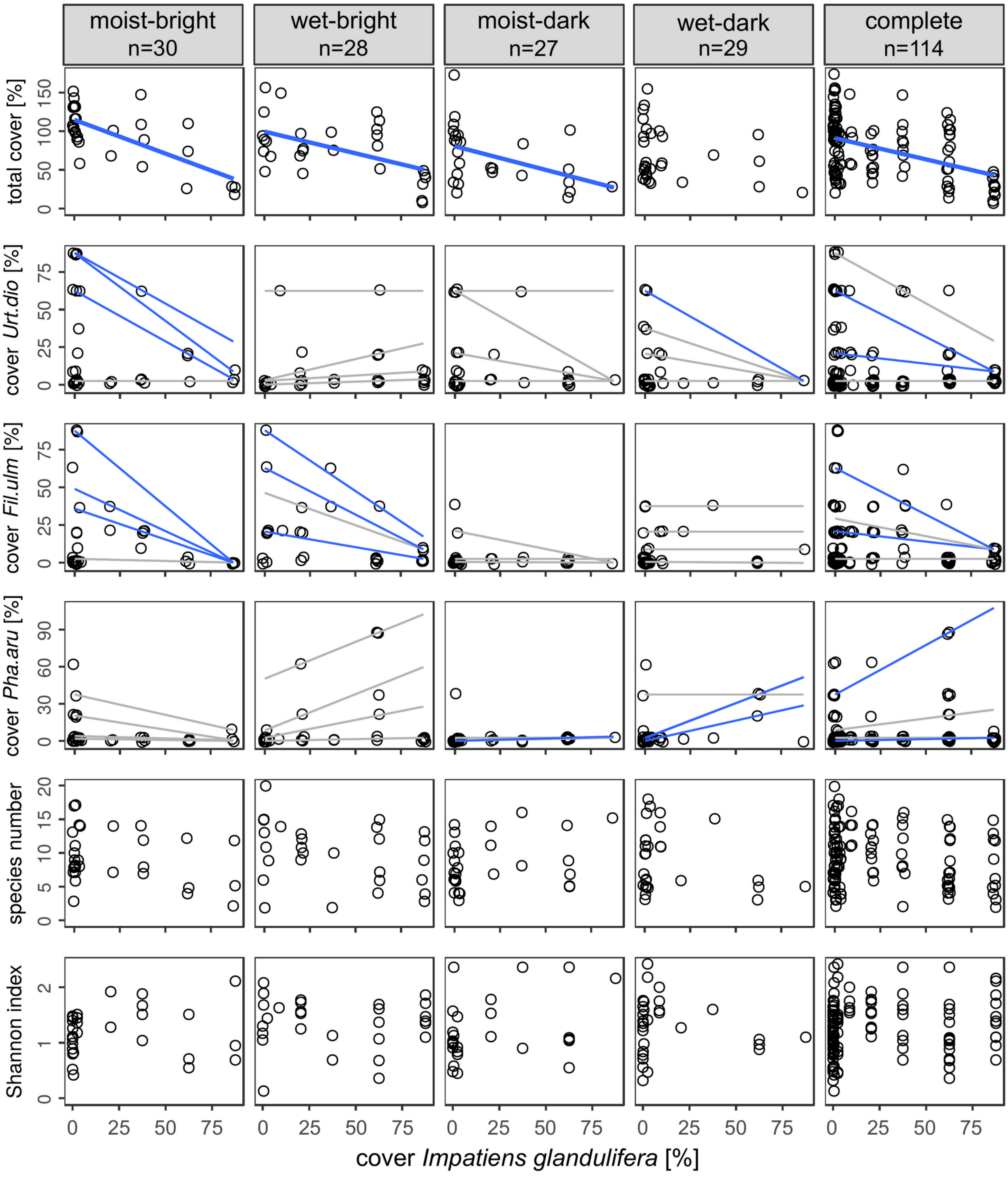


Supplementary file 4: Table 1. Result of the automated model selection approach identifying environmental variables that affected the cover of *Impatiens glandulifera* in summer 2016 and spring 2017. The approach started with one global model stating that the cover of *I. glandulifera* depended on all predictor variables listed in the table (light, indices for constantly wet soils, cover of *Alnus glutinosa* (Aln.glu), Ellenberg indicator value N (eiv N), indicex for periodically wet soils, cover of *Acer pseudoplatanus* (Acer.pse), tree species number, cover of *Fraxinus excelsior* (Fra.exc), *Salix fragilis* (Sal.fra), *Betula pendula* (Bet.pen), soil water content (squared), and Ellenberg value R (eiv R) and using site as random factor. Next a set of models with combinations of all parameters was generated from the global model and weighted by their AICc. In the table, the best models with delta AICc < 2 are shown giving the estimates of the contained predictors, numerator degrees of freedom (df), AICc, delta AICc (delta) and AICc weight. For each predictor the relative importance [%] was calculated as the sum of AICc weights of all those models with a ΔAICc > 2 including the variable. The number (N) of models containing the particular variable is also given.

		predictors														result		
		Intercept	**light ^2**	**index constantly wet**	**Aln. glu**	**eiv N**	**index periodi-cally wet**	**Acer pse**	**tree species number**	**Fra. exc**	**Sal. fra**	**Bet. pen**	**soil water content ^2**	**eiv R**	**df**	**AICc**	**delta**	**weight**
summer 2016 (n = 114)	model 1	0.20	-0.25	-0.25		0.23	0.29	-0.32	0.22	-0.22					10	311.21	0.00	0.21
	model 2	0.18	-0.22	-0.25		0.25	0.28	-0.32		-0.22					9	311.44	0.22	0.19
	model 3	0.19	-0.25	-0.36	-0.25		0.29	-0.23							8	311.48	0.26	0.18
	model 4	0.19	-0.25	-0.33	-0.28		0.33								7	312.81	1.60	0.09
	model 5	0.20	-0.26	-0.34			0.27	-0.30	0.24	-0.19					9	312.92	1.71	0.09
	model 6	0.18	-0.26			0.32	0.28	-0.29	0.23	-0.22					9	313.10	1.89	0.08
	model 7	0.20	-0.27	-0.34	-0.21		0.30	-0.25	0.18						9	313.14	1.93	0.08
	model 8	0.20	-0.26	-0.33			0.31	-0.28	0.23						8	313.15	1.93	0.08
	importance		**100**	**92**	**36**	**48**	**100**	**91**	**54**	**56**								
	N		**8**	**7**	**3**	**3**	**8**	**7**	**5**	**4**								
spring 2017 (n = 111)	model 1	-0.02		-0.30							0.31				5	303.26	0.00	0.27
	model 2	0.16	-0.17	-0.27							0.28				6	303.46	0.19	0.25
	model 3	0.26	-0.27	-0.26	-0.28							-0.25			7	304.53	1.27	0.15
	model 4	0.18	-0.24	-0.3	-0.28										6	305.00	1.74	0.12
	model 5	0.27	-0.28		-0.24	0.24						-0.28			7	305.12	1.85	0.11
	model 6	0.16	-0.18			0.24					0.23				6	305.18	1.91	0.11
	importance		**73**	**79**	**37**	**21**					**63**	**25**						
	N		**5**	**4**	**3**	**2**					**3**	**2**						

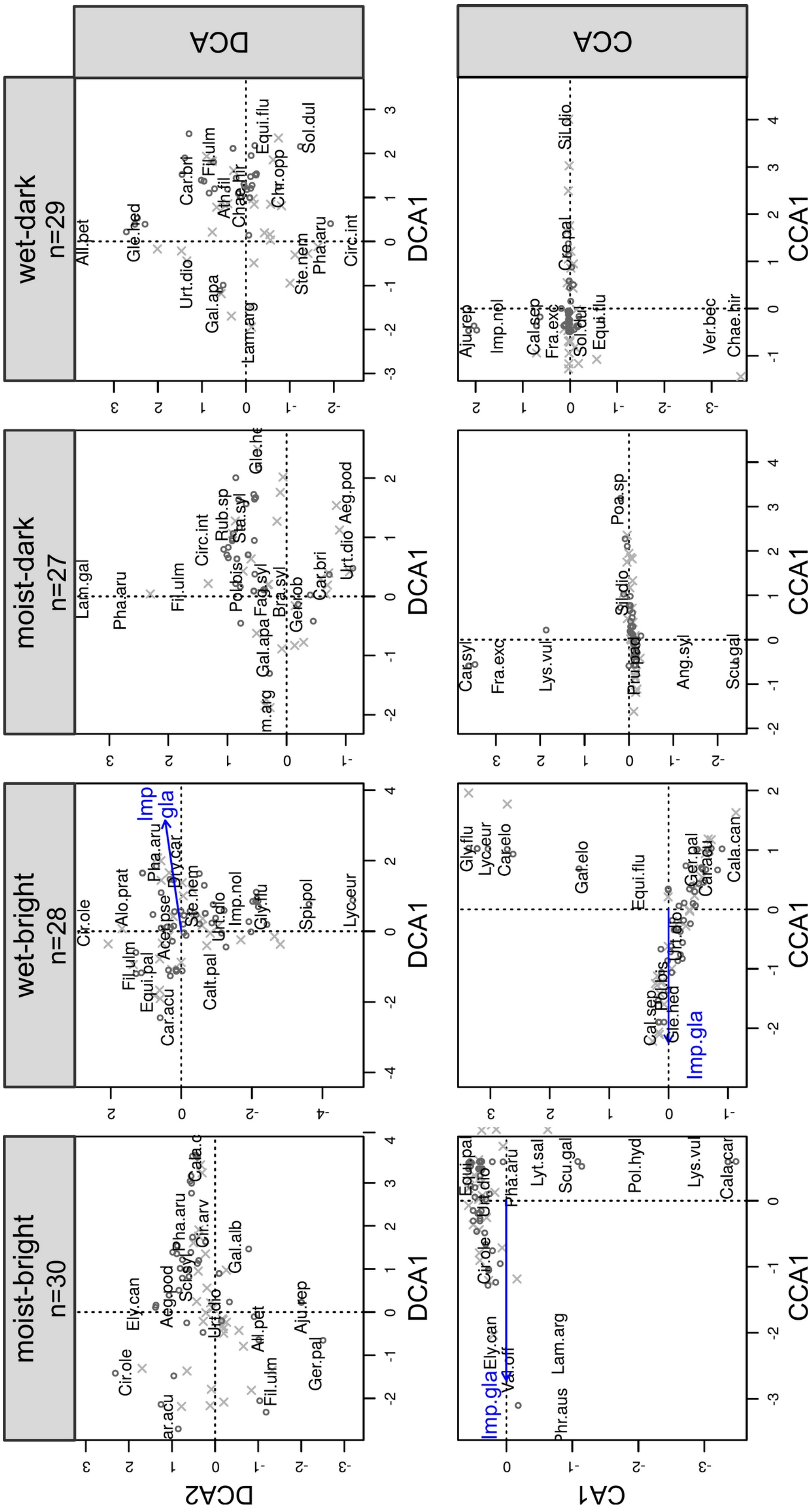
Supplementary material 6, Figure S2.

