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FACTORS CONTROLLING PLANT INVASION: COMMUNITY NICHE, VEGETATION STRUCTURE AND LOCAL ADAPTATION

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CONTENTS

SUMMARY

The main objectives of this dissertation are to contribute to the development of invasion ecology, and to improve the understanding of factors that control plant invasions. For this purpose, four research fields that currently strongly interact within invasion ecology were chosen, i.e., theoretical invasion ecology, macroecological research on plant invasions, community ecology, and evolutionary ecology.

Invasion ecology is a rather young discipline that has advanced considerably since its early beginnings. Nevertheless, it still remains difficult to explain, to predict and to manage biological invasions. Pointing out difficulties in invasion ecology, and looking for measures to overcome them can accelerate progress in the discipline. Basic and applied research in invasion ecology are confronted with difficulties arising within three main domains, i.e., (A) societal issues, such as divergent perception of invasive alien species, (B) the uniqueness of the invasion process itself, such as its complexity and context dependency, and (C) the scientific methodology in invasion ecology, such as imprecise formulation of hypotheses. Three key measures are proposed that can be used to overcome these difficulties: (1) a checklist for scientific definitions, (2) the implementation of a hierarchy of hypotheses (HoH), where general hypotheses branch into specific ones that are testable, and (3) platforms for improved communication. These measures may significantly increase conceptual clarity and enhance communication, and thereby advance the field of invasion ecology.

The invasion process suggests that invasive alien plant species invade different habitats sequentially. Differences in the relative frequency of phytosociological relevés with invasive aliens, and in the niche width of invasive aliens and native congeners were studied over three time periods in Germany. 8839 relevés were collected for three pairs of congener species covering different growth forms (*Impatiens noli-tangere*, *I. parviflora*; *Solidago virgaurea*, *S. canadensis*; *Prunus padus*, *P. serotina*) using the global index of vegetation plot databases (GIVD). The number and proportion of relevés with the native compared to those with the invasive alien were assessed, and ordinations and β-diversity were used to study niche width. An increase in the relative number of relevés with the invasive compared to the native species was observed. The niche space of the invasive alien species and the overlap of the niches of the native and the invasive species increased over time. The increasing similarity between community niches of congener species is possibly a consequence of biotic homogenization.

The identification of significant relationships between community mean functional traits related to competition, and the growth and fecundity of invasive alien plants, is proposed as a new method for the management of problematic invaders and the conservation of native biodiversity. This novel approach was tested in the prominent invader purple loosestrife (*Lythrum salicaria*), in two areas within its native and invaded range, respectively. Vegetation surveys were conducted, and community mean traits were calculated based on plant traits extracted from the TRY database. Growth and fecundity of the study species were explained by community traits using multiple linear regressions. Several community traits showed positive correlations with the growth and fecundity of *Lythrum salicaria*, especially plant height, leaf area, and specific leaf area. Interestingly, relative cover of graminoid species was negatively related to *Lythrum salicaria*. Results indicate that the proposed approach could become a successful method in invasion ecology. Based on the studied case, it is suggested that *Lythrum salicaria* is a strong competitor in tall vegetation with dense cover. However, its growth and fecundity were reduced in communities with a high abundance of grasses and sedges.

Evolutionary change can occur rapidly in invasive alien species, and has been shown to lead to local adaptation that enables plant species to persist under different conditions. The alien annual *Impatiens glandulifera* was used to investigate local adaptation to distinct habitats that were consecutively invaded. A reciprocal transplant experiment was performed using populations in alluvial deciduous forests, fallow meadows, and coniferous upland forests, and a greenhouse experiment for growing plants from these habitats under treatments reflecting the main habitat differentiators (shade, soil acidity, competition). Plant traits differed between habitats in the field experiment and between treatments in the greenhouse, but not between seed origins. Overall, there was no indication of local adaptation in both experiments. Nevertheless, *Impatiens glandulifera* is a successful invader in many habitats. Therefore, it is suggested that the species is coping with environmental variation by means of high phenotypic plasticity. The observed colonization sequence is likely to be based primarily on changes in propagule pressure. It is concluded that invasive alien plants can become dominant in distinct habitats without local adaptation.

The focus on four complementary fields within invasion ecology, i.e., theoretical invasion ecology, macroecology, community ecology, and evolutionary ecology, allowed addressing different objectives and using a diverse set of methods. Besides theoretical development of the discipline the results overall contribute to the idea that the interplay of invasiveness and invasibility drives plant invasion success. In the studied cases, invasion success depends mainly on time since introduction, vegetation structure and competition in resident plant communities, phenotypic plasticity of the invader, and propagule pressure.

ZUSAMMENFASSUNG

Die Hauptziele dieser Dissertation sind es, einen Beitrag zur Weiterentwicklung der Invasionsökologie zu leisten und das Verständnis der Faktoren, die Pflanzeninvasionen steuern, zu verbessern. Dazu wurden vier Forschungsbereiche ausgewählt, die zurzeit stark mit der Invasionsökologie interagieren, nämlich die theoretische Invasionsökologie, makroökologische Forschung über Pflanzeninvasionen, Synökologie und evolutionäre Ökologie.

Die Invasionsökologie ist eine junge Wissenschaft, die seit ihren Anfängen beträchtliche Fortschritte erzielt hat. Dennoch ist es nach wie vor schwierig, biologische Invasionen zu erklären, vorherzusagen oder zu managen. Der Fortschritt in der Disziplin kann beschleunigt werden, indem auf Schwierigkeiten in dem Forschungsgebiet hingewiesen wird und Maßnahmen zu ihrer Überwindung gesucht werden. Es wird erörtert, dass Grundlagenforschung und angewandte Forschung in der Invasionsökologie mit Schwierigkeiten konfrontiert sind, die aus drei Domänen entstehen, nämlich aus (A) gesellschaftlichen Aspekten, z.B. der unterschiedlichen Wahrnehmung von invasiven Fremdarten, (B) der Einzigartigkeit des Invasionsprozesses sowie seiner Komplexität und Kontextabhängigkeit und (C) der wissenschaftlichen Methodologie in der Invasionsökologie selbst, z.B. der unpräzisen Formulierung von Hypothesen. Drei Schlüsselmaßnahmen werden vorgeschlagen, die verwendet werden können, um diese Schwierigkeiten zu überwinden: (1) eine Checkliste für explizite Definitionen, (2) die Einführung einer Hierarchie der Hypothesen (HoH), bei der allgemeine Hypothesen sich in spezifische, präzise testbare Hypothesen verzweigen, und (3) Plattformen für eine bessere Kommunikation. Diese Maßnahmen könnten die konzeptuelle Klarheit steigern, die Kommunikation verbessern und damit die Invasionsökologie als Disziplin voranbringen.

Der Invasionsprozess deutet an, dass invasive Fremdarten verschiedene Lebensräume sequentiell besiedeln. Unterschiede in der relativen Anzahl von pflanzensoziologischen Relevés mit invasiven Fremdarten sowie der Nischenbreite dieser Arten und einheimischer Verwandter wurden über drei Zeitperioden in Deutschland untersucht. Dazu wurden 8839 Vegetationsaufnahmen für drei Artenpaare mit unterschiedlichen Lebensformen (*Impatiens noli-tangere*, *I. parviflora*; *Solidago virgaurea*, *S. canadensis*; *Prunus padus*, *P. serotina*) mit Hilfe des Globalen Indexes von Vegetationsplot Datenbanken (GIVD) zusammengetragen. Die Anzahl und das Verhältnis von Aufnahmen mit der einheimischen Art im Gegensatz zu Aufnahmen mit der Fremdart wurden festgestellt, und Ordinationen sowie die β-Diversität wurden verwendet, um die Nischenbreite zu untersuchen. Ein Anstieg der relativen Anzahl von Aufnahmen mit der invasiven Art im Vergleich zu der Einheimischen wurde festgestellt. Die Nische der invasiven Fremdarten und die Überschneidung der Nischen von verwandten einheimischen und fremden Arten haben über den Untersuchungszeitraum zugenommen. Die gesteigerte Ähnlichkeit zwischen den Nischen der verwandten Arten ist eventuell eine Konsequenz biotischer Homogenisierung.

Die Bestimmung signifikanter Beziehungen zwischen mittleren Arteigenschaften einer Pflanzengesellschaft, die mit Konkurrenz zusammenhängen, sowie Wachstum und Fruchtbarkeit von invasiven Fremdarten wird als eine neue Methode für das Management von problematischen Invasoren und den Schutz einheimischer Biodiversität vorgeschlagen. Dieser Ansatz wurde für *Lythrum salicaria* in zwei Gebieten im einheimischen und zwei im invadierten Verbreitungsgebiet getestet. Vegetationsuntersuchungen wurden durchgeführt und mittlere Arteigenschaften der Pflanzengesellschaften auf der Grundlage von Eigenschaften aus der TRY Datenbank berechnet. Wachstum und Fruchtbarkeit der untersuchten Art wurden in multiplen linearen Regressionen von mittleren Arteigenschaften erklärt. Einige mittlere Arteigenschaften waren positiv mit dem Wachstum und der Fruchtbarkeit von *Lythrum salicaria* korreliert, besonders Pflanzengröße, Blattfläche und spezifische Blattfläche. Interessanterweise stand die Deckung graminoider Arten in einer negativen Beziehung zu *Lythrum salicaria*. Die Ergebnisse deuten an, dass der vorgeschlagene Ansatz eine erfolgreiche Methode in der Invasionsökologie werden könnte. In dem untersuchten Fall wird deutlich, dass *Lythrum salicaria* ein starker Konkurrent in Beständen mit hoher Vegetation und dichter Deckung ist. Allerdings waren Wachstum und Fruchtbarkeit der Art in Pflanzengesellschaften mit hoher Abundanz von Gräsern und Seggen reduziert.

Bei invasiven Fremdarten können genetische Veränderungen schnell eintreten und zu lokaler Anpassung führen, die es den Pflanzen erlaubt, unter unterschiedlichen Bedingungen zu überdauern. Die fremde einjährige Art *Impatiens glandulifera* wurde verwendet, um lokale Anpassung an unterschiedliche Lebensräume zu untersuchen, die der Reihe nach besiedelt wurden. Ein reziprokes Experiment mit Populationen aus Auwald-, Brachwiesen- und Nadelwald-Habitaten wurde durchgeführt sowie ein Gewächshausexperiment, bei dem Pflanzen aus diesen Habitaten unter Behandlungen wuchsen, welche die Hauptunterschiede zwischen den Habitaten abbildeten (Schatten, Bodensäure, Konkurrenz). Pflanzeneigenschaften unterschieden sich zwischen den Habitaten im Feldexperiment und zwischen den Behandlungen im Gewächshaus, aber nicht zwischen Samenherkünften. Insgesamt wurden in beiden Experimenten keine Anzeichen für lokale Anpassung gefunden. Trotzdem ist *Impatiens glandulifera* ein erfolgreicher Invasor in vielen Lebensräumen. Daher deutet alles darauf hin, dass die Art durch phänotypische Plastizität mit Umweltvariation umgehen kann. Die beobachtete Einwanderungs-Sequenz ist daher wahrscheinlich eine Folge von Veränderungen im Ausbreitungsdruck. Es wird gefolgert, dass invasive Fremdarten in verschiedenen Habitaten dominant werden können, ohne lokal angepasst zu sein.

Die Kombination von vier aktuellen Forschungsansätzen der Invasionsökologie hat es ermöglicht, komplementäre Ziele zu erreichen. Neben der konzeptuellen Weiterentwicklung der Disziplin haben die Ergebnisse zu der Idee beigetragen, dass der Erfolg von Pflanzeninvasionen vom Zusammenspiel von Invasivität und Invasibilität gesteuert wird. In den untersuchten Fällen hing der Erfolg vor allem von der Zeit seit der Einführung, der Vegetationsstruktur und Konkurrenz in Pflanzengesellschaften, phänotypischer Plastizität sowie dem Ausbreitungsdruck ab.

GENERAL INTRODUCTION

Research on biological invasions is a well-established and active field within biology. Invasion ecology focuses on alien invasive species, and addresses issues that range from biogeography, evolutionary biology, community and ecosystem ecology over landscape and restoration ecology towards risk analysis and sociology (Richardson, 2011b). *Alien species* are defined as those species that occur at a location beyond their area of origin, whereby occurrence in the new area has been prevented in the past through a dispersal barrier (Heger *et al.*, 2013a). *Invasive species* are those aliens that sustain self-replacing populations over several life cycles, produce reproductive offspring and have the potential to spread over large distances (Richardson *et al.*, 2011).

Invasive alien species can cause significant ecological (Vilà *et al.*, 2011), economic (Pimentel *et al.*, 2001) and sociological impacts (Pejchar & Mooney, 2009), and biological invasions are regarded as one of the most important components of global change, and a major threat to biodiversity (Vitousek *et al.*, 1997; Mack *et al.*, 2000). Besides being a major source of impacts, biological invasions are especially interesting as they can be viewed as natural experiments across large spatio-temporal scales that enable researchers to observe ecological and evolutionary processed in real time (Sax *et al.*, 2007). Therefore, studying biological invasions allows new insights into many fields of biology, and continuing scientific research on the factors that control biological invasions is encouraged.

Factors controlling plant invasions

One major topic in invasion ecology is the question which factors drive invasions. Although major progress in answering this question has been achieved (Lockwood *et al.*, 2007; Davis, 2009; Richardson, 2011a), there are still knowledge gaps (see Davis, 2009), and current developments summarized as ‘global change’ further challenge explanation and prediction of biological invasions, e.g., climate change (Bellard *et al.*, 2013), increase in global trade (Hulme, 2009), and alterations in crop usage, e.g., use for biofuel production (Davis *et al.*, 2010).

The establishment and spread of plant species in a new area is driven by the interplay of traits of the species and environmental conditions (Richardson & Pyšek, 2006). Each species has certain traits that determine its success in establishing and spreading in a new area (‘*invasiveness*’). However, a species can only establish and spread successfully in a new area when the abiotic and biotic conditions of the habitat ‘match’ the species’ requirements. Therefore, environmental conditions equally determine if a species can establish and spread successfully (‘*invasibility*’). Some of the main factors determining invasiveness and invasibility are shown in Fig. 1. If environmental conditions in the new area differ from the native area or if trait expressions of individuals in the new area differ from those in the native area, e.g., due to genetic differences, the interplay between these groups of factors changes also. This can lead to different growth and fecundity of the species during establishment and spread which is a frequently observed phenomenon. For example, individuals of the same species often grow taller in the new than in the native area (Crawley, 1987), and colonize different habitats (DeWalt *et al.*, 2004).

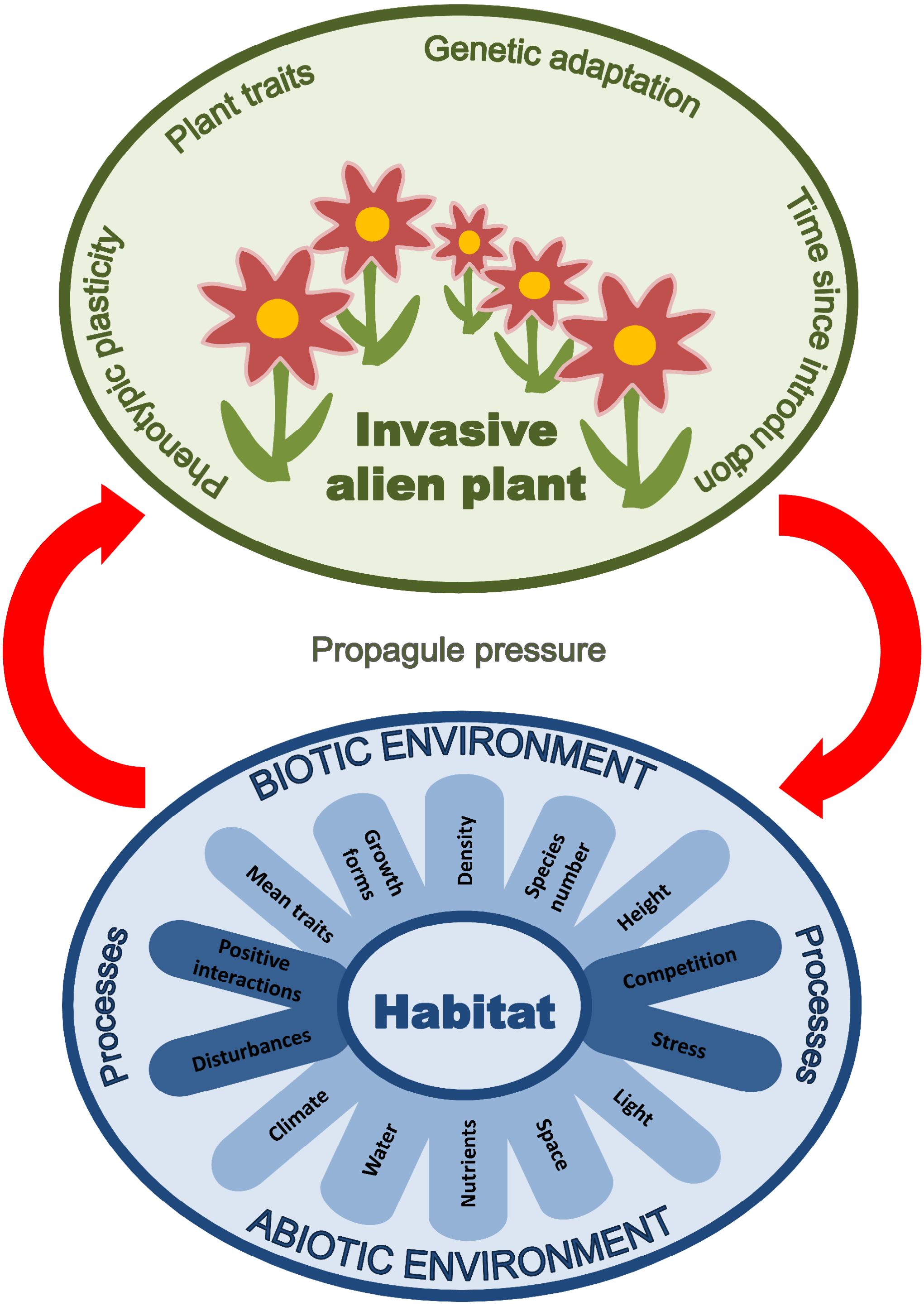


Fig. 1 Interplay of *invasiveness* of an alien plant species and *invasibility* of a habitat. Examples of factors that influence invasiveness and invasibility are given. Some processes are believed to facilitate invasions, others can be inhibitory.