Micro-habitat specific impact of *I. glandulifera* on the resident vegetation. With the complete dataset and four subsets representing different micro-habitats regarding light (relative PAR) and soil water content (see also Fig. 3) it was tested whether vegetation parameters depend on cover of *I. glandulifera*. Results of all statistical tests are given in Table 2. For total cover, species number, and Shannon index linear models were used. Resulting regression lines are shown if p < 0.001. For cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica* quantile regressions were applied using the 0.50, 0.75, 0.85 and 0.95 quantiles. Quantile regression lines are shown in blue color when R2 > 0.1 and p < 0.001 or in grey color when R2 < 0.1 and p > 0.001.



Supplementary material 7, Figure S3.

Micro-habitat specific impact of *I. glandulifera* on the resident plant species composition. With four data subsets representing different micro-habitats regarding light (relative PAR) and volumetric soil water content (see also Fig. 3) it was tested with DCA and CCA analyses whether the resident species composition changed depending on cover of *I. glandulifera*. In the case of significance cover of *I. glandulifera* is shown as arrow. All statistical results are given in Table 2.



Supplementary file 8, additional information: information on the published datasets

The datasets Supplementary file 9 and Supplementary file 10 include all data used for analysis.

Supplementary file 9, dataset plant cover

This dataset contains all data of plant cover. All plant species of the herb layer were recorded in summer 2016 and spring 2017, all species of the tree and shrub layer in summer 2017. In summer 2017 additionally the cover of *I. glandulifera* was recorded, but no other herb species. Each row of the dataset is the record of one species, its cover and information on location, date and vegetation layer.

explanation of column names:

plot.id	unique identifier of each plot foreign key to the environment and vegetation characteristics dataset
X_WGS84	X-coordinates of the plots, under the WGS84 system
Y_WGS84	Y-coordinates of the plots, under the WGS84 system
site	field site levels: "Ludwig" (Ludwigschorgast), "Neu" (Neunkirchen), "Weid" (Weidenberg), "Peg" (Pegnitz), "Waisch" (Waischenfeld)
layer	vegetation layer, levels "herb" (herb layer), "shrub" (shrub layer), "tree" (tree layer)
season	season of vegetation survey, "summer" or "spring"
year	year of vegetation survey, "2016" or "2017"
date	date of vegetation survey per plot
species.full	full species name, written-out genus, species and author
species.code	abbreviation of the species name
cover class	cover of each species, estimated according extended Braun-Blanquet scale
cover	cover of each species (cover class), converted into numeric values [%] according extended Braun-Blanquet scale

Supplementary file 10, dataset environment and vegetation characteristics

For each plot this dataset contains the (micro-)habitat, environmental variables and vegetation characteristics as total resident plant cover, diversity indices, and vegetation height.

Ellenberg indicator values were calculated per plot from the resident herb layer vegetation in summer, based on species presence not weighted by cover. Cover sums and diversity indices were calculated for summer and spring based on the vegetation dataset (Supplementary file 9). Vegetation height was calculated as mean of the height of the five tallest plants in the plot, regardless of the plant species (Supplementary file 2).

The term "resident vegetation" refers to all species except *Impatiens glandulifera*.

explanation of column names:

plot.id	unique identifier of each plot primary key within this dataset and foreign key to the plant cover dataset
X_WGS84	X-coordinates of the plots, under the WGS84 system
Y_WGS84	Y-coordinates of the plots, under the WGS84 system
site	field site levels: "Ludwig" (Ludwigschorgast), "Neu" (Neunkirchen), "Weid" (Weidenberg), "Peg" (Pegnitz), "Waisch" (Waischenfeld)
habitat	main habitat of the study site, see Table 1 in Materials and Methods levels: "forest" (alder / alder-swamp forest in Ludwig and Neu), "meadow" (abandoned meadow in Weid, Peg and Waisch)
micro.habitat	groups representing different micro-habitats regarding light and soil moisture; built by dividing the dataset according to the median of light (23.9 % PAR) and volumetric soil moisture (51.5 %). levels: "drybright", "wetbright", "drydark", "wetdark"
moist	volumetric soil moisture [%], measured with a SM-150 sensor (Delta-T Devices), median of four measurements per plot
par	light situation per plot, as relative photosynthetic active radiation [%], measured with a PAR-Sensor (licor), median of four point records within the plots divided by the particular logged reference matching in time
L	Ellenberg indicator value for light
F	Ellenberg indicator value for soil moisture
constant.wet	index for constantly wet soil, calcutated from Ellenberg indicator value F
periodic.wet	index for periodically wet soil, calcutated from Ellenberg indicator value F
R	Ellenberg indicator value for soil reaction
N	Ellenberg indicator value for soil nutrients
T	Ellenberg indicator value for temperature

cover.sum.r.summer	total COVER [%] of the RESIDENT vegetation in SUMMER, calculated as SUM of the cover off all species in the plot
cover.sum.r.spring	total COVER [%] of the RESIDENT vegetation in spring, calculated as SUM of the cover off all species in the plot
cover.total.tree	TOTAL COVER [%] of the TREE layer, estimated according extended Braun-Blanquet scale
n.spec.r.summer	NUMBER of SPECIES of the RESIDENT vegetation in SUMMER, derived from the vegetation dataset
n.spec.r.spring	NUMBER of SPECIES of the RESIDENT vegetation in SPRING, derived from the vegetation dataset
n.spec.tree	NUMBER of SPECIES of the TREE layer, derived from the vegetation dataset
H.r.summer	Shannon-index H of the RESIDENT vegetation in SUMMER, calculated from the vegetation dataset with vegan::diversity()
H.r.spring	Shannon-index H of the RESIDENT vegetation in SPRING, calculated from the vegetation dataset with vegan::diversity()
height.summer.i	maximum vegetation HEIGHT of IMPATIENS GLANDULIFERA in SUMMER
height.summer.r	maximum vegetation HEIGHT of the RESIDENT vegetation in SUMMER
height.spring.i	maximum vegetation HEIGHT of IMPATIENS GLANDULIFERA in SPRING
height.spring.r	maximum vegetation HEIGHT of the RESIDENT vegetation in SPRING

Supplementary material 9, Dataset plant cover

This dataset is to long for printing. It is online available under:
https://doi.org/10.3897/neobiota.57.51331.suppl9

Supplementary material 10, Dataset environment and vegetation characteristics

This dataset is to long for printing. It is online available under:
https://doi.org/10.3897/neobiota.57.51331.suppl10

5.3 Manuscript 3

Invasive *Impatiens glandulifera*: a driver of changes in native vegetation

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(* equal contributions)

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Own contribution: idea and concept: 30 %,, design: 70 %, search for study sites: 100 %, field work and data collection: 70 % (not including the help of 5 student workers), supervision of a master student: 60 %, data curation: 100 %, data analysis and figures of the manuscript: 100 %, writing original draft of the manuscript: 90 %, review and editing of the manuscript 40 %, corresponding author

Authors contribution: JB, ML, and HF had the idea. JB, SM, HF, and ML developed the study design. JB and SM performed the experiments and collected the data (with the help of 5 student workers, see acknowledgment). JB and SM analyzed, and visualized the data and wrote the initial draft. JB curated the data, prepared the figures and analyses as shown in the manuscript. JB, SM, ML, and HF reviewed the manuscript. ML and HF supervised the study and provided resources.

Author contribution adopted literally from the manuscript:
JB: Conceptualization (equal), Data Curation, Formal Analysis (leading), Investigation (leading), Methodology (equal), Project Administration (equal), Visualization (leading), Writing – Original Draft Preparation (leading), Writing – Review & Editing (equal)
SM: Formal Analysis (supporting), Investigation (supporting), Methodology (equal), Visualization (supporting), Writing – Original Draft Preparation (supporting), Writing – Review & Editing (supporting)
HF: Conceptualization (equal), Methodology (equal), Project Administration (equal), Resources (supporting), Supervision (equal), Writing – Review & Editing (equal)
ML: Conceptualization (equal), Methodology (equal), Project Administration (equal), Resources (leading), Supervision (equal), Writing – Review & Editing (equal)

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ORIGINAL RESEARCH

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Invasive *Impatiens glandulifera*: A driver of changes in native vegetation?