Invasiveness of a plant was related to a set of plant traits defining an 'ideal weed' (Baker, 1965). While single plant traits do not explain invasiveness very good, certain combinations of traits that define different ecological strategies may enhance invasiveness (Küster *et al.*, 2008). Additionally, high phenotypic plasticity (Richards *et al.*, 2006) and time since introduction (Haider *et al.*, 2010) can contribute to plant invasion success. Possible reasons for time effects include the requirement of time for the species to adapt genetically to new environments, or to develop larger and older populations that are able to donate more propagules, thereby increasing propagule pressure.

The invasibility of a habitat is driven by the abiotic and biotic environment a species faces during invasion. For example, climatic conditions and nutrient availability define if an invasive alien plant is generally able to grow in a certain habitat. The biotic environment also contributes to invasibility, e.g., although ecological interactions rarely enable communities to resist invasion, they may constrain the abundance of invasive species (Levine *et al.*, 2004). Competition between plants can be a process arising from the biotic environment that decreases invasion success, while positive interactions may be facilitating. Another process that can further facilitate invasions is disturbance (Davis *et al.*, 2000).

It has been shown recently that hypotheses that do not consider interactions between invasiveness and invasibility are less supported by empirical studies than those that do so (Jeschke *et al.*, 2012a). Therefore, it has to be kept in mind that invasiveness and invasibility should be addressed together, and the success of a species in a new area will depend on the interplay between both.

Current trends in invasion ecology

Invasion ecology consists of many research fields, such as macroecology, community ecology, and evolutionary ecology (Richardson, 2011b). Currently, some of these disciplines flourish because they are especially useful in the face of present developments summarized under the term 'global change'. To account for these current developments, I focus on four current trends in invasion ecology, i.e., theoretical invasion ecology, macroecological research on plant invasions, mechanistic community ecology, and evolutionary ecology on invasive alien plants.

Theoretical invasion ecology

Research on theory, concepts, and synthesis in invasion ecology has been very active recently (Blumenthal, 2006; Catford *et al.*, 2009; Blackburn *et al.*, 2011; Gurevitch *et al.*, 2011; Kueffer *et al.*, 2013). Invasion ecology is a rather young sub-discipline of ecology, new concepts and hypotheses are proposed frequently, and there have been several attempts to propose a unified framework for invasion ecology to advance the field (Catford *et al.*, 2009; Gurevitch *et al.*, 2011; Kueffer *et al.*, 2013). Nevertheless, the accumulating data often questions existing concepts, and it has been shown that evidence for established hypotheses in invasion ecology is uneven and declining (Jeschke *et al.*, 2012a).

Currently, invasion ecology seems to face some major difficulties, and it can be argued that there is potential for improving effectiveness of the discipline. Pointing out current difficulties and developing measures to overcome them, is proposed as a way to accelerate progress in invasion ecology.

Macroecology

Macroecology takes a broad perspective to search for generalized ecological patterns (Keith *et al.*, 2012). The discipline is mainly concerned with understanding the abundance and distribution of species at large spatial and temporal scales (Gaston & Blackburn, 2008). Macroecology and invasion ecology have joint forces to address questions of habitat invasibility (Pyšek *et al.*, 2010), patterns of the invasion process (Theoharides & Dukes, 2007) or species invasiveness (Cadotte *et al.*, 2006), e.g., as determined by plant traits (Küster *et al.*, 2008). During the past century, ecologists studied some geographical areas intensively, and accumulated a vast amount of data, for example co-occurrence data of plant species as in phytosociological relevés. Recently, these data have become accessible in large databases (Schaminée *et al.*, 2009; Jansen *et al.*, 2012a), that open new possibilities to study plant co-occurrence on large spatial and temporal scales, and facilitate investigation of questions usually raised in macroecology.

Co-occurrence data on large scales can be used to measure the width of realized niches in plants. For this purpose the spectrum of habitats colonized (Hejda *et al.*, 2009), as well as *β*-diversity are used (Fridley *et al.*, 2007a). During invasion, plant species spread into a region, and colonize additional habitats with time (Dietz & Edwards, 2006). This means, they require time to fill their potential range and realized niche. Thus, it can be asked whether or not niche width of invasive alien plants is smaller than of similar native taxa, and if it changes over time.

Community ecology

Community ecology addresses assemblages of species (Morin, 2011). One important goal in community ecology is to understand the origin, maintenance, and consequences of biological diversity within local communities (Morin, 2011). It is disputed how neutral and niche-based processes, such as environmental filtering, contribute to plant community assembly (Weiher *et al.*, 2011), and the roles of plant functional traits and phylogeny have received considerable attention recently (Kraft & Ackerly, 2010). Invasion ecologists are especially interested in the invasibility of communities (Levine, 2000), and it was even proposed to reassemble plant communities that are resistant to invasions (Funk *et al.*, 2008).

The structure of plant communities is driven by several mechanisms including interspecific competition (Grime, 2001). Competition can influence the development of each plant in a community. Invasive alien plant species can occur in similar communities in their native and invaded range, but their growth and fecundity should be related to the local level of competition in each place. Mean community traits that are related to competition, e.g., plant height, can be a mechanistic measure for competition in plant communities.

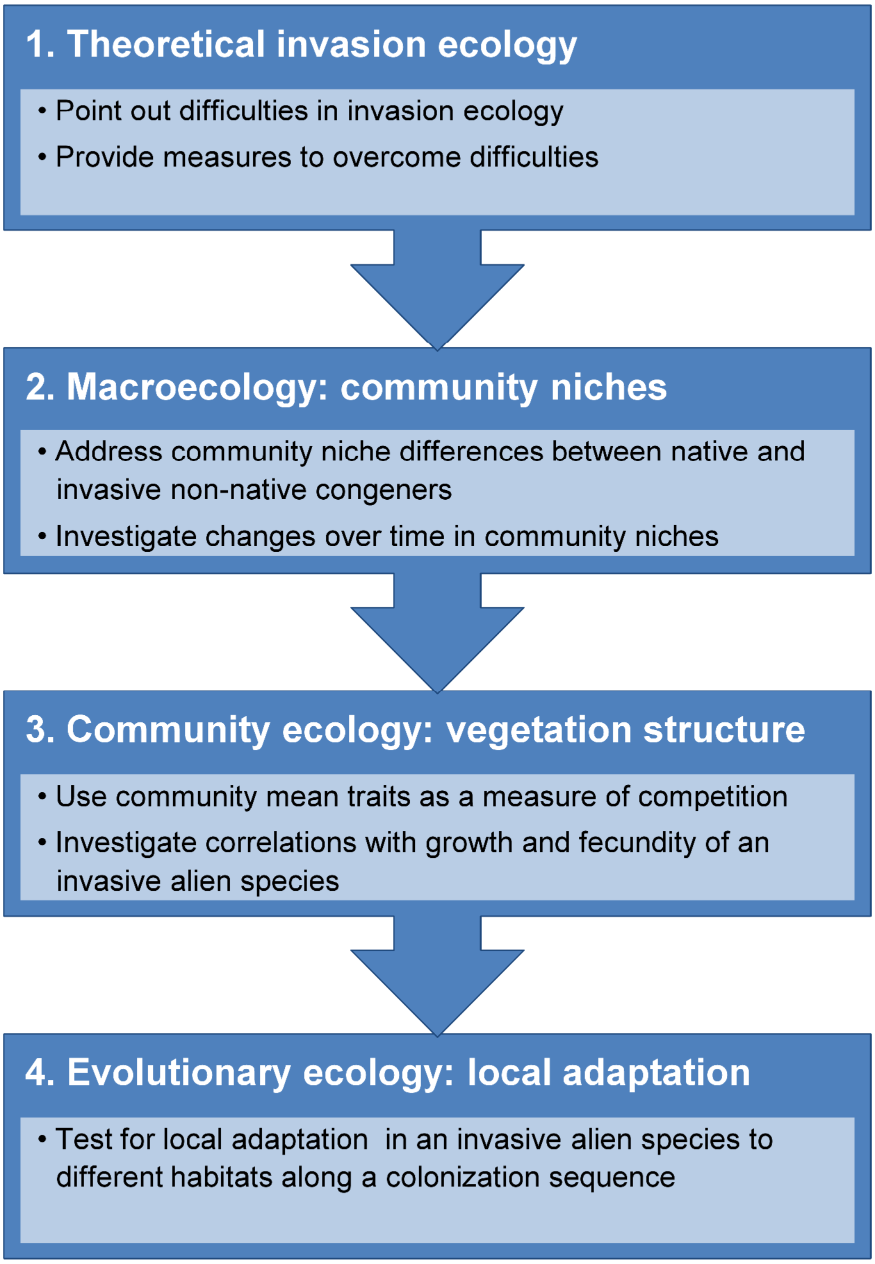
Evolutionary ecology

Evolutionary ecology is the field where ecologists and evolutionary biologists meet, sharing the common goal to understand the diversity of life, how it arises, how it is maintained, and why sometimes it is not (Mayhew, 2006). One core topic in evolutionary ecology is the study of variation within individuals, among individuals, among populations, and among species (Mazer & Damuth, 2001). Integrating an evolutionary perspective to invasion ecology is regarded as crucial, because conditions in a new environment may be considerably different from the native range, and this can present major adaptive challenges for invasive populations (Handley *et al.*, 2011).

It has been shown that evolutionary change can occur rapidly in invasive alien plants (Bossdorf *et al.*, 2005). Additionally, they may colonize additional habitats with different environmental conditions in a secondary stage of invasion (Dietz & Edwards, 2006). Within the invaded range, local adaptation to distinct habitat types has been proven for a number of species (Scott *et al.*, 2010; Godoy *et al.*, 2011b). When species invade habitats consecutively, a sequence of local adaptation that broadens the species ecological niche can be expected. However, ecological niches can also be broadened by high phenotypic plasticity (Richards *et al.*, 2006), and secondary invasions could also benefit from changes in propagule pressure.

Objectives

The objectives of this dissertation are to contribute to the theoretical development of invasion ecology, and to the understanding the most significant factors controlling plant invasions in the realms of the mentioned disciplines. The aims directly relate to the four disciplines, and are addressed in the four chapters of the dissertation (Fig. 2), i.e., (1) improving the conceptional basis of invasion ecology, (2) macroecological work on community niches, (3) mechanistic-ecological understanding of competition and vegetation structure, and (4) evolution during the invasion process.



1. Theoretical invasion ecology
- Point out difficulties in invasion ecology
- Provide measures to overcome difficulties

2. Macroecology: community niches
- Address community niche differences between native and invasive non-native congeners
- Investigate changes over time in community niches

3. Community ecology: vegetation structure
- Use community mean traits as a measure of competition
- Investigate correlations with growth and fecundity of an invasive alien species

4. Evolutionary ecology: local adaptation
- Test for local adaptation in an invasive alien species to different habitats along a colonization sequence

Fig. 2 Selected fields within invasion ecology that are especially promising. Main objectives for each field are given.

Chapter 1 – Theoretical invasion ecology: conceptual frameworks

Invasion ecology seems to struggle with the task to prove or to reject hypotheses on a large scale or to come up with a unified framework. To advance this process and to improve effectiveness of basic and applied research on invasions, difficulties that invasion ecology is currently facing are tackled. Circumstances that hinder or complicate basic or applied research in invasion ecology are assessed. Difficulties arising from three main domains are discussed, i.e., (A) society's impact and perception, (B) the peculiarity of the invasion process, and (C) the scientific methodology – with a special focus on the last domain. Progress can be made by overcoming the difficulties, and three key measures to do so are proposed.

Chapter 2 – Macroecology: community niches

The main objective of the second chapter is to address community niche differences between native and invasive non-native species, and their changes over time on a large spatial scale. It is hypothesized that relative frequency of invasive alien plant species compared to similar native taxa increases with time. Due to the ongoing colonization of additional habitats and plant communities, it is hypothesized that niche width is smaller in invasive alien species than in similar native taxa, and that the niche width of invasive species increases over time. Finally, the question is addressed if biotic homogenization leads to increased overlap in niches of invasive alien plants and similar native taxa.

Chapter 3 – Community ecology: vegetation structure

The third chapter seeks to identify significant relationships between community mean functional traits related to competition, and the growth and fecundity of a selected plant in its native and invaded range. As a basis for this, intercontinental variation in growth and fecundity of the study species is assessed. The proposed approach may be a useful new method for the selection of suitable species in restoration and management of invaded sites.

Chapter 4 – Evolutionary ecology: local adaptation

The main objective of the last chapter is to test for local adaptation in an invasive plant along a colonization sequence. It is hypothesized that local origins have a higher fitness compared to foreign ones when reciprocally sown to three different habitats. Additionally, it is tested if plants from the three habitats have higher fitness under greenhouse treatments that reflect the main environmental differences between the habitats. Finally, the question is addressed if local adaptation is more pronounced in habitats that have been colonized for a longer time.

Study systems

The study systems are briefly introduced to facilitate understanding and evaluation of the four chapters. The main study region was central Europe with a special focus on Germany. Nevertheless, data from other regions was also included to enable a comparison of populations in the native and invaded range of one species (Chapter 3). To answer the questions a set of study species was selected that spans the gradient from short-lived annuals to woody plants. Studied habitats include highly invaded ecosystems such as ruderal sites and wetlands, but also forest ecosystems.

Study regions

Due to history, central Europe has been an important area for species introductions for a very long time period (Kowarik, 2010). Introductions to central Europe already started with the human colonization in the Neolithic age (ca. 7000 years ago), but intercontinental exchange of species only started with the discovery of the Americas ca. 500 years ago, and increased significantly with the industrial revolution ca. 150 years ago. Since ca. 15 years, genetically modified organisms ('GMO') contribute as a new dimension to biological invasions (Kowarik, 2010).

The study region addressed in Chapter 2 is Germany as a part of central Europe. Despite of problems associated with using national borders to describe ecological phenomena, this was a useful choice as far as data from databases were compiled, and databases often have a national scope. In Chapter 3, plant communities within the native and invaded range of the perennial plant *Lythrum salicaria* were surveyed. Therefore, beside Bavaria in central Europe, three further study regions were used, i.e., the Greater Oslo area in southern Norway, which is also in the native range of the species, the St. Lawrence region in southeastern Canada, and upper New York State in northeastern USA; the latter two have been invaded for a relatively long time period by the species. In Chapter 4, adaptation of an invasive alien plant to different habitats is studied on a local scale. Therefore, a small study area of only ca. 140 km² in southern Germany was chosen that contained the addressed habitats.