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Abstract

Biological invasions are one of the major threats to biodiversity worldwide and contribute to changing community patterns and ecosystem processes. However, it is often not obvious whether an invader is the "driver" causing ecosystem changes or a "passenger" which is facilitated by previous ecosystem changes. Causality of the impact can be demonstrated by experimental removal of the invader or introduction into a native community. Using such an experimental approach, we tested whether the impact of the invasive plant *Impatiens glandulifera* on native vegetation is causal, and whether the impact is habitat-dependent. We conducted a field study comparing invaded and uninvaded plots with plots from which *I. glandulifera* was removed and plots where *I. glandulifera* was planted within two riparian habitats, alder forests and meadows. A negative impact of planting *I. glandulifera* and a concurrent positive effect of removal on the native vegetation indicated a causal effect of *I. glandulifera* on total native biomass and growth of *Urtica dioica*. Species α-diversity and composition were not affected by *I. glandulifera* manipulations. Thus, *I. glandulifera* had a causal but low effect on the native vegetation. The impact depended slightly on habitat as only the effect of *I. glandulifera* planting on total biomass was slightly stronger in alder forests than meadows. We suggest that *I. glandulifera* is a "back-seat driver" of changes, which is facilitated by previous ecosystem changes but is also a driver of further changes. Small restrictions of growth of the planted *I. glandulifera* and general association of *I. glandulifera* with disturbances indicate characteristics of a back-seat driver. For management of *I. glandulifera* populations, this requires habitat restoration along with removal of the invader.

KEYWORDS

causality of impact, context-dependency, plant invasion, planting experiment, removal experiment, riverside vegetation

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Feldhaar and Lauerer have contributed equally.

1 | INTRODUCTION

Biological invasions are an important aspect of anthropogenic global change and are considered to be one of the major threats to biodiversity worldwide (Sala et al., 2000). A well-documented impact of species invasions is to reduce native biodiversity, species abundances, change community patterns, and ecosystem processes such as nutrient cycling in invaded communities (Dogra et al., 2010; Ehrenfeld, 2010; Vilà et al., 2011). However, it is difficult to disentangle cause and effect of an invasion. An alien species can invade an intact ecosystem and cause changes there, thus be the "driver" of the changes (Bauer, 2012; Didham et al., 2005; MacDougall & Turkington, 2005). Alternatively, invasion may be facilitated by earlier ecosystem changes, such as global warming, land use change, or disturbances. Then the invasion is only a symptom, and the invader a "passenger" of the underlying change (Bauer, 2012; Didham et al., 2005; MacDougall & Turkington, 2005). Drivers and passengers are the extreme positions of a continuum, and several invasive species rather fall in-between those categories (Bauer, 2012). Such "back-seat drivers" benefit from previous changes, but once established they become drivers of further changes (Bauer, 2012). Another challenge in assessing the impact of an invader are context-dependencies. Invasion can, for example, depend on ecosystem, invasion stage, or species traits (Kueffer et al., 2013). The more an invader is a passenger of changes, characteristics of the native ecosystem such as habitat conditions and species composition of the receiving community should influence the outcome of invasion and lead to differences between habitats. Invasion of a passenger is rather unlikely the more it relies on previous ecosystem changes. Knowledge about driver and passenger characteristics of an invader and context-dependencies is important to understand invasion processes and to develop more targeted management plans.

Impatiens glandulifera originating from the Himalaya mountains is a very common invasive species in Central Europe. Rapid spread and population growth of this annual species are enabled by a large number of seeds and their effective dispersal. Seeds are catapulted over several meters due to an explosion mechanism of the capsule and subsequently often transported by water flows (Beerling & Perrins, 1993). *I. glandulifera* invaded various wet habitats such as mesotrophic grass- and woodlands but increasingly also forests and ruderal sites outside of the riparian zone (Beerling & Perrins, 1993; Čuda et al., 2017; Čuda et al., 2020; Pyšek & Prach, 1993, 1995). *I. glandulifera* is capable of suppressing native plants because of a high competitive effect along with a vigorous growth and the release of allelopathic substances such as 2-methoxy-1,4-naphthoquinone as shown in experimental studies (Bieberich et al., 2018; Gruntman et al., 2014; Loydi et al., 2015; Power & Sánchez Vilas, 2020; Ruckli et al., 2014; Vrchotová et al., 2011). Another factor benefiting *I. glandulifera* is, for example, release from natural enemies such as insect herbivores and parasitic rust fungi (Tanner et al., 2014). Under field conditions, it can form dominant stands with a height of up to three meters (Beerling & Perrins, 1993; Bieberich et al., 2020). Nonetheless, the impact of *I. glandulifera* on native plant communities is rated ambiguously, and it is not clear whether the impact is causal, thus *I. glandulifera* being a driver of ecosystem changes. Comparing invaded and uninvaded sites Hejda and Pyšek (2006), Hejda et al., (2009), and Diekmann et al., (2016) found only weak, but Kiełtyk and Delimat (2019) found strong differences of plant diversity and composition. From a previous study, we know that *I. glandulifera* and native vegetation cover correlated negatively, and the correlation depended on environmental conditions at a particular site (Bieberich et al., 2020). However, with these observational approaches, causality of impact is difficult to address (Hejda & Pyšek, 2006; Kumschick et al., 2015; Stricker et al., 2015). Some studies—also with ambiguous results—experimentally removed the invader *I. glandulifera* (Cockel et al., 2014; Čuda et al., 2017; Hejda & Pyšek, 2006; Hulme & Bremner, 2006). Such removal experiments can help to identify whether an effect is causal (Kumschick et al., 2015; MacDougall & Turkington, 2005). If the invader is a driver of changes, removal should rescue the state prior to invasion. However, also removal experiments have some drawbacks (Hulme & Bremner, 2006; Kumschick et al., 2015; Stricker et al., 2015). Response of the native community could also be caused by the disturbance of the treatment itself. Removal of any other, even native, species could have the same effect, for example, because this may lead to higher resource availability. The process of native community recovery could also take longer time than the study, and thus effects may not become visible yet, especially if there are legacy effects of the invasion. An effective method to study causal effects is to add the invader to the native community (Stricker et al., 2015). However, this is rarely implemented under field conditions because then, a careful handling of the invader is required.

The aim of this study was to investigate whether *I. glandulifera* has a causal negative impact on the native vegetation and whether this impact depends on the habitat. Due to its uneven distribution within one field site, *I. glandulifera* can be transplanted from an invaded patch into an uninvaded patch, without introducing the species to a new site. To disentangle cause and effect of invasion, we combined the classical approaches to compare invaded and uninvaded patches, and to remove *I. glandulifera* from invaded patches, with transplanting *I. glandulifera* into uninvaded patches. Thus, the transplanting represents a control for removal and vice versa. To test for habitat-dependence, we replicated this experimental approach in two different riverside habitat types, alder forests and meadows. We expect that *I. glandulifera* has a negative impact on the native vegetation, specifically on α-diversity, biomass and species composition of the resident vegetation, and on individual plant growth of resident species. For the latter, *Urtica dioica* was chosen as target species because it is one of the most frequent native co-occurring species of *I. glandulifera* in both habitats. Because of the high competitive and allelopathic effect of *I. glandulifera* on neighboring plants, especially native plant growth should be affected even within a short time leading to changed species abundances and plant performance at the spatial scale of the experimental plots. If *I. glandulifera* is a driver of changes having a causal impact, (a) removal of *I. glandulifera* is expected to have a positive (recovery) effect on the native vegetation, and (b) planting *I. glandulifera* into formerly uninvaded plots should have a negative impact on the native vegetation. Additionally, (c) establishment of planted *I. glandulifera* and impact of planting and removal are expected to depend on the habitat because plant growth and species interactions are shaped by environmental conditions. If *I. glandulifera* has no causal impact on the resident vegetation, its removal should have no recovery effect, and its planting should have no negative impact on the resident vegetation. The native vegetation could still differ between invaded and uninvaded patches if *I. glandulifera* has no causal impact but is only a passenger of changes.

2 | MATERIALS AND METHODS

2.1 | Implementation of the field experiment

Field studies were conducted at four riverside sites around Bayreuth, Germany, also used in a previous study (Bieberich et al., 2020). Among them were two open sites comprised of abandoned meadows with tall herbaceous vegetation (Waischenfeld 49°49.98′N 11°20.17′E, Weidenberg 49°56.95′N 11°42.15′E) and two alder swamp forests, also with tall herbaceous vegetation (Ludwigschorgast 50°6.66′N 11°35.20′E, Neunkirchen 49°55.20′N 11°38.05′E). Each site consisted of a mosaic of patches with and without *I. glandulifera*.