Study species

Recently, Kueffer *et al.* (2013) suggested to use model organisms for in-depth research in invasion ecology. For this dissertation, five study species (Fig. 3; Table 1) were chosen mainly based on their suitability to answer the questions of each chapter. Moreover, the selected species are among the most problematic invaders and best-studied invasive alien species, and meet the criteria that define promising model organisms by Kueffer *et al.* (2013): (1) well-studied species for which data, tools, infrastructure and knowledge are available, (2) versatile species that are suitable for studying multiple questions, and are attractive to funding agencies and collaborators, (3) amenable species that are useful for studying and experiments because of their characteristics and accessibility, and (4) diverse sets of species covering a broad range of life forms, habitats and regions.

To study niche differences between invasive alien plants and similar native taxa (Chapter 2) it was necessary to choose species with native congeners available. Additionally, species had to be abundant in the study area for some time to increase their representation in vegetation databases. *Impatiens parviflora*, *Solidago canadensis*, and *Prunus serotina* met these criteria, and allowed to study a spectrum of life forms. To study intercontinental patterns in the native and introduced range of a species (Chapter 3), it was necessary to select a well-established invasive species occurring in relatively similar plant communities over a large range.

The prominent invader *Lythrum salicaria* was highly suitable, because this species has been studied in detail, and background information was particularly good. To study local adaptation to different habitats on a colonization sequence (Chapter 4), a species was needed that colonized different habitats consecutively. Additionally, a short life cycle was important to allow for potentially fast genetic evolution. *Impatiens glandulifera* met these criteria, and was also easy to handle in experiments because of good germination and vigorous growth.

Moreover, the study species have been well investigated. *Lythrum salicaria* and *Impatiens glandulifera* are among the most intensively studied invasive plants (Pyšek *et al.*, 2008; Kueffer *et al.*, 2013). *Lythrum salicaria*, *Solidago canadensis*, and *Impatiens glandulifera* together with its congeners were explicitly suggested as model organism for future research by Kueffer *et al.* (2013); and congeneric comparisons in the genus *Impatiens* were also encouraged. It was intended to work with a diverse set of invasive alien species, spanning from annuals over perennials to woody species. To enhance the relevance of the results invasive alien plants were selected that are known to have an ecological impact, e.g., the displacement of or competition with native plants. The selected species were introduced to the study areas ca. 160–350 years ago, and started spreading ca. 100–200 years ago, but are mostly still in the expansive stage of invasion.

Lythrum salicaria

Impatiens glandulifera

Impatiens parviflora

Prunus serotina

Solidago canadensis

Fig. 3 Pictures of the main study species (see Table 1 for further information on the species; picture of *Prunus serotina* by Johannes Kollmann).

Table 1 Main characteristics of the five selected study species.

	***Impatiens glandulifera* Royle**	***Impatiens parviflora* DC.**	***Lythrum salicaria* L.**
Family	Balsaminaceae	Balsaminaceae	Lythraceae
Common name	Ornamental jewelweed[2]	Smallflower touch-me-not[2]	Purple loosestrife[2]
German name	Drüsiges Springkraut[1]	Kleines Springkraut[1]	Blut-Weiderich[1]
Life form	Therophyte[1] (annual)	Therophyte[1] (annual)	Hemicryptophyte[1] (perennial)
Reproduction	Seeds[3]	Seeds[1]	Seeds and vegetatively[3]
Native range	Himalaya[1]	North-eastern Asia[1]	Europe, Asia[1]
Main habitats	(no information)	(no information)	Wetlands[1]
Invaded range	Europe, New Zealand, North America[3]	Europe[4]	Australia, North America, Africa[3]
Main habitats	Coniferous forests, deciduous forests, fallow meadows, riverbanks, weed communities[1]	Coniferous forests[1], deciduous forests[1], weed communities[1]	Wetlands[3]
Main impacts	Displacement of native plants[3], increasing erosion[3], competition for pollination[3]	Competition with native plants[1]	(?) Displacement of native plants[3], (?) reduction of invaded sites suitability for wildlife and recreation[3]
Study	Chapter 4	Chapter 2	Chapter 3
Study area(s)	Freising, Germany	Germany	SE Canada; NE USA (S Norway; S Germany)[6]
Introduction	ca. 160 years ago	ca. 180 years ago	ca. 200 years ago
Spread	ca. 100 years ago	ca. 130 years ago	ca. 200 years ago

	Prunus serotina **Ehrh.**	***Solidago canadensis*** **L.**
Family	Rosaceae	Asteraceae
Common name	Black cherry[2]	Canada goldenrod[2]
German name	Späte Traubenkirsche[1]	Kanadische Goldrute[1]
Life form	Nanophanerophyte, phanerophyte[1] (woody)	Geophyte, hemicryptophyte[1] (perennial)
Reproduction	Seeds and resprouting[4]	Seeds and vegetatively[1]
Native range	Eastern North America[1]	North America[1]
Main habitats	Forests[4], woodland[4]	Forests[1], prairies[1], ruderal sites[1]
Invaded range	Europe[4]	Europe, Australia, New Zealand, Japan, China, Taiwan, Caucasia, Siberia[5]
Main habitats	Coniferous forests[1], deciduous forests[1]	Deciduous forests[1], meadows[1], riverbanks[1], ruderal sites[1], weed communities[1]
Main impacts	Competition with native plants[4], alteration of humus composition[4], toxicity[4]	Displacement of native plants[1]
Study	Chapter 2	Chapter 2
Study area	Germany	Germany
Introduction	ca. 330 years ago	ca. 350 years ago
Spread	ca. 190 years ago	ca. 160 years ago

[1] www.floraweb.de; www.floraweb.de/neoflora/ (19 September 2013)
[2] http://plants.usda.gov (19 September 2013)
[3] http://www.issg.org (19 September 2013)
[4] www.europe-aliens.org (19 September 2013)
[5] www.nobanis.org (28 November 2013)
[6] See Table 8; Fig. 9
(?) These impacts are disputed (see Lavoie, 2010)

Study habitats

Invasive alien plants occur in all habitats of Europe (Kowarik, 2010). Highest levels of invasion are found in habitats that are associated with human- and water-induced disturbances, high fertility, and high propagule pressure (Chytrý *et al.*, 2008). The selected study species mainly occur in ruderal sites and weed communities, open wetlands and (fallow) meadows, and woodlands and forests (Fig. 4). Therefore, these three broad habitat categories are briefly introduced here.

Ruderal habitats and weed communities

Ruderal habitats are characterized by ample supply of nutrients, water, light and warmth as well as high levels of disturbance (Jansen *et al.*, 2011), and are among the most invaded habitats in central Europe. It has been shown that a high proportion of ruderal plants is a reliable predictor of alien plant invasion (Jansen *et al.*, 2011), which is in accordance with the fluctuating resource availability theory by Davis *et al.* (2000). It is not surprising that many alien plants grow well in disturbed habitats as many of them are ruderals (Hierro *et al.*, 2006). Some of the most frequent invasive alien plants in central European ruderal habitats are *Ailanthus altissima*, *Ambrosia artemisiifolia*, and *Senecio inaequidens*. Additionally, three of the study species occur frequently in ruderal habitats and weed communities, i.e., *Impatiens parviflora, Solidago canadensis*, and *Impatiens glandulifera* (see Table 1).

Open wetlands and (fallow) wet meadows

Open wetlands and fallow wet meadows include a variety of open habitats with soil conditions ranging from moist to wet. Disturbance intensity and nutrient inputs span a broad gradient in these habitats, because management and use through humans are highly variable. For example, wet grasslands are infrequently disturbed and subject to nutrient pulses of variable intensity, while base-rich fens are only occasionally disturbed and nutrient pulses are rather low (Pyšek *et al.*, 2010). Invasive alien plants rarely become dominant in regularly used central European meadows, but if sites are abandoned, colonization by invaders becomes more likely (Kowarik, 2010). Invasive species that are often found in fallow meadows include *Solidago canadensis*, *Solidago gigantea*, and *Impatiens glandulifera.*

Central European fens and peatlands do not harbor many invasive alien plants as long as they are quite pristine, but if wetlands are drained, invasion can become an important issue (Kowarik, 2010). Prominent invaders of drained fens in central Europe are e.g., *Heracleum mantegazzianum*, and *Fallopia japonica*, while *Vaccinium angustifolium x V. corymbosum* is an example of an alien plant invading peatlands. It has been argued that wetlands are especially vulnerable to invasions, because they act as landscape sinks that accumulate debris, sediments, water, and nutrients which facilitates invasion (Zedler & Kercher, 2004). The central European native *Lythrum salicaria* is a prominent invasive alien plant in North American wetlands. Overall, three of the study species occur in wetlands and wet meadows, i.e., *Impatiens glandulifera, Lythrum salicaria*, and *Solidago canadensis* (see Table 1).

Ruderal habitat invaded by *Solidago canadensis*.

Wetland invaded by *Lythrum salicaria*.

Coniferous forest invaded by *Impatiens glandulifera*.

Fig. 4 Pictures of three of the study habitats in Bavaria (upper picture by Johannes Kollmann).

Woodlands and forests

Woodlands and forests in central Europe harbor less invasive alien plants than other habitats, but this is rather a consequence of dispersal limitation than resistance to invasion (Kowarik, 2010). For these habitat types, distinction of coniferous and deciduous forests as well as of woodland and artificial plantations is important. In deciduous woodlands disturbances and pulses of high nutrients are generally rare, while in coniferous plantations strong disturbances pulses of nutrients are present in the initial establishment (Pyšek *et al.*, 2010). Riverine alluvial deciduous forests are another habitat that is characterized by high disturbance and nutrient input. As waterways are known to act as dispersal corridors for many invasive alien species such as *Impatiens glandulifera* (Malíková & Prach, 2010), they harbor many invasive alien plants. Most of the study species occur in coniferous and/or deciduous forests, i.e., *Impatiens glandulifera*, *Impatiens parviflora*, *Prunus serotina*, and *Solidago canadensis* (see Table 1).

Methodological overview

This dissertation combines a variety of methods, i.e., conceptual methods (Chapter 1), the analysis of a large amount of vegetation data compiled from databases (Chapter 2), a descriptive intercontinental field survey (Chapter 3), a manipulative field and greenhouse experiment (Chapter 4). Statistical analyses also involve a set of different approaches, including ordination (Chapter 2), analysis of variance and Kruskal-Wallis test (Chapter 3), multiple linear regression (Chapter 3), and finally linear mixed models (Chapter 4). Throughout the dissertation statistics were calculated using the open-source software R (Crawley, 2009; R Core Team, 2013). The complementary use of different up-to-date methods was especially promising, and the use of big sample sizes enhances the relevance of the results.

Chapter 1 – Theoretical invasion ecology

The approach taken to address current difficulties in the scientific field of invasion ecology and develop measures to overcome these difficulties was based on expert discussions. In March 2010 a workshop of the specialist group 'Theory in ecology' of the Ecological Society of Germany, Austria, and Switzerland (GfÖ) on '*Tackling the emerging crisis of invasion biology: how can ecological theory, experiments, and field studies be combined to achieve major progress*' was held in Benediktbeuern, Germany (organized by Tina Heger, Sylvia Haider, Anna T. Pahl & Jonathan M. Jeschke); 22 participants from six countries discussed and summarized existing difficulties in invasion ecology, and developed measures to overcome them (Heger, 2010). Group discussions can be a useful approach to identify research priorities and emerging issues (Sutherland *et al.*, 2011). Discussions during the workshop were very fruitful, and results were summarized afterwards by a subgroup of the participants.

Chapter 2 – Macroecology

Community niche differences between native and invasive non-native species and their changes over time were addressed in three pairs of congener plant species representing different life forms, including always one native and one invasive non-native species. Phytosociological relevés with the selected species from Germany were compiled from several databases listed in the 'Global Index of Vegetation-Plot Databases' (Jansen *et al.*, 2012a). Ecological variation in relevés was analyzed using ordination and calculation of Whittaker's β-diversity.

Chapter 3 – Community ecology

Populations in two native and two introduced areas were sampled to assess patterns in growth and fecundity of the study species. Plant height, cover, and total cumulative shoot length served as measures of growth and fecundity. To assess the competition in the community, plant species in a plot around the study species were sampled and their cover measured. While plant height of each species in the plot was measured directly, other traits related to competition were compiled from the TRY database (Kattge *et al.*, 2011b). Community mean traits weighted by abundance were calculated for each plot. Relationships between multiple community mean traits related to competition, and growth and fecundity of the study species were investigated using multiple linear models.

Chapter 4 – Evolutionary ecology

Local adaption in the study species to different habitats along a colonization sequence was studied by using a reciprocal field experiment and a greenhouse experiment. Seed material of five populations from each of the three different habitats was used in both experiments. Treatments in the greenhouse included the main differentiators between the three habitats, i.e., shade, soil acidity, and competition. Plant biomass was used as a proxy for fitness. Additionally, specific leaf area, plant height, and relative growth rate were measured to detect plastic responses to the main habitat differentiators. Linear mixed models were used to analyze the data.

CHAPTER 1

CONCEPTUAL FRAMEWORKS AND METHODS FOR ADVANCING INVASION ECOLOGY

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Abstract

Invasion ecology has much advanced since its early beginnings. Nevertheless, explanation, prediction, and management of biological invasions remain difficult. We argue that progress in invasion research can be accelerated by, first, pointing out difficulties this field is currently facing and, second, looking for measures to overcome them. We see basic and applied research in invasion ecology confronted with difficulties arising from (A) societal issues, e.g., disparate perceptions of invasive species; (B) the peculiarity of the invasion process, e.g., its complexity and context dependency; and (C) the scientific methodology, e.g., imprecise hypotheses. To overcome these difficulties, we propose three key measures: (1) a checklist for definitions to encourage explicit definitions; (2) implementation of a hierarchy of hypotheses (HoH), where general hypotheses branch into specific and precisely testable hypotheses; and (3) platforms for improved communication. These measures may significantly increase conceptual clarity and enhance communication, thus advancing invasion ecology.

Keywords

communication platforms • definitions and terminology • hierarchy of hypotheses

• invasive alien species • synthesis • transdisciplinarity

Introduction

Studying biological invasions can yield insights into numerous basic ecological, evolutionary, and biogeographical topics (Sax *et al.*, 2005). As some invasive species threaten biodiversity, are vectors of human diseases, and cause socio-economic costs, their investigation also has an applied focus. From its beginning, invasion ecology has combined these basic and applied aspects. The first written accounts of invasive species date back to the eighteenth century (Chew, 2006), but the publication of Elton's (1958) book "The ecology of invasions by animals and plants", which conveys an explicit conservation point of view, is generally considered to be the starting point of focused research on biological invasions (Richardson & Pyšek, 2008). In the 1980s, invasion ecology emerged as a specific research field (Richardson & Pyšek, 2007). This was in part due to the international program of the Scientific Committee on Problems of the Environment (SCOPE) on biological invasions (Drake *et al.*, 1989). The program focused on three questions, again addressing basic as well as applied aspects: (i) What factors determine whether a species will become an invader or not? (ii) What are the properties that determine whether an ecological community is vulnerable or resistant to invasions? (iii) How should effective management strategies be developed?

Some answers to these questions are now available, and have been summarized in various journal articles and books (Lockwood *et al.*, 2007; Blackburn *et al.*, 2009; Davis, 2009; Richardson, 2011a). Based on Elton's work and the SCOPE program, invasion ecologists have produced plenty of hypotheses and data. New methods such as modeling approaches, multi-scale comparisons and molecular methods are being applied, and new topics such as *propagule pressure* (the pattern in which propagules arrive; Simberloff, 2009) and post-introduction evolution have been raised (Richardson & Pyšek, 2008). It should be expected, thus, that knowledge has increased considerably since the beginning of invasion research. Nevertheless, progress towards satisfactory explanation and prediction of invasions as well as management of invasive species is rather slow (Puth & Post, 2005; Lockwood *et al.*, 2007; Blackburn *et al.*, 2009; Davis, 2009; Richardson, 2011b; Moles *et al.*, 2012).

Several authors have already called for an improvement of the implementation of existing knowledge into policies and management (Hulme, 2006; Lodge *et al.*, 2006). In this paper, we focus on invasion science itself: We think there is much potential for improving the effectiveness of basic and applied research on invasions. We argue that progress in invasion ecology can be accelerated by, first, explicating difficulties that basic and applied research on invasions are facing today and, second, developing measures to overcome them. By difficulties, we here mean circumstances that hinder or complicate basic or applied research. Difficulties for invasion ecology arise from: (A) society's impact and perception; (B) the peculiarity of the invasion process; and (C) the scientific methodology. Overlaps between these three domains exist, but this classification is helpful to structure our considerations. In Table 2, Table 3, and Table 4, we summarize difficulties of all three domains as well as measures to overcome them. Some of these difficulties and measures have been pointed out before and are covered by the references provided. Here, our focus is on new possibilities to improve the effectiveness of basic and applied research on biological invasions, especially regarding domain C.