To choose positions for the plots, a grid of 20 m × 20 m was laid over each study site (Figure 1a), ten meters shifted to the grid of our previous study (Bieberich et al., 2020). In March to April 2016, all grid intersection points were checked for suitability to conduct either removal or planting of *I. glandulifera* there (Figure 1a). Suitability was predefined as an area of 2 m × 4 m homogeneous herbaceous vegetation, in spring either invaded by *I. glandulifera* with 5%–40% cover for the removal trial or uninvaded with a maximum of five *I. glandulifera* plants for the planting trial. Additionally, suitable positions in alder forests had to have a more or less closed canopy and positions in meadows had to be not covered by trees as far as possible. Out of all suitable positions, four positions per study site and trial (planting, removal) were randomly chosen for usage. On each chosen position, a pair of 1.5 m × 1.5 m plots was established with a gap of 0.5 m between the single plots. One randomly chosen plot of the pair was left unchanged either as an invaded control or an uninvaded control, respectively (Figure 1b). Within the second plot of the pair, occurrence of *I. glandulifera* was manipulated in May (2016-05-09/27). For the removal treatment, all *I. glandulifera* plants were removed. Plots were checked and, if necessary, removal repeated every other week for the first 2 months and then at larger intervals since only few *I. glandulifera* plants emerged. Initially removed *I. glandulifera* had a stem length of 21 ± 12 cm mean ± *SD* ($n = 65$ with five plants randomly chosen and measured per plot) and in total 6–87 g dry biomass of *I. glandulifera* was removed per plot (mean 26 g, $n = 13$ plots). For the planting treatment, 63 *I. glandulifera* plants, corresponding to about 5%–10% cover in spring, were transplanted into each plot with always 20 cm distance between individual plants (mean stem length 19 ± 5 cm, $n = 65$ with five plants randomly chosen and measured per plot). Transplanted individuals were always collected and transplanted within the same study site. After about 10 days, we checked whether the transplanted individuals had grown and replaced failed individuals once. We wanted to achieve that the uninvaded plots and plots where *I. glandulifera* was removed were free of *I. glandulifera* over summer, while naturally growing and planted *I. glandulifera* developed 15%–75% cover. This

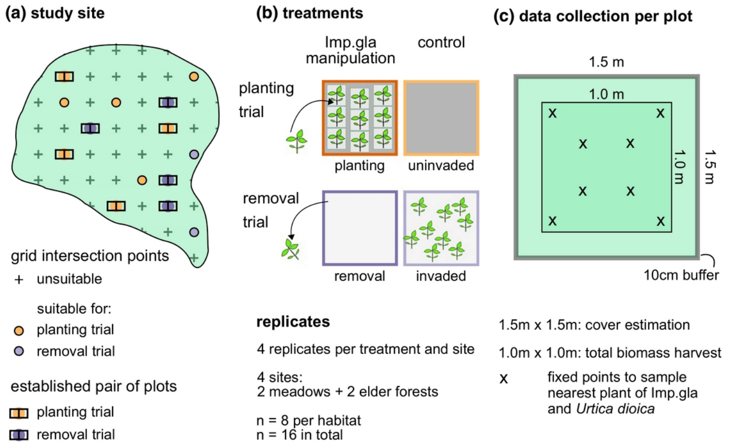

FIGURE 1 Study design. (a) Concept of selection of suitable plot positions along a grid laid over each study site. From the suitable positions, it was randomly chosen which positions were used to either conduct the planting or the removal trial there. (b) In total, there were four treatments: planting of *I. glandulifera* within uninvaded plots and a paired uninvaded control, removal of *I. glandulifera* from invaded plots and a paired invaded control. (c) Data collection within each plot: cover and vegetation height were gathered within the total 2.25 m^2 plot; total biomass was harvested within the central 1 m^2; individual plants of *I. glandulifera* and *U. dioica* were harvested within the total plot except a 10-cm buffer margin, whereby those eight plants being nearest to the eight fixed points in the plot were sampled

moderate cover of *I. glandulifera* was aimed for because a very high cover of *I. glandulifera* in the removal trial could make the measurement of a recovery effect difficult. For a recovery effect in particular, a certain amount of native vegetation is required. During summer, in total three pairs of plots belonging to the removal trial were destroyed by fallen trees and wild boars in three different study sites. This resulted in $n = 13$ for the removal trial and $n = 16$ pairs of plots for the planting trial.

Effect of the *I. glandulifera* manipulations on the resident vegetation was evaluated in autumn 2016. To study the effect on traits of individual plant growth, *U. dioica* was chosen as native target species because it was the only species that was sufficiently abundant in all sites and treatments. When *I. glandulifera* or *U. dioica* occurred in a plot, their cover was estimated within the total plot on 2016–08-19/25 according to extended Braun-Blanquet scale which was afterward converted into the numerical values 0, 0.1, 0.5, 2.5, 8.8, 20.5, 37.5, 62.5, 87.5 percent cover (Braun-Blanquet, 1964; Reichelt & Wilmanns, 1973). Data on vegetation height and biomass were collected on 2016–08-30/10-04. Maximum vegetation height of the resident vegetation was recorded with a folding ruler as mean height of the five highest plants in the plot, regardless of plant species. In one pair of plots, the plants were not totally upright due to rainfall or wind, and thus we could not measure vegetation height. When occurring, eight individual plants each of *I. glandulifera* and *U. dioica* were harvested per plot. The respective plants nearest to one of eight fixed points in the plot were chosen whereby the outermost 10 cm margin of the plot was ignored (Figure 1c). In some cases, there were only six or seven plants of *U. dioica* in a plot, and accordingly sample size decreased. Of each sampled plant, stem length was measured with a folding ruler and dry weight of the vegetative plant parts and the infructescence were measured separately. Within the central 1 m^2 of each plot, all vascular plants were harvested and the biomass sorted by species. Species were determined using standard literature (Eggenberg & Möhl, 2013; Jäger, 2017; Jäger et al., 2013; Schmeil et al., 2011), and total dry weight was recorded per species. To measure dry weight, all plant material was dried at 90°C for 2 days and weighed to the nearest 0.01 g (weighing scale Mettler PM 4,600). Thus, all biomass data, hereafter, are given as dry mass.

2.2 | Statistical analysis

All statistical analyses were done with the software package R 4.2.0 (2020–06–22), R Studio 1.3.959. In addition to the core packages, lme4 (Bates et al., 2015), vegan (Oksanen et al., 2019), car (Fox & Weisberg, 2019), and broom (Robinson et al., 2020) were used for statistical analyses, plyr (Wickham, 2011), dplyr (Wickham et al., 2020), and reshape2 (Wickham, 2007) for data handling, ggplot2 (Wickham, 2016), cowplot (Wilke, 2019), and RColorBrewer (Neuwirth, 2014) for visualization. Linear models were used to test whether total biomass, cover, individual plant biomass, and stem length of *I. glandulifera* depended on whether *I. glandulifera* was planted or grew naturally and whether in the habitat meadow or alder forest. In the case of individual plant biomass and stem length ($n = 8$ per plot) plot was applied as random factor. Species number, Shannon index, total biomass, and vegetation height of the resident vegetation (all species except *I. glandulifera*) were compared between invaded and uninvaded control treatments and between habitats using linear models. Likewise, total biomass, cover, stem length, vegetative biomass, and infructescence biomass of *U. dioica* were compared between invaded and uninvaded control situations with linear models, and additionally total biomass of the most frequent native species with Mann-Whitney-*U* tests. However, habitat-dependency could not be tested with these parameters because sample size per habitat was too low. In the case of individual plant growth of *U. dioica* mean values per plot were used making the use of plot as random factor unnecessary. For all linear models, either pair of plots or study site was applied as random factor whenever possible. In some cases, it was not possible to use the random factor because its variance was estimated zero. Use of error distribution family was decided per parameter based on visual inspection of the model residuals, resulting in generalized linear models where necessary.

To quantify impact intensity of manipulation of *I. glandulifera* within each pair of plots, the relative interaction index RII was calculated (Armas et al., 2004; Gruntman et al., 2014) comparing manipulation and control, according to the equation (manipulation - control)/(manipulation + control). RII is bound to the range from −1, to + 1, is symmetrical around zero (no effect), and the algebraic sign shows whether the effect of the manipulation is negative or positive. Because of these properties, RII enables further analysis with classical statistical methods (Armas et al., 2004). Planting of *I. glandulifera* is expected to have a negative impact on the resident vegetation, indicated by a negative RII, while removal of *I. glandulifera* is expected to have a positive effect, indicated by a positive RII. RII was applied for the above-mentioned parameters of the resident vegetation and of *U. dioica* and the biomass of the most frequent species. For *U. dioica* individual plant biomass and stem length, RII was calculated with the mean values of 6–8 plants per plot. For each parameter, it was tested whether impact intensity RII of *I. glandulifera* planting and removal in the two habitats differs from zero using a one-sample Wilcoxon test. Additionally, we used linear models to test whether the RII of species number, Shannon index, total biomass and vegetation height depended on the trials (planting and removal of *I. glandulifera*), the habitats (meadow and alder forest), and their interaction term.

To analyze whether plant species composition and abundance differ between the natural control situations (uninvaded or invaded) and whether *I. glandulifera* manipulations (removal or planting) have an effect on them, multivariate analyses were performed with biomass data of all species. For visualization, a nonmetric multidimensional scaling (NMDS) was performed based on Bray-Curtis dissimilarity index (max. 80 numbers of random starts, 3 dimensions, package vegan). Differences between treatments, habitats, and their interaction were tested with PERMANOVA analyses also based on Bray-Curtis dissimilarities (command adonis of package vegan). Study sites were given as groups within which permutations were constrained.