Table 2 Invasion ecology is confronted with three domains of difficulties. Domain A: Difficulties arising from society and its relationship to biological invasions, measures that can be taken to overcome them and consequences for the scientific approach of invasion ecology; letters and numbers in parentheses refer to Table 4.[1]

	Difficulty	**Measures**	**Consequences for the scientific approach**
A1	Deliberate introductions, influenced by commercial interests and changing fashions	• Risk assessment protocols • Black, white and gray lists[i] • International cooperation to prevent trade with risky species[ii] • Raising public awareness[iii]	• Commercial interests and changing fashions should be considered for explanation and prediction (C8)
A2	Accidental introductions, promoted by globalization	• Quarantine measures[iv] • International cooperation to prevent accidental introductions[2] • Raising public awareness[3]	• Changes in transportation pathways should be considered for explanation and prediction (C8)
A3	Inconsistent evaluation of invasive species	• Development of management strategies based on knowledge about public attitudes[v]	• Public attitudes should be investigated and considered (C8)
A4	Little motivation for management measures due to little prospect of success[vi]	• Improve information about feasibility of management strategies[vii]	• Need for clear management guidelines (C6)

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[i] Verbrugge et al. 2010
[ii] Perrings et al. 2010b
[iii] Bremner and Park 2007, Burt et al. 2007, Byron 2008
[iv] Mack et al. 2000, Moore et al. 2010
[v] Fischer and van der Wal 2007
[vi] Andreu et al. 2009
[vii] Bodey et al. 2010

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Domain A: difficulties arising from society and its relationship to biological invasions

Society causes biological invasions, and biological invasions influence society. This feedback not only complicates effective prevention and management (A1–A4 in Table 2) but also has consequences for the scientific approach (right column in Table 2). An example is the perception of invasive species by the general public. The general public has only limited knowledge of the phenomenon of biological invasions (Gellis Communications, 2008), and perception as well as evaluation of invasions are not at all homogeneous across societal groups (Fischer & van der Wal, 2007; Gherardi, 2011; Rotherham & Lambert, 2011) (A3 in Table 2). Especially in case of deliberate introductions related to agriculture, forestry, fisheries, and biological control, species can cause benefits as well as costs (Gozlan, 2008). Thus, species ranked as highly problematic by conservation scientists sometimes are regarded as not harmful or even desirable by the public. For example, conservation scientists perceive the tree of heaven (*Ailanthus altissima*) as a harmful invader with the potential to threaten native species; on the other hand, many people on the Mediterranean islands appreciate its ability to grow on dry soils and to provide shade (Bardsley & Edwards-Jones, 2007).

Such disparate perceptions have consequences for applied research on invasions: research on managing invasions and strategies tailored to address actual societal needs cannot be efficient unless these needs are uncovered. An increasing amount of work already aims to include social and economic demands into invasion research (Fischer & van der Wal, 2007; Berghöfer *et al.*, 2010; Perrings *et al.*, 2010a). Such efforts are in high demand, and more inter- and transdisciplinary collaborations should be established to foster them (Richardson, 2011b; see below).

Domain B: difficulties arising from the peculiarity of the invasion process

In addition to problems related to society, a major obstacle for research is that invasion processes are notedly difficult to analyze, explain, and predict. Invasion processes are complex (Lodge, 1993; Hayes & Barry, 2008) (B1 in Table 3) and context-dependent (Zedler & Kercher, 2004; Gurevitch *et al.*, 2008; Blackburn *et al.*, 2009) (B2 in Table 3). This creates the need for methods that are able to explain and predict multiple interacting influences (Heger & Trepl, 2003), and to take into account the history of current invasions for their explanation (Cassey *et al.*, 2005) (see right column in Table 3).

Global transportation networks and other socio-cultural activities (such as horticulture or fishery) not only cause difficulties for the prevention and management of invasive species, but also create the need to integrate socio-cultural sciences into research (Kowarik, 2003;

Niggemann *et al.*, 2009; Tatem, 2009) (B3 in Table 3). One example is the spread of New Zealand bittercress (*Cardamine corymbosa*) to Europe and the U.S., which is largely due to a combination of ecological traits (e.g., active short-distance seed dispersal) and socio-economic activities that include international plant auctions and exchanges of container-grown plants among nurseries, garden centers, and private gardens (Hoste *et al.*, 2008). An increasing number of studies already integrate socio-cultural analyses into approaches to study invasions (Dehnen-Schmutz & Williamson, 2006; Skou *et al.*, 2012), and invasion ecologists increasingly collaborate with socio-cultural scientists. An example is the workshop organized by C. Kueffer, in Bielefeld, Germany, August 2012 (http://www.uni-bielefeld.de/(en)/ZIF/AG/2012/08-27-Kueffer.html), where half of the participants where socio-cultural scientists and the other half natural scientists. To improve effectiveness of explanation, prediction and management, similar efforts should be strengthened (see key measure 3 below).

Table 3 Invasion ecology is confronted with three domains of difficulties. Domain B: Difficulties caused by the peculiarity of the invasion process, and consequences for the scientific approach of invasion ecology; letters and numbers in parentheses refer to Table 4.[2]

	Difficulty	**Consequences for the scientific approach**
B1	Complexity: many different factors interact in determining invasion success	• Synthesis needed to integrate the interacting influence of multiple factors (C2)
B2	Context dependence: invader success varies in time and space	• Historic data are relevant (C4) • Case studies needed, but also synthesis (C2)
B3	Cultural influences at each stage of the process	• Socio-cultural sciences have to be integrated for explanation and prediction (C8)

Domain C: conceptual and methodological difficulties

Invasion ecology has to cope with several conceptual and methodological difficulties, many of which are related to or produced by society and the peculiarity of the invasion process (see right columns in Table 2 and Table 3). The scientific methodology in invasion research is facing difficulties concerning the conceptual basis and theory of invasion ecology (C1–C3 in Table 4), empirical research (C4 and C5 in Table 4), and the need for integration with other scientific disciplines and societal groups (C6–C8 in Table 4). We will focus on some particularly important difficulties and propose three key measures to overcome them.

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Table 4 Invasion ecology is confronted with three domains of difficulties. Domain C: Conceptual and methodological difficulties, and measures to meet them. C1 to C3 relate to the conceptual basis and theory of invasion ecology, C4 and C5 to empirical research, and C6 to C8 to the need of integration with other scientific disciplines and societal groups. Letters and numbers in parentheses refer to difficulties given in Table 2, Table 3.[3]

	Difficulty	**Measures**
C1	Terminology: unclear concepts and definitions	• Explicit definitions (see checklist in Box 1)
C2	Insufficient synthesis; sub-division of invasion ecology (e.g., taxonomic groups)	• Hierarchy of hypotheses (HoH) with precise, testable hypotheses at lowest level
C3	Imprecise hypotheses (a) different versions of hypotheses (b) lack of testability	• HoH
C4	Lack of data to test hypotheses (a) lack of data on unsuccessful introductions (b) lack of large-scale experimental data (c) lack of long-term data	• Funding of large-scale and long-term research • 'Indirect' methods (e.g., retrospective analyses and model simulations instead of long-term experiments) • Online databases • Citizen science and monitoring programs by the general public
C5	Bias in data collection (a) invasion events (most research on successful species in areas with high density of researchers) (b) methods of data collection	• Frequent reviews with connection to HoH; aim: identification of gaps and biases
C6	Necessity of communication of research results to concerned stakeholders (A4)	• Focus on output valuable for applications • Up-to-date networks and platforms • Joint conferences and discussions
C7	Complexity (B1) creates the need to integrate other biological subdisciplines	• Integration of HoH into other disciplines • Joint conferences and discussions
C8	Influence of socio-economic and cultural processes on invasions (A1, A2, B3) creates the need for transdisciplinary research	• Communication and collaboration with researchers of humanities and social sciences • Joint conferences and discussions

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Terminology: unclear terms and concepts

As many other research fields, invasion ecology is still plagued by the ambiguous use of terms and unclear concepts (Richardson *et al.*, 2011; McGeoch *et al.*, 2012) (C1 in Table 4). Inconsistent terminology can cause difficulties when it comes to the communication of research rationales and results, both within science, and between science and the broader public; therefore explicit definitions are needed. However, they are not equally necessary for all publications. General treatments of biological invasions (such as this publication) can cover different definitions of invasive species, whereas comparisons of sets of native and invasive species need explicit definitions and consistent applications of underlying concepts (van Kleunen *et al.*, 2010).

Creating a single set of definitions that suits all purposes seems impossible (Hodges, 2008), as different research goals create different ideas of what is peculiar about invasions (Kueffer & Hirsch Hadorn, 2008). We therefore suggest to accept that different stakeholders use different definitions (cf. Heger *et al.*, 2013a). However, it is important to clarify how *alien* or *invasive species* is defined by a given person or text. We propose to use the following checklist to achieve such clarity.

Key measure 1: checklist for explicit definitions

The checklist we suggest consists of five questions that are important to define alien species, and four additional questions for defining invasive species (Box 1). Depending on the research context (e.g., basic or applied focus), different answers are possible for each question. The references included below can help deciding which answers are most reasonable for a given context.

Question 1: How did the species arrive in areas beyond their native range? Is human-mediated transport regarded a condition to call a species alien? If the answer is 'yes', it should be stated how unintentional species introductions are distinguished from natural dispersal events. In cases where information on the pathway is lacking, proxies can be used (e.g., geographical distribution, see Webb, 1985). Additionally, it is helpful to state what is meant by human-mediated transport: are indirect effects of human action, e.g., habitat change, included or excluded? An excellent example clarifying this and similar aspects can be found in Pyšek *et al.* (2004).

Question 2: Are continuously spreading species ('leading edge dispersal', Wilson et al., 2009) regarded as alien? Climate change alters species distributions; hence spontaneous colonization events from neighboring geographic regions may become more frequent in the near future (Walther *et al.*, 2009). If continuously spreading species are not viewed as alien, the definition will need to include a criterion to distinguish continuous from non-continuous

Box 1 Checklist for definitions: questions that should be answered when defining alien or invasive species.[4]

ALIEN SPECIES

1. Is human-mediated transport a necessary criterion?

   If yes:
   - How are unrecorded, unintentional introductions distinguished from natural dispersal?
   - Does human mediation include indirect effects such as habitat change?

2. Are species that continuously expand their range regarded as aliens?

   If not:
   - Which criterion is used to distinguish continuous from non-continuous spread (e.g., distance between populations, existence of a barrier to dispersal)?

3. Are species that originate in the region by hybridization of alien and native species regarded as aliens?

4. Are species regarded as aliens if they evolved in the region, became extinct, and were reintroduced?

5. Are species regarded as aliens even if they have been present in the new region for quite a long time?

   If not:
   - After which time period do we consider them to be native?

INVASIVE SPECIES

6. Can native species also be invasive, or are invasive species a subset of alien species?

7. Is impact a necessary criterion?

   If yes:
   - How is impact defined? Which is the threshold to consider an impact relevant?

8. Is success a necessary criterion?

   If yes:
   - How is success defined? Indicators may be large distribution, high local abundance, or fast spread.

9. Is occurrence in natural habitats a necessary criterion?

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spread. For example, Richardson *et al.* (2000) suggested that a new occurrence of plant species should be regarded as alien if it is more than about 100 km away from the closest native population. Another option is to consider species as alien as soon as they overcome a species-specific barrier to dispersal (Heger & Trepl, 2003).

Question 3: Are species that originate in the region by hybridization of alien and native species regarded as aliens? In the strict sense of many definitions of alien species, these hybrids have to be regarded as natives, because they evolved in the region. If authors do not agree with this view, it should be stated clearly (see e.g., Pyšek *et al.*, 2004).

Question 4: *Are species regarded as alien if they evolved in the region, became extinct, and were re-introduced?* When answering this question, the time scale has to be explained. Some authors argue species that were native in an area but became extinct during the last glaciation should be viewed as alien (Webb, 1985; Pyšek *et al.*, 2004).

Question 5: Is residence time within an area regarded as an important criterion? In this case, it is useful to specify after which residence time a species is considered to be native (see Carthey & Banks, 2012).

The previous questions all relate to the term *alien species*; questions 6–9 can be used to clarify definitions of *invasive* species.

Question 6: Can native species also be called invasive? The term *invasive* species is sometimes used for species expanding their range, no matter whether they are alien or native (Myster, 1993; Valéry *et al.*, 2008; Catford *et al.*, 2009; Carey *et al.*, 2012). Davis (2009), as an example, proposes to focus on similarities between processes of species redistributions instead of trying to separate aliens from range-expanding native species (SPRED-ecology, pp. 191–192). It is useful to state whether this view is shared, or invasive species are regarded as a subset of alien species (see e.g., ISSG (2000) or Richardson *et al.* (2011) for respective definitions).

Question 7: Do invasive species necessarily have a negative impact in their new environment? Some definitions apply the term *invasive* to those alien species that spread, regardless of their effects in the new environment (e.g., Heger & Trepl, 2003). If impact is used as a condition (as e.g., in ISSG, 2000), it should be specified what kind of impact is meant, e.g., economic, social, and/or ecological impact, and which is the threshold to consider the impact relevant.

Question 8: Do invasive species have to be successful? Some authors propose that success is an important criterion to define invasive species (Valéry *et al.*, 2008). As *success* can be indicated by a large distribution, high local abundance, dominance, fast spread, or a combination of these, it should be explained which measure of success the definition uses.

Question 9: Do invasive species have to occur in semi-natural communities? As some alien species at first only occur in heavily modified habitats (Richardson *et al.*, 2000), the colonization of semi-natural or natural habitats is sometimes viewed as a useful criterion to define invasive species (Reichard & Hamilton, 1997). According to such definitions, alien species quickly spreading in agricultural habitats are excluded from the invasive species category.

Explicitly answering these nine questions can help solving the problem of unclear terminology. The implementation of this checklist could, for instance, be accomplished in a working group or regular symposia. Increased consciousness of a growing number of authors, editors, and reviewers will help to minimize misunderstandings and misinterpretations.

Invasion theory: lack of synthesis and imprecise hypotheses

Each of the many existing hypotheses in invasion ecology covers specific aspects of the general mechanisms behind biological invasions. Some recent studies offer ideas for a synthesis of invasion theory (Colautti & MacIsaac, 2004; Blumenthal, 2006; Catford *et al.*, 2009; Davis, 2009; Gurevitch *et al.*, 2011). These approaches each put together different pieces of available knowledge in a specific and valuable way, but each approach is limited in what it covers. Additionally, invasion ecology still struggles to overcome a taxonomic bias, especially a division into plant-oriented studies on the one hand and animal-oriented studies on the other hand (Pyšek *et al.*, 2008; Jeschke *et al.*, 2012b). As a result, our overall knowledge about the mechanisms driving invasions is still patchy. Although a few treatments of both invasive plants and animals are available (Blackburn *et al.*, 2011), a general synthesis of invasion ecology is still missing (C2 in Table 4).

As an additional difficulty, studies testing widely used hypotheses often report contradictory results (Jeschke *et al.*, 2012a; Moles *et al.*, 2012). This is oftentimes due to the context dependency of invasions (see above). Contradictory results become a problem as soon as the respective hypothesis is at stake: it is not clear if hypotheses with ambiguous evidence are worth keeping, or if they should be discarded (cf. Jeschke *et al.*, 2012a). For example, the biotic resistance hypothesis (also known as 'diversity-invasibility hypothesis') states that ecosystems with a high biodiversity are more resistant to invaders than ecosystems with a low biodiversity (Elton, 1958; Levine & D'Antonio, 1999; Mack *et al.*, 2000; Fridley *et al.*, 2007b; Davis, 2009). Several small-scale experiments have supported this hypothesis, whereas large-scale studies hardly ever do so (Fridley *et al.*, 2007b). The latter sometimes even show the opposite pattern of what is predicted (Levine, 2000; Stohlgren *et al.*, 2003; Stohlgren *et al.*, 2006). Second, the enemy release hypothesis (Keane & Crawley, 2002), which states that the absence of enemies is one cause of invasion success, is supported by several studies (Wolfe, 2002; Mitchell & Power, 2003), but questioned by others (Frenzel & Brandl, 2003; te Beest *et al.*, 2009).

One reason for these contradictory results is that considerable variation exists with respect to the wording of many current hypotheses (C3a in Table 4), and studies addressing them are not always explicit about which version they focus on. If two studies claim to test a certain hypothesis but are in fact testing different variants of this hypothesis, they may have opposite conclusions even if their empirical results are similar. The biotic resistance hypothesis, for example, is sometimes formulated as above, stating that ecosystems with a high biodiversity are more resistant to invaders than ecosystems with a low biodiversity. According to another, very general formulation of this hypothesis, ecosystems with a high biodiversity and a low level of disturbance should be more resistant to invaders than ecosystems with a low biodiversity and a high level of disturbance (Jeschke & Genovesi, 2011). Yet another formulation focuses on disturbance and leaves out diversity (Mack *et al.*, 2000), and other factors have also been tested to see if they influence an ecosystem's resistance to invaders, e.g., the presence of keystone predators (Carlsson *et al.*, 2010).

A related difficulty is that many existing versions of hypotheses are too imprecise to be actually testable (C3b in Table 4). In fact, the number of variants of some hypotheses probably keeps rising exactly because existing versions are not testable. The biotic resistance hypothesis in the version stating that ecosystems with a high biodiversity are more resistant to invaders than ecosystems with a low biodiversity can be tested only if 'biodiversity' and 'resistance' are specified. Existing studies have quantified biodiversity in different ways, for example by measuring richness of native species (Arndt, 2006; Capers *et al.*, 2007) evenness (Wilsey & Polley, 2002; Mattingly *et al.*, 2007). Resistance has also been quantified in different ways, for example, by counting the number of invasive species (assuming that fewer invasive species will be found in resistant ecosystems as compared to other ecosystems; e.g., Arndt, 2006; Capers *et al.*, 2007), or by calculating the fraction of introduced species that have become established (Blackburn & Duncan, 2001; Jeschke & Genovesi, 2011). Existing studies have thus focused on different forms of biodiversity and resistance (see also Jeschke *et al.*, 2012a), and have consequently tested different formulations of the resistance hypothesis, in most cases without stating which exact version of the hypothesis has been addressed.

Another example is the enemy release hypothesis. Its general version contains several different possible mechanisms and processes, hence no single study can be designed to test it in its full extent. Studies addressing enemy release can only focus on some of its aspects, and often do so without explicitly discussing this limitation. For example, some studies compare populations of invasive species in the new range to populations of the same species in the indigenous range and quantify infestation, i.e., abundance or diversity of predators or parasites that can be found on the species (Mitchell & Power, 2003; Vignon *et al.*, 2009). Other studies use the same comparison but quantify damage typically caused by predators, e.g., leaf damage (Lewis *et al.*, 2006; Ebeling *et al.*, 2008). Another approach is to compare invasive to similar or related native species, and again, in some cases infestation is quantified (Frenzel & Brandl, 2003; Blakeslee & Byers, 2008), in others damage (Carpenter & Cappuccino, 2005; Sugiura, 2010). The case is even more complicated by the fact that some comparisons analyze the importance of generalist predators (Jogesh *et al.*, 2008), others that of specialist predators (Memmott *et al.*, 2000; Liu *et al.*, 2007). It is often stated that the data confirm or reject the enemy release hypothesis without stating that only some aspects have been tested (see also Davis, 2011).

Key measure 2: a hierarchy of hypotheses (HoH)

The difficulty of imprecise hypotheses and lacking synthesis can be overcome by what we call a hierarchy of hypotheses (HoH). We suggest arranging hypotheses in an inverted tree-like structure, in which general hypotheses (i.e., hypotheses including too many aspects to be tested in single case studies) at the top branch into more and more specific hypotheses at the bottom. The most specific hypotheses (at the bottom) are very precise, and each can be approached with case studies. An accumulation of evidence for or against individual hypotheses can then help evaluate the more general predictions represented by this branch (cf. Jeschke *et al.*, 2012a).

A HoH is able to structure the various aspects contained within many existing hypotheses. Let us use the enemy release hypothesis as an example. Its general formulation can be situated at the top of a branch (Fig. 5). A hypothesis addressing the rate of infestation in the new compared to the native range could be situated below, and further branch into hypotheses focused on generalist or specialist predators only (Fig. 5). Other lower-level hypotheses and aspects of the enemy release hypothesis could be fanned out in the same way; where necessary, hypotheses could also be specified with respect to certain taxa or habitats.

Such an explicit formulation of testable lower-level hypotheses could be used to structure research on biological invasions. Every study could explicitly state which lower-level hypothesis is tested, whether it is confirmed or rejected, and what that means for higher-level hypotheses. To construct a HoH for invasion ecology will not be easy, and it has to be worked out how exactly the lower-level hypotheses contribute to the rejection or confirmation of the higher-level hypotheses. We think of a HoH as an evolving structure, at all times able to integrate new insights. As soon as it is constructed, it will be much easier than it is today to see whether lower-level hypotheses for a given higher-level hypothesis reach similar levels of empirical support, or whether certain lower-level hypotheses are better supported than others. Furthermore, it would be possible to see which hypotheses apply under which environmental conditions, for which scales, for which taxonomic groups and habitats. In other words, important information would be available to decide which hypotheses are valuable as a basis for prediction and management for given conditions.

Within a HoH, higher-level hypotheses are also connected to each other. For example, the enemy release hypothesis is connected to the novel weapons hypothesis. The latter hypothesis suggests that invasive species can have a competitive advantage over native species because they possess a trait that the native species are not evolutionarily adapted to and therefore affects them negatively (Callaway & Ridenour, 2004). A shared idea is that missing eco-evolutionary 'experience' of the resident species with the invader can be advantageous for alien species. We suggest calling this the 'lack of eco-evolutionary experience hypothesis' (Fig. 5).

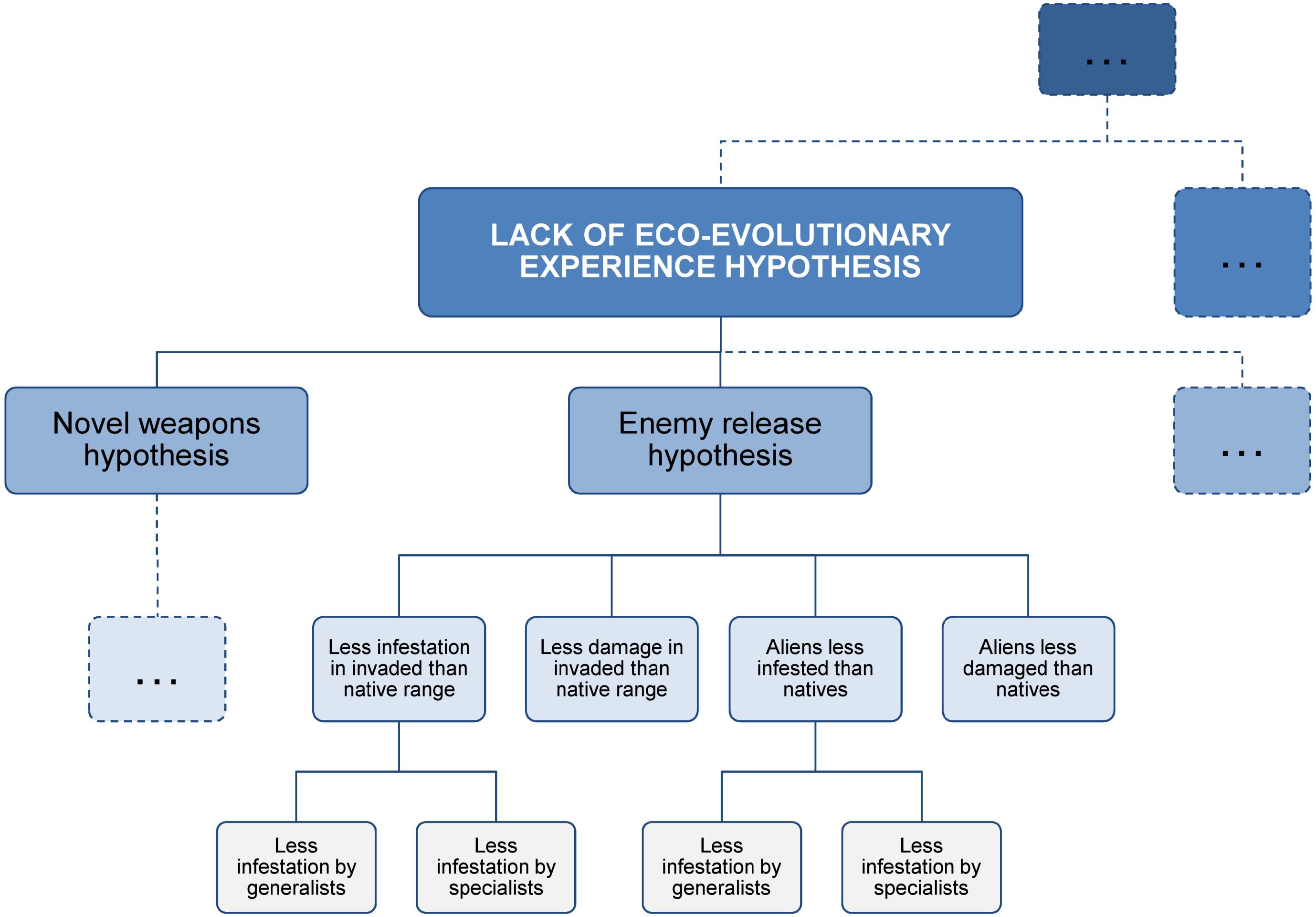

Fig. 5 Sketch of a possible hierarchy of hypotheses (HoH) for invasion ecology. Overarching ideas branch into more precise, better testable hypotheses at lower levels. ‘Infestation’ means abundance or diversity of predators or parasites that can be found on the species. Empty boxes indicate that the hierarchy may be extended (Included here with kind permission from Springer Science+Business Media B.V. (original copyright). Box 1 in Heger et al. (2013, *Ambio* 42: 527-540).).

In a HoH for invasion ecology, every existing hypothesis would find its place within an interlinked system of other hypotheses. Every hypothesis could be classified as a basic building block at a lower level (i.e., testable but with small cover and extent) or be located at a higher level. Different formulations of similar ideas (e.g., formulations of the biotic resistance hypothesis described above) could be neighbors on one level and be integrated into an overarching idea at a higher level. In this way, a novel possibility for synthesis becomes visible. Research could aim at precisely determining which hypotheses hold in which situations, finding more and more interconnections among hypotheses and ideas, and search for more higher-level theories synthesizing those at lower levels. Future research should focus on building and maintaining such a HoH. It could be implemented as an online tool and updated regularly to integrate new data and hypotheses.

Empirical evidence: lack of data and biases in data collection

In addition to conceptual issues, a lack of data to test hypotheses (McGeoch *et al.*, 2010) is a difficulty in invasion ecology (C4 in Table 4). For example, information on failed invasions following accidental introductions is often not available, especially for plants and invertebrates, sometimes not even for vertebrates. This problem affects many hypotheses in invasion ecology (Jeschke, 2009; Lockwood *et al.*, 2009; Rodriguez-Cabal *et al.*, 2009). Invasion ecology also lacks homogeneous data at large spatial scales, and long-term data are rare as well (but see Meiners *et al.*, 2004). While short-term effects of invasive species are often known, their long-term effects are rarely investigated and hard to predict (Strayer *et al.*, 2006). The history of invasion processes sometimes can be recovered through the study of herbarium specimens in combination with molecular research and literature reviews. Model simulations can additionally help fill this gap to some degree (Strayer *et al.*, 2006). The study of ongoing changes in the effects of invasive species is necessary for predicting future effects. Unfortunately, the collection of long-term data is often hampered by difficulties to acquire funding for more than a few years. Citizen science has proven useful to gather large amounts of data, with a spatial and temporal coverage that would be hard to achieve for individual research teams (Dickinson *et al.*, 2012). More citizen science programs to engage the general public into invasion research should be started. Online databases such as DAISIE (Delivering Alien Invasive Species Inventories for Europe; http://www.europe-aliens.org), GISD (Global Invasive Species Database; http://www.issg.org/database), or NOBANIS (European Network on Invasive Alien Species; http://www.nobanis.org) have proven very useful, but they can only summarize data that are actually available.

Another difficulty for data analysis is that data collection is often biased, e.g., taxonomically, geographically, or methodologically (C5 in Table 4). Research on successful invaders is concentrated in those areas where most funding is available (Wilson *et al.*, 2007; Pyšek *et al.*, 2008). Similarly, researchers preferentially use those research methods that are easier to put into practice. Finally, initial introduction seems to be much less studied than other phases of the invasion process (Puth & Post, 2005). These difficulties could be overcome, at least partly, if review studies that summarize existing data and identify research gaps and biases, such as the one by Pyšek *et al.* (2008), would be undertaken more frequently. A coherent framework, like the hierarchy of hypotheses suggested above, could help structure such summaries.

Lack of communication with the public, and with other scientific disciplines

In addition to the discussed possibilities for improvement of the scientific methodology of invasion ecology concerning theory and data, there is a considerable potential for improvement concerning communication. Enhanced communication of applied research results to relevant stakeholders could help advance implementation of existing knowledge into policy and management (see Driscoll *et al.*, 2011; Jones-Walters & Çil, 2011) (C6 in Table 4), and invasion ecology could profit considerably from an improved communication among scientists of different disciplines e.g., community ecology, macroecology, biological control, weed science, conservation biology, global change biology, biogeography, and evolutionary biology; Davis *et al.*, 2001; C7 in Table 4). A hierarchy of hypotheses could help implement knowledge exchange: a similar hierarchy could be developed for other disciplines, and these HoHs could be interconnected on a higher level.

As pointed out above, invasion processes are influenced by socio-economic and cultural activities in many different ways, which also creates the need for transdisciplinary research (C8 in Table 4). An increasing number of studies already advance in that direction, e.g., by analyzing historic catalogues (Dehnen-Schmutz *et al.*, 2007; Blackburn *et al.*, 2010), by explaining patterns in alien species richness based on indicators of current and historic socio-economic conditions (Hulme, 2009; Essl *et al.*, 2011), or by considering factors like economic value of species and invasions (Born *et al.*, 2005; Gozlan *et al.*, 2010). Another way to bridge the gap between ecology and social sciences is to combine vector science (Carlton & Ruiz, 2005) with the study of continually shifting global decentralized networks (Barabási, 2002).

Key measure 3: platforms for improved communication

We suggest to establish platforms for improved communication among scientists of different disciplines and with other societal groups (Fig. 6). Conference series explicitly addressing biological invasions already exist (e.g., 'Neobiota' or 'Biolief'). By inviting contributions from non-ecological disciplines, especially social sciences, these conferences could be used as forums for integrative, transdisciplinary research. Such transdisciplinary conferences would also benefit from frequent opportunities for open discussions. Moderated discussions in small groups can strongly promote the exchange of ideas and views, and are able to yield valuable insights. Smaller workshops addressing specific inter- or transdisciplinary questions would foster exchange of views and the development of novel approaches to invasion research. To permanently establish a culture of inter- and transdisciplinary communication at invasion conferences, it might be necessary to have one or more institutions guiding the process (cf.

Aronson *et al.*, 2010 concerning integrative communication in ecological economics). Therefore, existing organizations such as Neobiota (http://www.oekosys.tu-berlin.de/menue/neobiota/) should be used as a starting ground for such inter- and transdisciplinary efforts. Establishing an international transdisciplinary society for invasion science could be the next step.

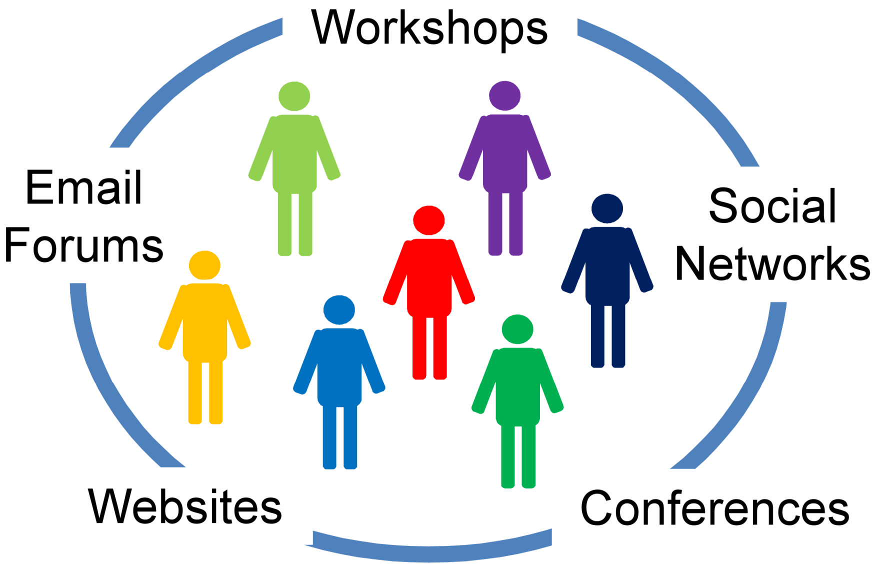

Fig. 6 Possibilities to improve communication among scientists of different disciplines, managers, politicians, and other stakeholders (represented by different colors). [5]

The internet is providing possibilities for communication that should be better utilized for invasion research. In particular, social networks could be used for increasing communication among invasion scientists (cf. Nisbet *et al.*, 2010 for similar recommendations to enhance communication regarding climate change research). Websites can also be set-up for citizen science approaches where volunteers can post the observations of alien species on a website (Dickinson *et al.*, 2012; http://www.waarnemingen.be). Websites and apps of networks that connect science and policy can be very helpful as well, e.g., the Network-Forum for Biodiversity Research Germany (NeFo, http://www.biodiversity.de). It has been shown that stakeholders prefer free and easily accessible information on biological invasions (Bayliss *et al.*, 2012). Two recently established websites (http://www.lifewatch.eu and http://www.congressgenetics.eu/) offer a combination of easily accessible information and communication platforms for researchers and stakeholders involved in biodiversity management. These initiatives could serve as a guide for launching a similar website for biological invasions. The HoH as described above could become the basis for such a website. It could become an evolving online platform, integrating knowledge from different

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[5] Included here with kind permission from Springer Science+Business Media B.V. (original copyright). Figure 2 in Heger et al. (2013, *Ambio* 42: 527-540).

subdisciplines and providing easy access to existing knowledge for other societal groups. Email forums, integrated in existing or newly founded organizations and invigorated at workshops and symposia, could further enhance communication within science as well as among scientists and other stakeholders.