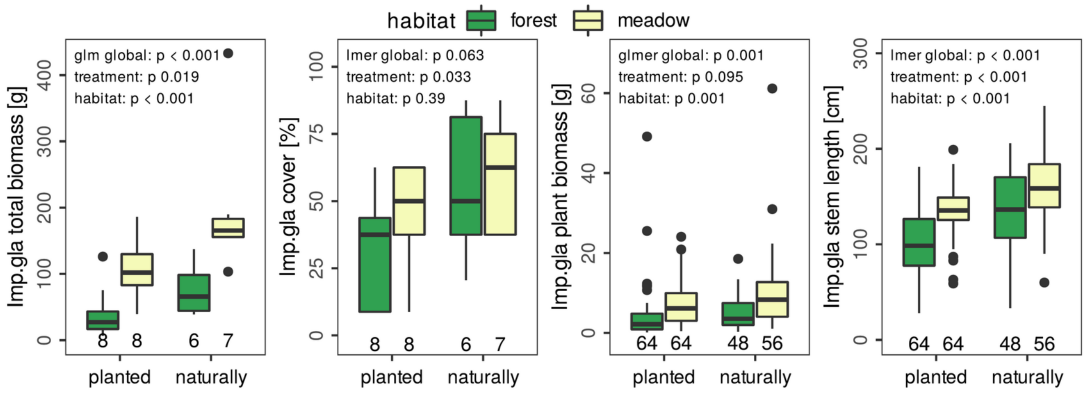

FIGURE 2 Comparison of planted and naturally grown *I. glandulifera* in the habitats alder forest and meadow. With generalized-linear models, it was tested whether total dry biomass, cover, individual plant dry biomass, and stem length of *I. glandulifera* depended on treatment and habitat. Study site was used as random factor (lmer or glmer) unless its variance was estimated zero, thus no random factor was used (glm). For total biomass and individual plant biomass, a gamma error distribution was applied. Resulting *p*-values are given and total sample sizes indicated at the bottom line in the graphs. Individual plant biomass and stem length $N = 8$ plants per plot

3 | RESULTS

3.1 | Dependence of *I. glandulifera* performance on treatment and habitat

In the uninvaded control as in the removal treatment *I. glandulifera* remained mostly absent or occurred at very low abundances only (*I. glandulifera* dry biomass median 0.00 g, max. 0.87 g, cover less than 5%). On average 47 of the 63 planted *I. glandulifera* plants, corresponding to 74%, established. However, survival was lower in alder forests than in meadows (51% versus 85%, $p = .012$, Wilcoxon-test). The planted *I. glandulifera* added up to a biomass of 7–186 g per plot (median 75 g, Figure 2). In natural occurrences in contrast, a higher *I. glandulifera* biomass was recorded (39–433 g, median 137 g, Figure 2). Cover of *I. glandulifera* ranged from 10% to 90% (Braun-Blanquet classes 2a to 5) and correlated strongly with biomass (combining planted and natural occurrences, Pearson correlation coefficient $r = 0.797$, $p < .001$, Figure A1). Planted *I. glandulifera* plants reached similar, but slightly smaller sizes as those naturally grown (Figure 2): with 0.1–61 g biomass (median 4.8 g) plants did not differ significantly in biomass but planted ones had shorter stems than the naturally grown ones (median 126 versus 153 cm). Abundance and plant growth of both, planted and naturally grown *I. glandulifera* was lower in alder forests than in meadows (Figure 2).

3.2 | Habitat-dependent impact of *I. glandulifera* on the resident vegetation

In total 71 resident species were recorded (Table A1). Besides *I. glandulifera*, *Lamium argentatum* occurring in two pairs of plots was the only alien plant species. In the control treatments, resident species number ranged from 2 to 16 per 1 m^2 and did not differ between invaded and uninvaded plots and between habitats, and likewise the Shannon index did not differ (Figure 3a). Total biomass and height of the resident vegetation in contrast were significantly higher in uninvaded plots than in invaded ones, biomass by about 124 g and vegetation height by almost 50 cm. Both were lower in alder forests than in meadows. However, for vegetation height, this difference was not significant because of a high variation between study sites (mixed-effect model). Species composition and abundance differed between invaded and uninvaded plots and also between habitats (Table 1, Figure 4). For example, *Galeopsis tetrahit* and *Cardamine amara* tend to have more biomass in invaded control plots, while for *Carex acutiformis*, *Aegopodium podagraria*, and *Chaerophyllum hirsutum* this is the case in uninvaded ones. *Cirsium oleraceum*, *Ajuga reptans* and *Carex brizoides* only occurred in uninvaded control plots. Comparing habitats regarding their species composition *Geranium palustre*, *Carex acutiformis*, and *Mentha longifolia*, for example, were specific to meadows, while *Circaea lutetiana*, *Dryopteris carthusiana*, *Chrysosplenium oppositifolium*, and *Ch. alternifolium* to forests. The common species *Urtica dioica*, *Galium aparine*, *Filipendula ulmaria*, *Phalaris arundinacea*, *Stellaria nemorum*, *Agrostis caninus*, *Galeopsis tetrahit*, *Aegopodium podagraria*, and *Chaerophyllum hirsutum* occurred consistently across both habitats although biomass could vary.

A causal negative impact tested by planting or removal of *I. glandulifera* on resident vegetation characteristics was only indicated for total biomass of the resident vegetation and the impact intensity did not depend on habitat (Figure 3b, Table 2). On average, *I. glandulifera* planting decreased total resident biomass by 20 g (RII −0.08), and removal increased it by 17 g (RII + 0.08). At maximum, planting resulted in a decrease of total resident biomass from 189 to 118 g (RII −0.23) and removal of *I. glandulifera* in an increase from 95 to 203 g (RII 0.36). Pooling both habitats, RII of planting and removal

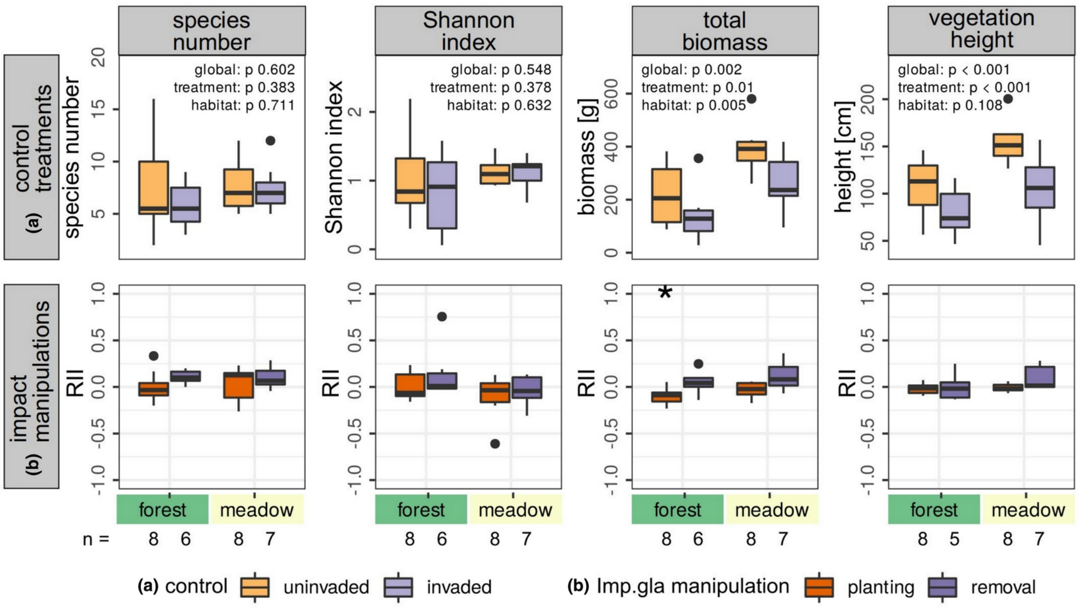

FIGURE 3 Resident vegetation characteristics in the control treatments (a) and impact intensity of *Impatiens glandulifera* planting and removal (b) depending on the habitat. With linear mixed-effect models using site as random factor, it was tested whether the shown parameters differed between control plots invaded and uninvaded by *I. glandulifera* and between habitats (*p*-values given). Impact intensity of *I. glandulifera* manipulation on each parameter is expressed by relative interaction index (RII) among manipulation and appropriate control per pair of plots. RII of −1 shows most negative impact, 0 no impact, and + 1 most positive impact. For planting and removal in both habitats separately, it was tested with a one-sample Wilcoxon test whether RII differs from zero (result indicated by asterisks). Sample sizes are given at the bottom of the graphs

TABLE 1 Multivariate effect of treatment and habitat on species composition and abundance, tested with a PERMANOVA based on Bray-Curtis dissimilarities of dry biomass per species

Data subset	Coefficient	*df*	R^2	F	*p*-value
1) Control treatments: invaded and uninvaded by *Impatiens glandulifera*	Treatment	1	0.130	4.759	.001
	Habitat	1	0.116	4.246	.001
	Treatment:habitat	1	0.070	2.565	.017
	Residual	25	0.684		
2) *Impatiens glandulifera* planting and uninvaded control	Treatment	1	0.004	0.156	.924
	Habitat	1	0.194	6.873	.831
	Treatment:habitat	1	0.012	0.421	.642
	Residual	28	0.790		
3) *Impatiens glandulifera* removal and invaded control	Treatment	1	0.019	0.516	.766
	Habitat	1	0.156	4.258	.858
	Treatment:habitat	1	0.016	0.422	.823
	Residual	22	0.809		

Note: The PERMANOVA was separately conducted for 1) the invaded and uninvaded control treatments, 2) planting trial, and 3) removal trial. Study sites were used as groups within which permutations were constrained.

on total resident biomass was different from zero (planting *p* = .016 and removal *p* = .033, one-sample Wilcoxon test). Differing between habitats, median RII of planting on total resident biomass was negative and removal positive in both habitats, but only planting within alder forests showed a RII significantly different from zero (Figure 3b). Species composition was neither changed by *I. glandulifera* planting nor by removal, and this did not depend on habitat (Table 1, Figure 4).

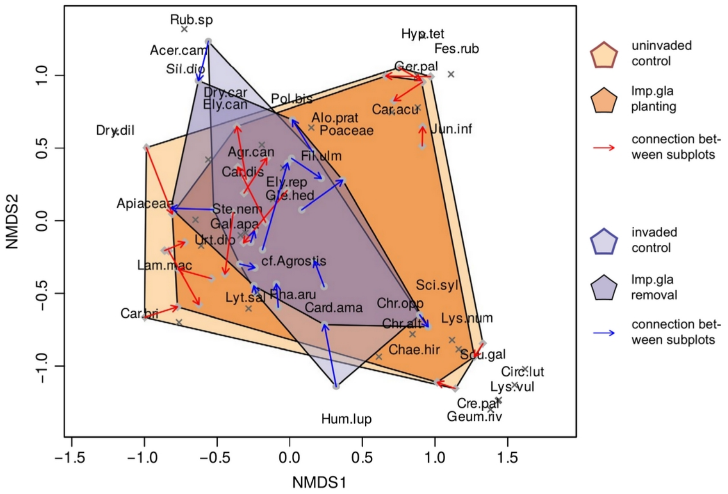

FIGURE 4 Ordination analysis of the resident species composition and abundance showing differences between invaded and uninvaded controls, respectively, and effect of *I. glandulifera* planting and removal. A nonmetric multidimensional scaling (NMDS) was performed based on Bray-Curtis dissimilarity index of plant dry biomass, dimensions 3, stress 0.136, $n = 58$ plots. Sites are indicated by points with arrows connecting a control treatment with its corresponding plot where *I. glandulifera* was manipulated. Species are given as crosses, the most frequent ones were labeled with priority. Results of a PERMANOVA testing the differences are given in Table 1. For abbreviations of the species names see Table A1

TABLE 2 Habitat-dependency of impact intensity (RII) of *I. glandulifera* manipulation on resident vegetation characteristics

Response	Model	Global *p*-value	R^2	Trial	Habitat	Trial:habitat	*N*	*df*
RII species number	lm	.484	−0.017	0.207	0.67	0.735	29	3
RII Shannon index	lmer	.222		0.188	0.213	0.549	29	6
RII total biomass	lmer	**.003**		**<0.001**	0.183	0.979	29	6
RII vegetation height	lm	.106	0.124	0.66	0.84	0.272	28	3

Note: With linear models, it was tested whether the impact of *I. glandulifera* depended on trial (planting and removal of *I. glandulifera*), habitat (meadows and alder forests), and their interaction term. Study site was used as random factor (lmer) unless its variance was estimated zero, thus no random factor was used (lm). *p*-values <.05 are given in bold.

3.3 | Impact of *I. glandulifera* on *Urtica dioica* and other frequent species

Urtica dioica grew significantly better in uninvaded than in invaded control plots regarding total biomass, cover, individual stem length, and individual vegetative biomass (Figure 5a). *U. dioica* total biomass was not changed by *I. glandulifera* manipulations while cover was slightly, but not significantly, decreased by *I. glandulifera* planting and increased by removal (Figure 5b). Individual plants of *U. dioica*, however, were affected by the manipulations regarding all considered parameters (Figure 4). Impact intensity on stem length was low but significant for planting. Impact on individual plant biomass of *U. dioica* was slightly higher. Median RII through planting was −0.11 with a maximum decrease from 6.2 to 2.6 g (RII −0.41), median RII through removal was 0.23 with a maximum increase from 1.2 to 4.8 g (RII 0.59). Impact intensity on infructescence biomass was very high but only significant in the removal trial (Figure 5b).

Besides *U. dioica*, the most frequent resident species were *Galium aparine*, *Filipendula ulmaria*, *Stellaria nemorum*, and *Phalaris arundinacea*. Total biomass of *P. arundinacea* was higher in invaded plots, but total biomass of the other species was independent of invaded or uninvaded situations (Figure A2a). RII of *I. glandulifera* planting and removal on each of those frequent species was highly variable and never significantly different from zero (Figure A2b). However, median total biomass of *G. aparine* decreased by planting and median total biomass of *F. ulmaria*, *G. aparine*, and *S. nemorum* increased by removal.

4 | DISCUSSION

In this field study, we experimentally removed *Impatiens glandulifera* from invaded plots, and planted *I. glandulifera* in formerly uninvaded plots in order to test whether *I. glandulifera* has a negative impact on the native vegetation in riparian meadows and alder forests, and whether the impact is causal or not. We found that *I. glandulifera* had a causal impact indicated by a negative effect of planting and a positive effect of removal of *I. glandulifera* on total resident biomass and individual plant growth of *Urtica dioica* but not on α-diversity, species composition, vegetation height, and total biomass of the most frequent co-occurring species. Impact of the manipulations depended only slightly on the habitat.

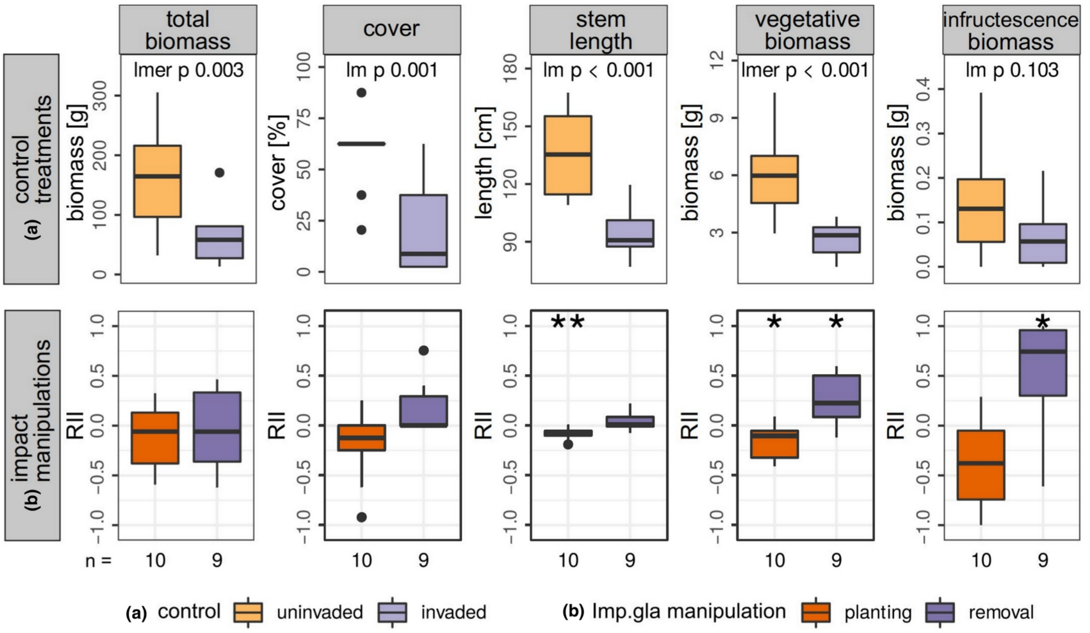

FIGURE 5 *Urtica dioica* in the control treatments (a) and impact intensity of *Impatiens glandulifera* planting and removal (b). With linear models, it was tested whether the shown parameters differed between control plots invaded and uninvaded by *I. glandulifera* (*p*-values given). Study site was used as random factor (lmer) unless its variance was estimated zero, thus no random factor was used (lm). Impact intensity of *I. glandulifera* manipulation on each parameter is expressed by relative interaction index (RII) among manipulation and appropriate control per pair of plots. RII of −1 shows most negative impact, 0 no impact, and + 1 most positive impact. For planting and removal separately, it was tested with a one-sample Wilcoxon test whether RII differs from zero (result indicated by asterisks). Sample sizes are given at the bottom of the graphs. Only pairs of plots are considered in which *U. dioica* occurred in both plots. Stem length, vegetative, and infructescence biomass of *U. dioica* represent mean values of 6–8 plants per plot

4.1 | *Impatiens glandulifera* had low but causal impact on native vegetation

Removal of *Impatiens glandulifera* had a positive and planting a negative effect on total resident plant biomass and growth of *Urtica dioica* individual plants. This indicates that *I. glandulifera* is a driver of ecosystem changes having a causal negative impact on the resident vegetation. A causal impact of *I. glandulifera* on native vegetation is also indicated by Hejda and Pyšek (2006), Hulme and Bremner (2006), and Cockel et al., (2014) who all found positive, but often only slight effects of *I. glandulifera* removal on riparian plant species diversity and composition, which were, however, not affected in the present study. A causal impact on *U. dioica* plants as found in the present study is underpinned by experimental studies on competitive and allelopathic interactions of both species (Bieberich et al., 2018; Gruntman et al., 2014; Tickner et al., 2001). However, the impact of *I. glandulifera* on *U. dioica* competing in a pot experiment was much stronger (relative interaction index RII about −0.7, in Gruntman et al., (2014) and Bieberich et al., (2018)) than under the field conditions in the present study (median RII planting −0.09). Taken together the impact of *I. glandulifera* can be rated as low. Total resident biomass and individual plant growth of *U. dioica* were affected by planting and removal indeed, but only to a small extend, and α-diversity, species composition, vegetation height, and total biomass of the most frequent co-occurring species were not affected by the manipulations at all.