Conclusion

This contribution is meant to increase awareness about existing difficulties in basic and applied invasion research, and to motivate efforts to more efficiently push to the limits of explanation, prediction, and management. Much can be done to increase clarity in communication, within science as well as between science, management, and the public. The proposed checklist for definitions can be useful to find a common language, and the proposed networking activities will provide opportunities to meet and exchange knowledge and ideas. Finally, the implementation of a hierarchy of hypotheses in invasion ecology can sharpen and synthesize existing hypotheses and can make scientific knowledge better available and thus more useful for understanding and managing invasions.

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CHAPTER 2

CHANGES IN THE COMMUNITY CONTEXT OF NATIVE AND INVASIVE NON-NATIVE PLANT SPECIES IN GERMANY

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Abstract

Insights to the process of plant invasions suggest that invasive non-native plant species colonize different habitats and plant communities consecutively. This study aims to show that the relative frequency of relevés with presence of invasive non-native plants in Germany has increased during the past 60 years, and to detect differences in community niche width of native and invasive non-native congeners over three time periods. Phytosociological relevés (8839) from Germany were collected from the global index of vegetation plot databases (GIVD) for three time periods and three congener species pairs covering different growth forms and a wide range of habitats (*Impatiens noli-tangere*, *I. parviflora*; *Solidago virgaurea*, *S. canadensis*; *Prunus padus*, *P. serotina*). Differences in number and proportion of relevés were assessed, and niche widths of the species were studied by ordination and β-diversity. There was an increase in the relative number of relevés with the invasive congeners compared to the native species in the three observation periods. Niche width was not necessarily smaller in invasive species compared to congeners, but different for each species pair. Invasive species niche width increased over time. Interestingly, the overlap of the niches of the native and the invasive species increased over time for all three species pairs. The increasing similarity between community niches of congener species is possibly a consequence of biotic homogenization.

Keywords

β-diversity • community niche • congener • global index of vegetation databases (GIVD) • *Impatiens* • invasive non-native plant • niche width • *Prunus* • *Solidago*

Introduction

Biological invasions are processes that involve species introduction to a new area, establishment and spread (e.g., Heger, 2001; Theoharides & Dukes, 2007). After establishment, invasive non-native species require time to fill their potential range (Williamson *et al.*, 2009), while natives are expected to have filled their potential range to a larger extent (Pearson & Dawson, 2003). Besides that, invasive species also require time to colonize the spectrum of abiotic and biotic conditions they potentially can, i.e., suitable habitats and communities. Therefore, species distribution models calibrated for early stages of invasion tend to underestimate the potential range compared to models that are built for later stages (Václavík & Meentemeyer, 2012).

It has been shown that invasive non-native plants occur in a smaller range of habitats in the invaded compared to the native range (Hejda *et al.*, 2009), and potentially invade additional habitats with time since establishment (Dietz & Edwards, 2006). Introduced plant species often first colonize disturbed, resource-rich and climatically benign habitats, and then spread into less disturbed, (semi)natural ones (Dietz & Edwards, 2006). Thus, the realized niche of invasive non-native plants should change over time, while the one of native plants is expected to be rather stable.

Realized niche width of a plant species can be addressed as the spectrum of habitats colonized which has been shown to differ considerably among non-native species (Hejda *et al.*, 2009). However, habitat-based estimates of species niches can potentially be misleading as habitats are not discrete (Fridley *et al.*, 2007a). Nevertheless, plant species co-occur and assemble to communities (Lortie *et al.*, 2004), and thus, co-occurrence data can be used to measure realized niche width without defining discrete habitats (Fridley *et al.*, 2007a). Taxonomic dissimilarity of invaded communities might serve as a mechanistic measure of the niche occupied by a species. This 'community niche' should reflect the spectrum of biotic and abiotic conditions occupied by a plant species. The community context of plant species can be investigated by using phytosociological relevés (Rasmussen & Kollmann, 2004), and β-diversity has been proposed as a quantitative measure of niche width (Fridley *et al.*, 2007a). High β-diversity (or high variation of species composition between relevés) means that the species occurs in different communities and has a wide niche, while low β-diversity means that the species occurs in less different communities and has a narrower niche (Botta-Dukát, 2011). As central Europe has been intensively studied by community ecologists during the 20th century, the number of available relevés from this region is high. Recent attempts to make this information accessible in large databases have facilitated the use of existing relevés (Schaminée *et al.*, 2009; Jansen *et al.*, 2012a), and these databases now open new possibilities to study the community niche of plants over large areas.

Changes in niche width of invasive non-native species could also be attributed to a generally increasing similarity in species compositions. This biotic homogenization has been attributed to the introduction and spread of common non-native species and/or declines in rare native species (McKinney & Lockwood, 1999), and to other environmental modifications such as urbanization (Kühn & Klotz, 2006). Changes in similarity of plant communities have been addressed in different areas with overall outcomes between –0.6% and 3.9% (Olden *et al.*, 2011). However, it has been shown that introduction of non-native species can also contribute to differentiation rather than homogenization (Lososová *et al.*, 2012). In Germany, homogenization effects were shown for native and long resident non-native species (introduced before 1500) assemblages, but not for more recent non-natives (Kühn & Klotz, 2006). When investigating changes in niche width of native and invasive non-native species, contributions of biotic homogenization have to be kept in mind.

Comparisons of invasive non-native species either to native species or to non-invasive non-native species in the introduced or native range are a common approach in invasion ecology (van Kleunen *et al.*, 2010). Several studies have compared non-native invasive plants to natives, mainly focusing on differences in plant traits (Küster *et al.*, 2010) and plasticity (Davidson *et al.*, 2011; Godoy *et al.*, 2011a), or assessing enemy release (Dang *et al.*, 2009), but also discussing differences in habitat association (Kühn *et al.*, 2003; Chytrý *et al.*, 2008). In such comparisons biases associated with phylogenetic distance can be minimized by selecting species from the same genus (Burns, 2004; Skálová *et al.*, 2011). It can also be crucial to select native species that are non-invasive elsewhere, for example when focusing on traits associated with invasiveness (Muth & Pigliucci, 2006). However, for comparing the community niche in the introduced range, invasiveness elsewhere is of minor importance. For this aim, time since introduction of the non-native species will be of crucial importance as additional habitats and communities are colonized with time.

Here, changes in the community niche during plant invasion in Germany are studied for three pairs of congeners including annual, perennial and woody species. Phytosociological relevés were compiled from different sources, and their number, the most frequent species and taxonomic dissimilarity among relevés with native or invasive non-native species were assessed for different time periods. With respect to invasion history, it is hypothesized that (1) relative frequency of relevés with presence of the invasive non-native congener increases over time; (2a) community niche width is smaller in invasive non-native plant species, especially when time since introduction is short; and (2b) community niche width increases over time, while it remains stable for native congeners; and (3) more recent relevés show increasing niche overlap of congeners because of biotic homogenization.

Material and methods

Study species

To test these hypotheses, three pairs of congeners were chosen representing different growth forms, i.e., the annual herbs *Impatiens noli-tangere* and *Impatiens parviflora* (Balsaminaceae), two perennial herbs *Solidago virgaurea* and *Solidago canadensis* (Asteraceae), and two small trees, *Prunus padus* and *Prunus serotina* (Rosaceae). In each genus, one species is native to Germany and one is introduced and invasive non-native. For categorization, invasive non-native species were defined as those that have been introduced to the study area, and spread considerably regardless of impact (cf. Richardson *et al.*, 2011). Native *Impatiens noli-tangere* has – to the best of our knowledge – not been reported invasive anywhere outside its range; *Solidago virgaurea* can be found at horticultural stores in North America, but has not naturalized (Hill & Kotanen, 2012); and *Prunus padus* is invasive in North America (Center for Invasive Species and Ecosystem Health & National Park Service, 2013). Time since introduction varies between species, as *Impatiens parviflora* was introduced ca. 180 years ago, *Solidago canadensis* ca. 350 years ago, and *Prunus serotina* ca. 330 years ago (Bundesamt für Naturschutz, 2013), but lies within the estimated time needed for the mean range size of invasive non-native species to reach a maximum (150–300 years; Williamson *et al.*, 2009).

Impatiens noli-tangere and *Impatiens parviflora* share many biological attributes, e.g., life form, height, reproduction and competitivity, and have similar ecological requirements (Godefroid & Koedam, 2010). They co-occur in shaded and humid forests (Coombe, 1956; Skálová & Pyšek, 2009). It has been suggested that *Impatiens parviflora* has a wider ecological niche than its congener (Godefroid & Koedam, 2010), and that *Impatiens noli-tangere* reaches its maximum development in areas that are too wet for *Impatiens parviflora* (Coombe, 1956). However, vegetation associated with both species differed only slightly (Vervoort & Jacquemart, 2012).

Solidago is primarily a North American genus with exception of *Solidago virgaurea* which is native in central Europe, where it occurs on rocky outcrops, in disturbed areas, and old fields (Hill & Kotanen, 2012). Invasive *Solidago canadensis* is a successful invader throughout much of Europe (Weber, 2001), and occurs mainly in ruderal sites, abandoned fields, along roads and railways (van Kleunen & Schmid, 2003).

Prunus padus and *Prunus serotina* are small deciduous trees (Leather, 1996; Vanhellemont *et al.*, 2009). Native *Prunus padus* occurs in moist or wet forests, along rivers and streams, or on edges of cultivated land on calcareous or neutral soils (Leather, 1996). Invasive *Prunus serotina* was planted for various purposes widely in central Europe (Starfinger *et al.*, 2003). The species was reported to have a broad ecological range (Godefroid *et al.*, 2005; Zerbe, 2007), including pine forests, and natural acidic oak forests (Zerbe & Wirth, 2006). The two species are known to co-occur (Annighöfer *et al.*, 2012).

Data collection and processing

Phytosociological relevés were collected from several databases (Table 5), most of them listed in the ‘Global Index of Vegetation-Plot Databases’ (Dengler *et al.*, 2011; 'GIVD'; Jansen *et al.*, 2012). All relevés were included that contained at least one of the six target species, were sampled between 1950 and 2009 in Germany and had information on geographic location (e.g., latitude and longitude or narrative location name).

Table 5 Relevés that contain at least one of the six study species were compiled from 13 databases, most of them listed in the global index of vegetation databases ('GIVD'; Dengler *et al.*, 2011).

Database name	GIVD ID	Citation	Version	Relevés (n)	Proportion (%)
VegMV: The Vegetation Database of Mecklenburg-Vorpommern	EU-DE-001	Jansen *et al.* (2012b)	28.10.2010	3678	41.6
Post-Mining Vegetation Database Eastern Germany	EU-DE-023	Jünger *et al.* (2012)	22.11.2010	2049	23.2
Vegetation Database of Strict Forest Reserves in NW-Germany	EU-DE-016	Schmidt *et al.* (2012a)	17.01.2011	900	10.2
Vegetation Database of Successional Permanent Plots in Göttingen	EU-DE-015	Schmidt *et al.* (2012b)	03.01.2011	775	8.8
VegetWeb: The National Online-Repository of Vegetation Plots From Germany[1]	EU-DE-013	Ewald *et al.* (2012)	10.11.2010	651	7.4
Vegetation Database of Pine Forests on Acidic Soils in Germany	EU-DE-019	Heinken (2012a)	10.11.2010	332	3.8
Vegetation Database of Deciduous Forests on Acidic Soils in NW Europe	EU-00-008	Heinken (2012b)	11.11.2010	297	3.4
BioChangeFields: Vegetation Database of Arable Plant Communities in Central Germany	EU-DE-027	Meyer *et al.* (2012)	21.12.2010	71	0.8
Vegetation Database Frankenalb	EU-DE-022	Hemp (2012)	25.01.2011	32	0.4
Nauener Forst	(not listed)	(T. Heinken, unpublished)	11.11.2010	22	0.2
Disturbances and Biodiversity at Grafenwöhr Training Area	EU-DE-025	Alt *et al.* (2012)	25.01.2011	18	0.2
Disturbances and Biodiversity in the Fichtelgebirge	EU-DE-024	Jentsch *et al.* (2012)	25.01.2011	9	0.1
BioChangeMeadows: German Meadows in the 1950s, 1990s and in 2008	EU-DE-009	Wesche & Krause (2012)	10.12.2010	5	0.1

[1] Project codes of VegetWeb data sources that were used: Bohn, LANUV (Landesamt für Natur, Umwelt und Verbraucherschutz, http://www.lanuv.nrw.de), vNWR, T251, T252, T254 (Fuchs 2005), T255 (Gehlken 2005), T262 (Dengler *et al.*, 2006), T269 (Heerde *et al.*, 2006), T271 (Dengler *et al.*, 2007), T272 (Klauck 2007), T273 (Brandes & Nitzsche 2007), T281 (Otte *et al.*, 2008), T291 (Rüter & Klotz 2006), T294 (Schrautzer *et al.*, 2009).

Since most of Germany has been well studied with regard to plant communities the data set should represent the occurrence of the study species rather well (cf. Rasmussen & Kollmann, 2004).

Relevés were compiled to a uniform dataset in Turboveg (Version 2.86a, Hennekens & Schaminée, 2001). Taxonomy was unified based on the reference list GermanSL Version 1.1 (Jansen & Dengler, 2008) to species level, i.e., subspecies or varieties were omitted. Different cover scales were transformed to presence-absence data to account for variation in estimating coverage by different authors. Wilson (2012) showed that environmental correlations can be well described with presence-absence data, and concludes that in large-scale survey, abundance information is unnecessary and may even be misleading.

Data analyses

All analyses were done with R version 3.0.1 (R Core Team, 2013) including the packages ‘vegan’ version 2.0-9 (Oksanen *et al.*, 2013) and ‘MASS’ version 7.3-29 (Ripley *et al.*, 2013). Data for each species pair was analyzed separately, i.e., *Impatiens* sp., *Solidago* sp., and *Prunus* sp. Relevés were classified into nine groups according to sampling time (three periods, i.e., 1950–1969, 1970–1989, 1990–2009) and status (native, invasive non-native or both species present; see Table 6). As samples were unbalanced and regionally biased, a random subsample of up to 25 relevés was used (less in some cases due to availability; Table 6), from each group weighted by geography. Thereto, a raster cell was assigned to each relevé based on geographic information (in one decimal degree steps). Probability P of sampling was calculated as follows: where n_g is the total number of relevés in the respective group g, and n_{gc} is the number of relevés in the group and respective cell c:

$$P = 1 - (n_g^{-1}\, n_{gc})$$

The subsamples were used to analyze ecological variation by ordination and niche width by calculation of Whittaker’s β-diversity. Individual detrended correspondence analyses (DCA) were calculated for each genus, using the function ‘decorana’ and the option for downweighting rare species (‘iweigh’ = 1); study species were excluded from the analysis. DCAs were plotted showing the relevés of each time period separately and the species status in different color. Whittaker’s β-diversity was calculated from smoothed data for each species and time period separately using the original code by Botta-Dukát (2011).

Table 6 Total number of relevés found for three sampling periods of the three pairs of native and invasive non-native species (*Impatiens noli-tangere, I. parviflora; Solidago virgaurea, S. canadensis; Prunus padus, P. serotina*), and percentages for relevés with the native, the invasive non-native or both species present. A subsample of up to 25 relevés was chosen for each category (see Methods), subsamples were smaller in categories with ≤5%; percentages do not necessarily sum up to 100% because of rounding.

Sampling period	*Impatiens*	*Solidago*	*Prunus*
1950–1969	**395**	**370**	**127**
native	83%	95%	79%
invasive non-native	16%	5%	21%
both	2%	0%	0%
1970–1989	**491**	**565**	**152**
native	72%	22%	57%
invasive non-native	23%	77%	38%
both	6%	2%	5%
1990–2009	**2753**	**3245**	**1228**
native	41%	30%	36%
invasive non native	52%	70%	62%
both	7%	<1%	1%

Results

The total number of relevés with the invasive or both species present increased over time for all three genera. Overall, 3639 relevés for *Impatiens*, 4180 for *Solidago*, and 1507 for *Prunus* were found in the databases (Table 6). The relative proportion of relevés with presence of the native species decreased significantly from 86% to 36% (mean for the three species; Spearman correlation, rho = –0.83, $P = 0.006$), while that of relevés with the invasive species increased from 14% to 62% (Spearman correlation, rho = 0.79, $P = 0.010$). Proportion of relevés with both species present was generally rather small and trends were less clear (Spearman correlation, rho = 0.39, $P = 0.302$). For *Impatiens* it increased from 2% to 7%. For the other two genera highest proportion of relevés containing both species was in the second time period (1970–1989), with 2% for *Solidago* and 5% for *Prunus*.

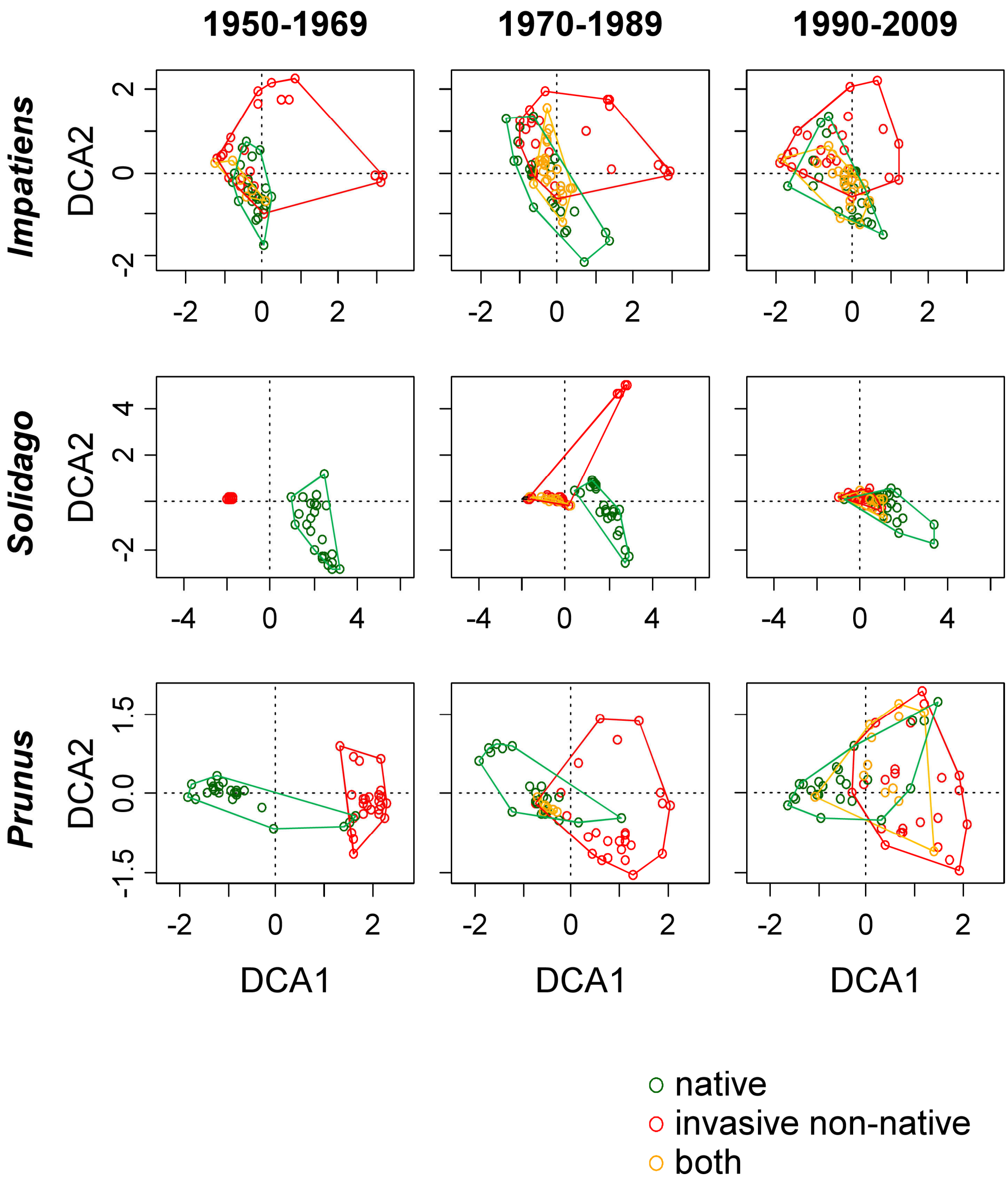

Fig. 7 Ordination diagrams from detrended correspondence analyses (DCAs) for relevés with a native and an invasive non-native plant species of the genera *Impatiens* (Eigenvalues: axis 1, 0.42; axis 2, 0.35), *Solidago* (axis 1, 0.65; axis 2, 0.44), and *Prunus* (axis 1, 0.57; axis 2, 0.30), respectively. Each panel shows relevés from only one of three considered time periods within a single DCA (native species, green; invasive species, red; both, yellow).

The ordination diagrams (DCA, Fig. 7) show relevés with the native, the invasive or both species present, separately for the three considered time periods. For the two *Impatiens* species the first axis represented a gradient from more acid and nitrogen-poor sites (*Galium saxatile*; Appendix 1 for species with high and low scores on DCA axes) to more basic and nitrogen rich sites (*Euphorbia helioscopia*), while the second axis showed a moisture gradient from wet (*Berula erecta*) to drier conditions (*Anthericum liliago*). Overlap between relevés with the native and the invasive species was already high in 1950–1969. For the native *Impatiens noli-tangere* the distance between relevés increased over time. For the invasive *Impatiens parviflora* distances between relevés were smallest in the most recent period. In this genus, the number of relevés with both species was especially high. These were mainly placed within or in close proximity to ordination space of the native species. Both *Impatiens* species were closely associated with trees as *Fagus sylvatica* and *Fraxinus excelsior* (see Appendix 2 for most frequent species); *Alnus glutinosa* was another frequent tree species in relevés with the native *Impatiens noli-tangere* or both species, and *Quercus robur* in those with the invasive *Impatiens parviflora*. *Urtica dioica* was among the most frequent species for both species in each of the three time periods. Additionally, *Circaea lutetiana*, *Oxalis acetosella* and *Deschampsia cespitosa* were frequent, but differences between time periods and the native or invasive species were minor. Overall, temporal changes in the ordination of relevés with native and invasive *Impatiens* were rather small.

For the two *Solidago* species the DCA axis 1 represented a gradient from nitrogen-rich (*Lamium maculatum*; Appendix 1) to nitrogen-poor conditions (*Tofieldia calyculata*); the second axis represented a gradient from dry, slightly shaded (*Lathyrus niger*) to moist conditions with high light availability (*Potentilla palustris*). The ordination separated relevés with native *Solidago virgaurea* clearly from those with invasive *Solidago canadensis* on the first axis in the first time period. This separation was reduced for the second time period, and disappeared for the last period where overlap was considerable. Relevés with the native species were strongly lumped together in the first period. This aggregation enlarged only very slightly during time. However, for the second time period there were three relevés that differed considerably from the others on axis 2, and might represent outliers. In *Solidago*, relevés with both species mainly overlapped with those relevés containing the invasive species. The native *Solidago virgaurea* was associated to some tree species, such as *Fagus sylvatica* and *Pinus sylvestris*, as well as species of grasslands, e.g., *Dactylis glomerata* and *Hypericum perforatum* (Appendix 2). Its invasive congener *Solidago canadensis* was more associated to ruderal plants as *Cirsium arvense*, *Calamagrostis epigejos* and *Taraxacum officinale*. *Achillea millefolium* was a frequent species in relevés with the native, the invasive and both *Solidago* species, especially in the most recent time period. To sum up, there was a clear separation between ordination space of the native and invasive *Solidago* species that reduced with time.

The first axis of the DCA for the two *Prunus* species represented a gradient from nitrogen-rich, shaded sites (*Lamium maculatum*; Appendix 1) to nitrogen-poor, sun-exposed sites (*Polygonatum odoratum, Linaria vulgaris*); the second axis represented a gradient from rather acid (*Teucrium scorodonia*) to basic conditions (*Origanum vulgare*). Separation of relevés with the native and the invasive species along the first axis was distinct for the first time period. The native species occupied mainly the nutrient-rich, shaded side of the gradient, while the invasive species concentrated on the nutrient-poor, light-exposed side. This separation diminished over time, and overlap of all three groups was marked in the most recent time period. Relevés that contain both species were similar to both those with the native *Prunus serotina* and those with the invasive *Prunus padus*. In relevés with *Prunus* woody species played a major role. Native *Prunus padus* was associated with *Fraxinus excelsior* and *Alnus glutinosa*, while *Pinus sylvestris* was the most frequent tree in relevés with invasive *Prunus serotina* (Appendix 2). Both *Prunus* species shared an association with *Quercus robur* and *Betula pendula*. Overall, the ordination for *Prunus* clearly showed an increasing overlap of the ordination spaces of the native and invasive species, as well as increasing ordination space for the invasive species.

Niche width measured as Whittaker's β-diversity increased significantly over time for the invasive non-native species (Fig. 8; Spearman correlation, rho = 0.95, $P < 0.001$), while there was no correlation between β-diversity and time for the native species (Fig. 8; Spearman correlation, rho = 0.20, $P = 0.474$).

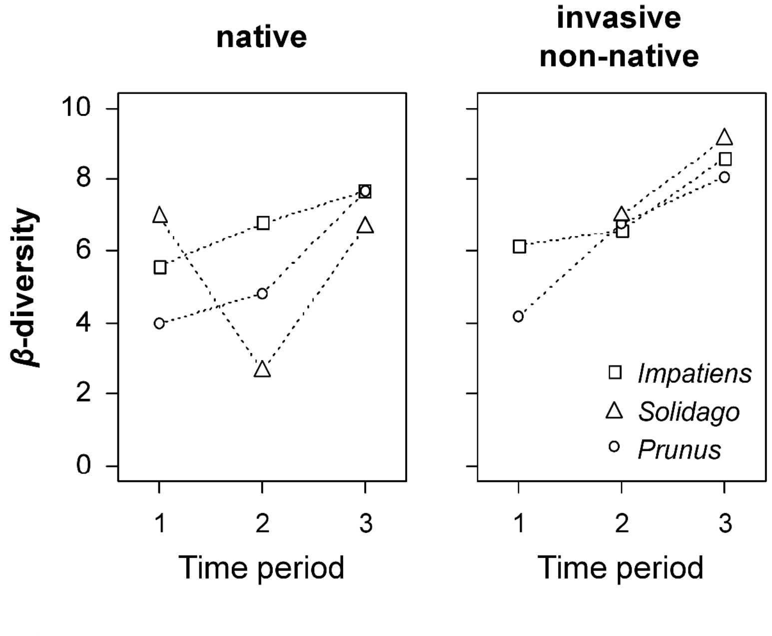

Fig. 8 Whittaker's β-diversity calculated from smoothed data for three native and three invasive non-native species (square, *Impatiens;* triangle, *Solidago;* circle, *Prunus*) in three time periods (1, 1950–1969; 2, 1970–1989; 3, 1990–2009).

Discussion

A marked increase in relative number of relevés with the invasive congener compared to the native over time was shown by this study (*Hypothesis 1*). Niche width measured as ordination space and as *β*-diversity was not necessarily smaller in invasive species compared to congeners, but different for each species pair (*Hypothesis 2a*). Invasive species niche width as *β*-diversity increased over time in all genera, while increase in ordination space was only clear in *Prunus* (*Hypothesis 2b*). Interestingly, the overlap of the niches of the native and the invasive species increased over time for all three species pairs (*Hypothesis 3*).

The increased proportion of relevés with the invasive congener might reflect an increase in abundance of the three invasive non-native species in Germany. Additionally, the hypothesized increase of community niche width in invasive non-native species over time was observed for ordination space of *Prunus serotina*, and for *β*-diversity in all three genera. This is in accordance with the recent ranking of the three invasive non-native species as having high potential for spread and being currently in the expansive stage of the invasion process in Germany (Nehring *et al.*, 2013). *Prunus serotina* invasion is markedly accelerating at the moment in the Czech Republic (Pyšek *et al.*, 2012a), and spread of *Solidago canadensis* is regarded as not finished yet (Weber, 2001). Nevertheless, *Impatiens parviflora* was reported to be less dominant than three decades ago in the Czech Republic (Pyšek *et al.*, 2012a). Indeed, the observed increase in proportion of relevés with invasive non-native species might also be an artefact that could be attributed to a data bias, increasing interest in invasive species since the 1970s (Pyšek *et al.*, 2012b), or a past tendency of researchers to select weakly or non-invaded sites for sampling. The used data were not specifically produced for the present study; thus, inequalities in representation of communities, different sampling dates and plot sizes are likely to exist (see Rasmussen & Kollmann, 2004). However, differences in cover estimation were excluded by using presence-absence data, and regional bias was minimized by using geographically weighted subsamples. Moreover, a comparison of stratified-random sampled and preferential sampled relevés indicated that estimates of the level of invasion from vegetation databases may be only weakly affected by preferential sampling (Michalcová *et al.*, 2011). Thus, it can be assumed that the observed pattern is only marginally biased, and the increase in proportion of relevés with the invasive non-native species reflects a true increase in abundance of invasive compared to native congeners.

The results indicate that the relative size of the community niche width of invasive compared to native species is case-specific. The hypothesized smaller niche width in invasive species was only indicated by a smaller ordination space for non-native *Solidago*. In the other two genera ordination spaces were more or less similar, and *β*-diversity did not differ consistently between natives and invasive non-natives. All three invasive species have been introduced rather long time ago, i.e., 180–350 years ago. When a mean lag phase of ca.150 years between introduction and invasive spread is assumed (as shown for woody species by Kowarik, 1995), the studied time periods should represent the phase of invasive spread rather well. However, the duration of a lag phase is highly species dependent (Kowarik, 1995). *Impatiens parviflora* started spreading ca. 130 years ago (Trepl, 1984), *Solidago canadensis* ca. 160 years (Weber, 1998), and *Prunus serotina* ca. 190 years (Kowarik, 1995). Keeping these time frames in mind, the study species had already spread for 70–130 years before the first studied time period (ca. 60 years ago). Therefore, niche width might have been already developed to a level similar to that of a native species. Nevertheless, investigation of a more recently invading species was not possible. We searched for relevés with more recent invasive non-natives, but availability was too low to perform a reliable analysis. For example, only 39 relevés in total were found for *Acer negundo* (data not shown) which first established in Germany in 1919 (Nehring *et al.*, 2013).

A highly interesting result is that ordination space overlap increased over time for all three species pairs, and β-diversity increased significantly in the invasive non-native species. The observed increase of niche space overlap may relate to general 'biotic homogenization' (e.g., McKinney & Lockwood, 1999). Co-occurrence occurred in all three genera, but relevés with both species were either placed mainly within the ordination space of the native congener as in *Impatiens*, or mainly within that of the invasive congener as in *Solidago*, or were distributed to both spaces as in *Prunus*. This suggests that invasive *Impatiens parviflora* and native *Solidago virgaurea* colonize sites with congeners, while the congeners might not be able to do the same. It was suggested before that sites with *Impatiens noli-tangere* might be too wet for *Impatiens parviflora* (Coombe, 1956), but our results rather indicate that sites with *Impatiens parviflora* might be not sufficiently moist for *Impatiens noli-tangere*. Godefroid & Koedam (2010) compared ecological preferences of the two species and reported that *Impatiens parviflora* is a species of dry soils in Belgium. The authors also showed that communities including both species are more similar to those with only *Impatiens noli-tangere* and concluded that invasive *Impatiens parviflora* can perfectly colonize many habitat of native *Impatiens noli-tangere*, but that the contrary is not true (Godefroid & Koedam, 2010). This is in perfect accordance with the present results. The pattern for *Solidago* is the opposite suggesting that native *Solidago virgaurea* might colonize sites with invasive *Solidago canadensis*, while the contrary is not true, because sites with *Solidago virgaurea* might be too nitrogen-poor for the invasive species. *Solidago canadensis* was shown to decrease biomass as soil nitrogen decreases in a common garden experiment in the native range (Kiger, 2006).