Criteria of a clear driver of changes were only partially met for *I. glandulifera* in the present study. If the species was a clear driver, planted *I. glandulifera* should establish and clearly suppress natives, while removal would lead to recovery of the native vegetation (Bauer, 2012; Didham et al., 2005; MacDougall & Turkington, 2005). In the present study, planted *I. glandulifera* reached similar, but slightly smaller sizes than naturally growing ones. Establishment and growth of *I. glandulifera* were lower in alder forests than in meadows. Thus, *I. glandulifera* growth was slightly restricted by resident vegetation and native plant species α-diversity was not affected at all. Species composition, vegetation height, *U. dioica* total biomass, and *U. dioica* cover differed among invaded and uninvaded plots. However, they were not subsequently affected by removal and planting of *I. glandulifera*. On the one hand, this can indicate that differences between invaded and uninvaded plots were not caused by *I. glandulifera* but are due to other factors, such as habitat conditions or disturbances. If these factors already differed between plots before *I. glandulifera* invasion, they themselves could be one reason for the invasion success at a particular patch. In this case, only comparing invaded and uninvaded patches observationally could lead to the false conclusion that *I. glandulifera* has a negative impact on native vegetation. On the other hand, a response of the native vegetation to the *I. glandulifera* manipulations indicating a causal effect could take longer time than the study duration of one season (Cockel et al., 2014; Rusterholz et al., 2017). Also between-year variations could obscure long-term effects. However, the manipulations affected total native biomass and performance of *U. dioica*, the response of which is faster and more sensitive in comparison with diversity measures. This indicates a fast competitive and allelopathic effect on the growth of neighboring plants as known for the annual *I. glandulifera* from the seedling stage onwards (Bieberich et al., 2020; Gruntman et al., 2014). Another limitation of this experimental study design is that the removal and planting of any other plant species could have the same effect as the removal and planting of *I. glandulifera*, and thus the results might not be specific to *I. glandulifera*. However, results of the present study are corroborated by a previous observational study within the same sites, which underpins that *I. glandulifera* has no impact on α-diversity, species composition, and vegetation height, but on abundance of *U. dioica* (Bieberich et al., 2020). We suggest that continuing the manipulations for more than one season may lead to a change of total abundance of *U. dioica* as a consequence of the reduced growth of individual plants.

If *I. glandulifera* is not a strict driver of changes, it could be a back-seat driver, whose invasion is favored by previous ecosystem changes until it becomes a driver of further changes itself (Bauer, 2012). Affinity of *I. glandulifera* to habitats with natural and anthropogenic disturbances and changed land use (Ammer et al., 2011; Beerling & Perrins, 1993; Čuda, Rumlerová, et al., 2017; Čuda et al., 2020; Pyšek & Prach, 1993, 1995) also indicates characteristics of a back-seat driver. However, to clearly distinguish a back-seat driver from a driver is not possible with the present study. To this end, it would be necessary to test whether removal of the invader would result in recovery of the initial state of an ecosystem only in combination with habitat restoration (Bauer, 2012).

4.2 | Causal impact of *I. glandulifera* depended only slightly on the habitat

We found a consistent effect of *I. glandulifera* manipulations on native vegetation in alder forests and meadows: In both habitats, *I. glandulifera* caused a reduction of total resident biomass but had no causal impact on species composition, α-diversity, and vegetation height. According to a linear model, RII on total biomass did not differ between the two habitats, alder forests and meadows. However, there was a small difference between habitats, as the RII on total biomass was significantly different from zero in alder forests but not in meadows in the *I. glandulifera* planting trial. This indicates a higher impact in elder forests, where both, the biomass of *I. glandulifera* and the resident vegetation was lower than in meadows. In contrast, in our previous study within the same study sites, we found negative correlations between cover of *I. glandulifera* and cover of *U. dioica*, *F. ulmaria* and total cover, which were stronger under bright conditions with higher *I. glandulifera* cover than under dark site conditions (Bieberich et al., 2020). Comparing invaded and uninvaded sites, also Diekmann et al., (2016) suggested a higher impact of *I. glandulifera* in open than in more shady habitats. Thus, the correlative impact seems to be stronger habitat-dependent than the short-time causal impact and more pronounced in bright habitats.

4.3 | Implications for assessment of impact and for nature conservation

We found that the impact of *I. glandulifera* on native vegetation was causal but low. The response of the native vegetation to the *I. glandulifera* manipulations was quite fast within one vegetation period, even if only some parameters were affected within the study duration. Also other field studies on *I. glandulifera* using a removal approach found effects on native vegetation within one season (Cockel et al., 2014; Hejda & Pyšek, 2006; Hulme & Bremner, 2006), whereas only in Hulme and Bremner (2006), the effect was quite high. This means that invasion can have a negative impact after a short period of time, but also removal as management measure could have a fast effect. However, the impact of *I. glandulifera* could also increase over time after invasion (Rusterholz et al., 2017), and longer lasting removal can also enhance a management effect (Cockel et al., 2014; Rusterholz et al., 2017).

We suggest that *I. glandulifera* is not a clear driver of changes, but it has some characteristics of a back-seat driver benefiting from previous changes such as disturbances or changed land use. This is relevant for nature conservation because drivers and back-seat drivers require a different management strategy. In the case of a driver, removal of the invader, which induced the changes, is ideally sufficient (Bauer, 2012). In contrast, in the case of a back-seat driver, habitat restoration is necessary in addition to removal of the invader (Bauer, 2012). Thus, management of a back-seat driver is more complicated because the previous changes that facilitated invasion have to be known and countered. Such previous changes can be all kinds of alterations of ecosystem properties such as land use change, pollution, nutrient input, or altered disturbance regimes (Bauer, 2012; Didham et al., 2005). Unfortunately, there is often no reliable information on the original community and ecosystem processes available (Parker et al., 1999). Special cases are natural disturbances and intentional anthropogenic ecosystem changes. Natural and anthropogenic disturbances are common in riparian habitats and can generally favor invasions (Richardson et al., 2007). Intentional ecosystem changes such as tree cutting or habitat restoration are sometimes associated with *I. glandulifera* invasion (for forests: Čuda et al. (2020), river restoration: Lapin et al. (2016)). In this case, it can be recommended to prevent the potential invasion of a back-seat driver while planning and conducting the disturbance (D'Antonio & Meyerson, 2002; Lapin et al., 2016). It is also possible that *I. glandulifera* invasions are favored by anthropogenic nutrient input as *I. glandulifera* has an affinity to nutrient-rich patches (Bieberich et al., 2020; Čuda et al., 2014). Thus, reducing the nutrient input into water bodies as a general aim of nature conservation may also reduce invasion of *I. glandulifera*. In the case of already established populations of *I. glandulifera*, it can be discussed if a management is reasonable, considering the rather low impact of *I. glandulifera* in combination with its high abundance and frequency in Central Europe. Since a population control can be very expensive (Leblanc & Lavoie, 2017), it should be reserved for sites which are particularly valuable in terms of nature conservation.

5 | CONCLUSION

Impatiens glandulifera had a causal but low impact on the resident vegetation in both riparian habitats, alder forests and meadows. The effect could be seen already after one season, but may also intensify over longer time. *Impatiens glandulifera* had some characteristics of a back-seat driver, which is facilitated by previous ecosystem changes but is also a driver of further changes having causal impact on the invaded ecosystem. If *I. glandulifera* has to be managed for nature conservation, this involves the need of ecosystem restoration along with removal of the invader.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

AUTHOR CONTRIBUTION

Judith Bieberich: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). **Stefanie Müller:** Formal analysis (supporting); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Heike Feldhaar:** Conceptualization (equal); Methodology (equal); Project administration (equal); Resources (supporting); Supervision (equal); Writing-review & editing (equal). **Marianne Lauerer:** Conceptualization (equal); Methodology (equal); Project administration (equal); Resources (lead); Supervision (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

All data of the manuscript are available at Dryad (https://doi.org/10.5061/dryad.59zw3r25z).

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APPENDIX

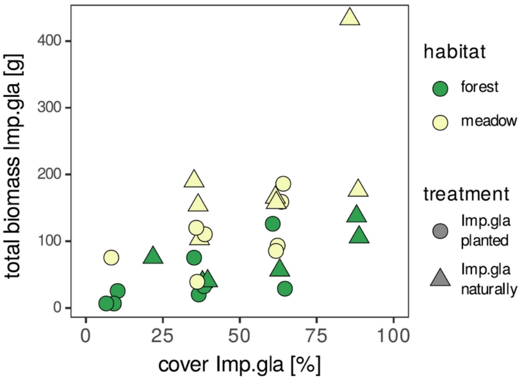

FIGURE A1 Correlation between total dry biomass and cover of *I. glandulifera*. Habitat and whether *I. glandulifera* was planted or grew naturally is indicated by point color and shape. To avoid overplotting of points, 2.5% random noise was added to *I. glandulifera* cover. Pooling both habitats and treatments, Pearson correlation coefficient was 0.726, $p < .001$. Biomass was harvested from the central 1 m^2 per plot and given as dry weight, while cover was estimated according Braun-Blanquet scale within the total 2.25 m^2 plot

TABLE A1 Abbreviations of species names as shown in Figure 4 and number of plot in which each species occurred

Abbreviation	Taxon name according to the determinable level	Occurrences
Acer.cam	*Acer campestre* L.	1
Acer.pse	*Acer pseudoplatanus* L.	5
Aeg.pod	*Aegopodium podagraria* L.	11
Agr.can	*Agrostis canina* L. (incl. *A.* cf. *canina* L.)	12
Aju.rep	*Ajuga reptans* L.	4
All.pet	*Alliaria petiolata* (M. Bieb.) Cavara et Grande	6
Alo.prat	*Alopecurus pratensis* L.	11
Ang.syl	*Angelica sylvestris* L.	1
Apiaceae	*Apiaceae*	1
Ath.fil	*Athyrium filix-femina* (L.) Roth	3
Cal.sep	*Calystegia sepium* (L.) R. Br.	2
Calt.pal	*Caltha palustris* L.	4
Car.acu	*Carex acutiformis* Ehrh.	15
Car.bri	*Carex brizoides* L.	4
Car.dis	*Carex disticha* Huds.	2
Card.ama	*Cardamine amara* L.	7
cf.Agrostis	probably *Agrostis*	2
Chae.hir	*Chaerophyllum hirsutum* L.	10
Chr.alt	*Chrysosplenium alternifolium* L.	3
Chr.opp	*Chrysosplenium oppositifolium* L.	5
Cir.ole	*Cirsium oleraceum* (L.) Scop.	6
Circ.int	*Circaea intermedia* Ehrh.	1
Circ.lut	*Circaea lutetiana* L.	2
Cre.pal	*Crepis paludosa* L. Moench	4
Dac.glo	*Dactylis glomerata* L.	2
Des.ces	*Deschampsia cespitosa* (L.) P. Beauv.	2
Dry.car	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	4
Dry.dil	*Dryopteris* cf. *dilatata* (Hoffm.) A. Gray	1
Ely.can	*Elymus caninus* (L.) L.	1
Ely.rep	*Elymus repens* (L.) Gould	1
Epi.ang	*Epilobium angustifolium* L.	1
Epi.sp	*Epilolium* sp.	1
Equi.flu	*Equisetum fluviatile* L.	8
Fes.rub	*Festuca rubra* L.	2
Fil.ulm	*Filipendula ulmaria* (L.) Maxim.	36
Fra.exc	*Fraxinus excelsior* L.	4
Gal.apa	*Galium aparine* L.	42
Gal.elo	*Galium elongatum* C. Presl	1
Gal.mol	*Galium mollugo* L.	1
Gal.tet	*Galeopsis tetrahit* L.	11
Ger.pal	*Geranium palustre* L.	8
Geum.riv	*Geum rivale* L.	2
Geum.urb	*Geum urbanum* L.	7
Gle.hed	*Glechoma hederacea* L.	7
Hum.lup	*Humulus lupulus* L.	1
Hyp.tet	*Hypericum tetrapterum* Fr.	1
Imp.nol	*Impatiens noli-tangere* L.	2
Jun.inf	*Juncus inflexus* L.	1
Lam.arg	*Lamium galeobdolon* ssp. *argentatum* (Smejkal) Duvigneau	3
Lam.mac	*Lamium maculatum* (L.) L.	6
Lat.pra	*Lathyrus pratensis* L.	2
Lys.num	*Lysimachia nummularia* L.	5
Lys.vul	*Lysimachia vulgaris* L.	3
Lyt.sal	*Lythrum salicaria* L.	1
Men.lon	*Mentha longifolia* (L.) L.	13
Myo.sco	*Myosotis scorpioides* L.	2
Pha.aru	*Phalaris arundinacea* L.	30
Poa.ang	*Poa angustifolia* L.	1
Poaceae	*Poaceae*	7
Pol.bis	*Polygonum bistorta* L.	7
Pri.ela	*Primula* cf. *elatior* (L.) Hill	1
Pru.pad	*Prunus padus* L.	1
Rub.sp	*Rubus* sp.	3
Rum.obt	*Rumex obtusifolius* L.	1
Sci.syl	*Scirpus sylvaticus* L.	3
Scu.gal	*Scutellaria galericulata* L.	2
Sil.dio	*Silene dioica* (L.) Clairv.	2
Ste.nem	*Stellaria nemorum* L.	30
Urt.dio	*Urtica dioica* L.	41
Val.dio	*Valeriana dioica* L.	3
Vib.opu	*Viburnum opulus* L.	1

(Continues)

TABLE A1 (Continued)

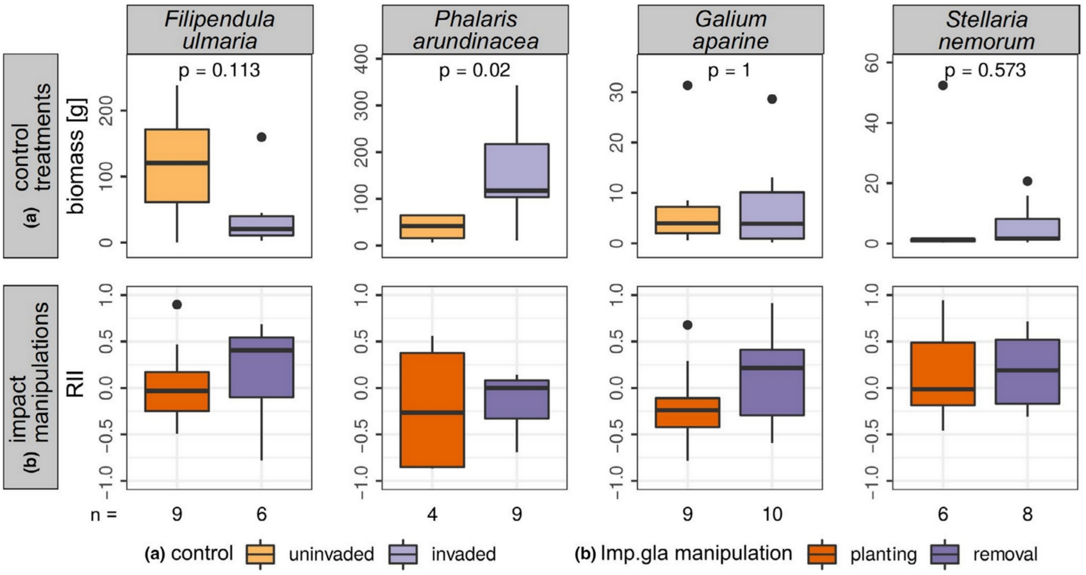

FIGURE A2 Total biomass per 1 m^2 of the most frequent resident species in the control treatments (a) and impact intensity of *Impatiens glandulifera* planting and removal (b). With a Mann-Whitney-*U* test, it was tested whether the shown parameters differed between control plots invaded and uninvaded by *I. glandulifera* (*p*-values given). Impact intensity of *I. glandulifera* manipulation on each parameter is expressed by relative interaction index (RII) among manipulation and appropriate control per pair of plots. RII of −1 shows most negative impact, 0 no impact, and + 1 most positive impact. For planting and removal separately, it was tested with a one-sample Wilcoxon test whether RII differs from zero (result indicated by asterics). Sample sizes are given at the bottom of the graphs. Only pairs of plots are considered in which the respective species occurred in both plots

6 Appendix

6.1 List of publications

publications of the thesis

Bieberich J, Feldhaar H, Lauerer M (2020) Micro-habitat and season dependent impact of the invasive *Impatiens glandulifera* on native vegetation. NeoBiota 57: 109–131. https://doi.org/10.3897/neobiota.57.51331.

Bieberich J, Lauerer M, Drachsler M, Heinrichs J, Müller S, Feldhaar H (2018) Species- and developmental stage-specific effects of allelopathy and competition of invasive *Impatiens glandulifera* on co- occurring plants. PloS ONE 13: e0205843. https://doi.org/10.1371/journal.pone.0205843.

Bieberich J, Müller S, Feldhaar H, Lauerer M (2021) Invasive *Impatiens glandulifera*: a driver of changes in native vegetation? Ecology and Evolution 11: 1320-1333. https://doi.org/10.1002/ece3.7135

other publication in invasion biology

Bieberich J, Lauerer M, Aas G (2016) Acorns off introduced *Quercus rubra* are neglected by European Jay but spread by mice. Annales off Forest Research 59(1). https://doi.org/10.15287/afr.2016.522

6.2 Presentations of my research

Contributions to conferences

date	conference	title	type
10/2015	Bayreuth Center for Ecology and Environmental Research, Workshop 2015 in Bayreuth	*Impatiens glandulifera*: Impact of an invasive plant species on the seedling development of co-occurring native species	Poster
06/2016	Cusanuswerk, Conference for PhD candidates in Oberwesel	Einfluss des invasiven *Impatiens glandulifera* auf Pflanzengemeinschaften: Stand des Forschungsprojektes	Talk
09/2016	46th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Marburg	Impact of the invasive *Impatiens glandulifera* on the growth of co-occurring native plant seedlings	Talk
06/2017	Cusanuswerk, Conference for PhD candidates in Ellwangen	Einfluss des invasiven *Impatiens glandulifera* auf Pflanzengemeinschaften: Stand des Forschungsprojektes	Talk
09/2017	1st International Conference of Community Ecology in Budapest	Impact of the invasive *Impatiens glandulifera* on co-occurring native plants	Talk
10/2017	Bayreuth Center for Ecology and Environmental Research, workshop 2017, in Bayreuth	Invasive *Impatiens glandulifera* reduces growth of native plants by allelopathy	Talk
05/2018	Cusanuswerk, Conference for PhD candidates, in Goslar	Einfluss des invasiven *Impatiens glandulifera* auf Pflanzengemeinschaften: Stand des Forschungsprojektes	Talk
10/2018	Bayreuth Center for Ecology and Environmental Research, workshop 2018, in Bayreuth	Invasive *Impatiens glandulifera*: micro niche and impact on plant community	Poster
09/2019	49th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Münster	Invasive *Impatiens glandulifera*: microhabitat and impact on native vegetation	Talk

Presentations at educational events

01/2018	Cusanuswerk. Workshop on introduction to scientific methods. Experimentelle Invasionsbiologie: Einfluss des invasiven Drüsigen Springkrautes auf einheimische Pflanzen
06/2018	Ecological-Botanical Gardens (EBG). Public event. Indisches Springkraut: ein durchsetzungsstarker Einwanderer?
06/2019	EBG. Public event. *Impatiens glandulifera*: Einfluss auf einheimische Vegetation und dessen Kontextabhängigkeit.

7 Declarations

(Eidesstattliche) Versicherungen und Erklärungen

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.

(§ 9 Satz 2 Nr. 4 PromO BayNAT)

Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.

(§ 9 Satz 2 Nr. 7 PromO BayNAT)

Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.

(§ 9 Satz 2 Nr. 8 PromO BayNAT)

Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.

....

Ort, Datum, Unterschrift