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CHAPTER 3

PLANT COMMUNITY TRAITS AS CORRELATES OF PLANT GROWTH AND FECUNDITY: THE CASE OF *LYTHRUM SALICARIA* (LYTHRACEAE) IN ITS NATIVE AND INVADED RANGES

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Abstract

- *Premise of the study:* Identifying significant relationships between community mean functional traits related to competition, and the growth and fecundity of alien plants, is a new method for the management of problematic invaders and the conservation of native biodiversity. This study tested this approach in the native and introduced ranges of purple loosestrife (*Lythrum salicaria* L.).

- *Methods:* Vegetation surveys were carried out in wetlands with *Lythrum salicaria* in two areas within its invaded and native ranges, respectively. Community mean traits, including plant height, leaf area and leaf dry matter content, were calculated based on species traits extracted from the TRY database. Multiple linear regressions were fitted to explain growth and fecundity of the study species as influenced by community traits.

- *Key results:* Several community traits showed positive correlations with the growth and fecundity of *Lythrum salicaria*, especially plant height, leaf area, and specific leaf area. Other community traits were negatively related to *Lythrum salicaria*, e.g., relative cover of graminoids. Most correlations were consistent among areas.

- *Conclusions:* Our study indicates that identifying relationships between community traits related to competition, and the growth and fecundity of alien plants, could become a new method for understanding and managing plant invasions. In our case, the results suggest that *Lythrum salicaria* is a strong competitor in vegetation having tall plants and dense cover, while its growth and fecundity are reduced in communities with a high abundance of grasses and sedges.

Keywords

Community mean traits • graminoids • leaf area • leaf dry matter • *Lythrum salicaria* • plant height • Purple Loosestrife • specific leaf area • TRY, wetlands.

Introduction

A major mechanism structuring plant communities is interspecific competition (Goldberg, 1996; Grime, 2001). Competition is an integrative concept that relates to plant cover and biomass; it includes the competitive response of a plant to its neighbors as well as competitive effects of neighbors on a plant (Goldberg & Landa, 1991). Neighboring plants are responsible for marked phenotypic responses in many species (Callaway *et al.*, 2003). Therefore, interspecific competition in a given community significantly influences growth and fecundity of the plants in the community (Clark *et al.*, 2011; Segarra *et al.*, 2013). Different plant communities within the range of a species may vary with regards to competitive strength, leading to differences in growth and fecundity.

So far, competition and vegetation structure have mostly been analyzed in terms of species numbers, growth forms, and cover (Cripps *et al.*, 2010; Alba & Hufbauer, 2012), while most functional traits have been neglected. Plant functional traits describe phenotypic variation that can influence ecosystem processes (Petchey & Gaston, 2006). Several key aspects of ecosystem functioning are controlled by functional traits (Díaz & Cabido, 2001; Garnier *et al.*, 2004; Mouillot *et al.*, 2011), thus, functional traits can serve as predictors of ecosystem dynamics and functioning (McGill *et al.*, 2006; Kattge *et al.*, 2011a). Garnier *et al.* (2004) suggested extending this approach to changes in community structure. Competition in a plant community could be described by means of functional traits in a more mechanistic way than has been done in most published studies. Competition within a plant community has been linked to several functional traits (Table 7; Grime, 2001; Cornelissen *et al.*, 2003b; Pywell *et al.*, 2003). Mean values of selected functional traits, weighted by species cover, could be tested for assessing competition in communities, and consequently the influence of competition on the growth and fecundity of selected species, which ultimately drives community assemblages. Until now few studies have compared effects of mean community traits on the growth and fecundity of focal species over large areas.

Correlations between community traits and focal plant growth and fecundity are especially interesting with regards to invasive alien plants. On the one hand, these species have colonized communities with great variation in vegetation structure, such as the North American prairie species *Solidago gigantea* Aiton that has invaded a wide range of habitats in central Europe, including ruderal roadsides, grasslands and wetlands (Weber & Jakobs, 2005). On the other hand, some invasive alien plants are restricted to vegetation types similar to their native communities, e.g., wetland plants invading similar habitats in their new range, such as *Lythrum salicaria* L. (Edwards *et al.*, 1998). Nevertheless, in these structurally analogous communities, mean functional traits are not necessarily similar. Numerous studies have described differences in the growth and fecundity of invasive alien plants in their native and introduced ranges (see Parker *et al.*, 2013). Several authors have suggested that reduced competition in the recipient community might contribute to increased growth of the invasive alien species (Callaway *et al.*, 2011; Hinz *et al.*, 2012). The influence of competition in communities with distinct taxonomic compositions is difficult to assess, and until now most field studies have focused on differences in abundance of different growth forms (Cripps *et al.*, 2010; Alba & Hufbauer, 2012). However, Byun *et al.* (2013) recently showed that the competitive effect on an invasive alien species can be related to sets of functional traits of resident plant communities, while species identity is less important. To our knowledge, community means of functional traits have not yet been used to explain the growth and fecundity of a species in both its native and introduced ranges.

Table 7 Selected plant traits and their relation to competition.

Plant trait	Advantages for competition
Plant height	Plant height is relevant for competitive strength as taller species are more able to suppress subordinate species, especially when nutrient availability is good and competition for light most important (Schamp *et al.*, 2008; Wang *et al.*, 2010).
Leaf area	Large leaves allow plants to capture light, thereby reducing growth of competitors (Weijschedé *et al.*, 2006; Craine & Dybzinski, 2013).
Specific leaf area (SLA)	Species with higher specific leaf area have higher metabolic rates per mass and higher relative growth rates, resulting in a competitive advantage (Marteinsdóttir & Eriksson, 2013).
Leaf dry matter content (LDMC)	Leaf dry matter content is generally negatively correlated with measures of growth such as relative growth rate (Thuiller *et al.*, 2010) and specific leaf area (Cornelissen *et al.*, 2003b); and should therefore be inversely related to competitive ability.
Seed mass	Large seeds usually contain more resources; this can lead to advantages for seedlings because it reduces mortality due to shading or herbivory (Moles & Westoby, 2004); this can result in higher establishment success (Schamp *et al.*, 2008; Marteinsdóttir & Eriksson, 2013).
Plant growth form	Plant growth form can have significant effects on competitive responses as graminoids were shown be suppressed more by heterospecific competitors than forbs (Semchenko *et al.*, 2013).
Species reproduction type	Species with clonal growth can have competitive advantages because they can share resources and redistribute photosynthates between ramets (Pennings & Callaway, 2000).

Lythrum salicaria is ideal for investigating the effects of variation in community mean functional traits on the growth of an invasive plant. It occurs in wetland habitats (Mal *et al.*, 1992), i.e., ‘azonal’ vegetation with relatively similar site conditions over large spatial scales, which allows intercontinental comparisons. Light, water, and nutrients are abundant in these communities, leading to a high biomass of competitive grasses and forbs. The effects of competition are further amplified because *Lythrum salicaria* develops and flowers comparatively late, leading to potential suppression by earlier developing wetland plants. Moreover, this species often shows higher performance and fecundity in the introduced range (e.g., Edwards *et al.*, 1998; Bastlová-Hanzélyová, 2001; Moloney *et al.*, 2009). These biogeographic differences have been linked to several hypotheses, including the evolution of increased competitive ability (EICA; e.g., Blossey & Nötzold, 1995), high phenotypic plasticity (Mal & Lovett-Doust, 2005; Chun *et al.*, 2007), and disturbance effects (Hager, 2004; Lavoie, 2010). However, the relationship between plant growth and community mean functional traits has hitherto not been investigated.

We studied *Lythrum salicaria* populations in two native and two introduced areas with comparable site conditions to investigate the relationship between community mean traits (used here as a proxy for competition), and the growth and fecundity of the species. The study areas are not true replicates due to phenological differences, but were used to explore the spatial consistencies of observed correlations. We hypothesized that *Lythrum salicaria* growth and fecundity is correlated with competition in the local plant community. To this end we first describe intercontinental variation in growth and fecundity of *Lythrum salicaria* (*Objective A*). We then investigate correlations of community mean traits representing competition with measures of *Lythrum salicaria* growth and fecundity (*Objective B*). Finally, we studied whether these correlations were consistent among areas of native and invasive occurrence of *Lythrum salicaria* (*Objective C*). To our knowledge, this is the first study using this novel method to measure competition between native and invasive alien plants.

Material and methods

Study species

Lythrum salicaria L. (purple loosestrife, Lythraceae) is a perennial forb native to Eurasia. It was introduced to North America in the early 1800s (Stuckey, 1980), and has spread widely since then (Thompson *et al.*, 1987). In late spring, *Lythrum salicaria* develops one to several aboveground shoots from winter buds on a persistent rootstock (Mal *et al.*, 1992). Sessile, lanceolate to ovate leaves grow along the square stems (Mal *et al.*, 1992). The plant grows 0.5–2.7 m tall, and the inflorescence is a terminal spike with many small cymes (Mal *et al.*, 1992). Plants flower from June to September or October, depending on the region (Mal *et al.*, 1992); plants from higher latitudes flower earlier (Montague *et al.*, 2008). The species mainly occurs in wetlands, including fens, shores of rivers and lakes, and coastal marshes (Mal *et al.*, 1992; Olsson & Ågren, 2002).

Study areas and sites

Community mean functional traits of wetlands with *Lythrum salicaria* were investigated in two areas that have been invaded for a relatively long time, i.e., St. Lawrence region, southeastern (SE) Canada; and Upper New York State, northeastern (NE) USA, and two within the native range, i.e., Greater Oslo area, southern (S) Norway; and Bavaria, southern (S) Germany (Fig. 9; Table 8; typical aspects in Appendix 3). The areas were selected to be climatically similar irrespective of latitude and the specific geomorphological setting. The latitudinal and altitudinal ranges covered by the European study sites are wider, while the annual mean temperature range is higher in the North American areas (Table 8). All study sites were wetlands with soils of high organic content, classifying them as histosols.

Areas were sampled June–August 2010/2011 during the early to peak flowering season of *Lythrum salicaria*. As the species develops rather late compared to neighboring plant species, the flowering stage represents an integration of the competition experienced by *Lythrum salicaria* over the spring and early summer. To control for possible phenological effects, we included in our analyses the number of days with temperature >8 °C (growing degree days, 'GDD' henceforth) in the study year until sampling (following Montague *et al.*, 2008). Ecophysiological experiments indicated that growth of *Lythrum salicaria* is prevented below 8 °C (Shamsi & Whitehead, 1977a). GDD were calculated from mean daily temperatures that were retrieved for the closest meteorological stations (Deutscher Wetterdienst, 2013; Government of Canada, 2013; National Oceanic and Atmospheric Administration, 2013; Norwegian Meteorological Institute, 2013).

Within each area, five study sites >25 km apart were selected to examine regional variation. Sites were chosen based on local expert knowledge of wetlands in the study areas, including data from a survey in SE Canada (Lavoie *et al.*, 2003), and are representative of wetlands with *Lythrum salicaria* in each area. A screening of suitable populations of *Lythrum salicaria* was done at all sites. True randomization of plots within study sites was not possible due to logistic constraints, and thus the five plots per study site were chosen haphazardly (5 × 5 m^2 each; 100 plots total).

Assessing growth and fecundity of **Lythrum salicaria**

For each plot, the height (i.e., shortest distance between upper tip of the plant and the ground level) of five *Lythrum salicaria* individuals was measured. If the species was abundant, the five plants were chosen randomly along a transect through the plot. In plots with less than five individuals, additional plants close to the plot were measured. The individual with median height was selected, and a subplot (0.5 × 0.5 m^2) was placed around it. *Plant height* (cm) of the selected individual and *cover* (%) in the subplot were used as measures of *Lythrum salicaria* growth. Cover was measured with a pin-point frame: a pin was lowered vertically to the ground at each of 16 points: the number of pins touching the species was recorded. Cover was calculated as a proportion of touched pins; if no pins where touched a cover of 0.1% was recorded.

Fecundity of *Lythrum salicaria* was evaluated using total cumulative length of all shoots of the selected individual plant (cm; hereafter '*shoot length*'). This variable is a suitable estimate of fecundity as it was closely correlated to cumulative flowering shoot length in S Norway and S Germany ($R^2 = 0.69$, $F_{1,48} = 108$, $P < 0.001$, data not shown). In addition, aboveground herbivory of *Lythrum salicaria* was estimated with six classes (Table 8).

Table 8 Characteristics of the four study areas, with five study sites each, within the introduced and native ranges of *Lythrum salicaria*. Normal annual precipitation and mean annual temperature from the nearest available weather station are shown (SE Canada 1971–2000, NE USA 1981–2010, S Norway 1961–1990, S Germany 1961–1990). Distances between the center of study sites and climate stations were always <25 km. Number of growing degree days >8 °C (GDD) were retrieved to control for possible phenological differences (see text for further information). Climate data from Government of Canada (2013), National Oceanic and Atmospheric Administration (2013), Norwegian Meteorological Institute (2013), and Deutscher Wetterdienst (2013). Herbivory was estimated in classes from 0 to 5. Mean values, ranges for latitude, longitude and altitude as well as standard deviation (±) are given.

Study area and site	**Latitude**	**Longitude**	**Altitude (m a.s.l.)**	**Normal precipitation (mm)**	**Normal temperature (°C)**
Introduced range					
SE Canada (CAN)	**42.5 – 43.4**	**-76.8 – -76**	**7 – 24**	**1054 ± 116**	**5.2 ± 0.9**
CAN1	42.98167	-76.82633	24	979	6.2
CAN2	43.14525	-75.98893	15	968	6.1
CAN3	42.49435	-76.35627	13	994	4.7
CAN4	42.78892	-76.12967	14	1085	4.7
CAN5	43.44744	-76.45504	7	1244	4.3
NE USA (USA)	**45.4 – 47.1**	**-73.8 – -70.8**	**105 – 364**	**1052 ± 93**	**8.3 ± 1.0**
USA1	45.38805	-73.75622	139	1073	8.6
USA2	45.65324	-73.46426	119	977	9.1
USA3	46.18829	-73.01531	327	947	8.2
USA4	46.38235	-72.36056	364	1182	6.7
USA5	47.05938	-70.81112	105	1078	9.0
Native range					
S Norway (NOR)	**47.8 – 48.7**	**11.1 – 12.4**	**4 – 111**	**829 ± 63**	**5.8 ± 1.1**
NOR1	48.36961	11.67735	14	779	6.6
NOR2	48.66348	11.36051	35	920	5.7
NOR3	48.08637	11.13395	4	765	6.9
NOR4	47.80653	12.44821	7	860	5.7
NOR5	48.62059	12.27202	111	820	4.1
S Germany (GER)	**59.1 – 59.9**	**10.3 – 11.1**	**369 – 529**	**1007 ± 407**	**7.4 ± 0.7**
GER1	59.46998	10.63250	443	788	7.5
GER2	59.68386	10.74655	369	715	7.8
GER3	59.05849	10.93431	529	972	7.4
GER4	59.74979	10.27594	524	1715	6.2
GER5	59.90856	11.11016	378	845	8.1

Study area and site	GDD in study year (n)	Species number (n)	Herbivory (classes 0–5)
Introduced range			
SE Canada (CAN)	**82 ± 3**	**10 ± 4**	**0 ± 1**
CAN1	84 ± 1	11 ± 3	0 ± 0
CAN2	81 ± 1	9 ± 2	1 ± 1
CAN3	87 ± 1	8 ± 3	1 ± 1
CAN4	80 ± 1	9 ± 1	0 ± 0
CAN5	78 ± 1	14 ± 4	1 ± 1
NE USA (USA)	**76 ± 6**	**9 ± 5**	**2 ± 2**
USA1	72 ± 9	11 ± 6	2 ± 1
USA2	75 ± 1	10 ± 3	2 ± 2
USA3	70 ± 1	10 ± 5	2 ± 2
USA4	72 ± 4	7 ± 4	3 ± 2
USA5	83 ± 1	11 ± 5	1 ± 1
Native range			
S Norway (NOR)	**123 ± 7**	**8 ± 3**	**2 ± 1**
NOR1	115 ± 1	9 ± 3	2 ± 1
NOR2	122 ± 0	8 ± 3	1 ± 1
NOR3	118 ± 1	6 ± 1	1 ± 0
NOR4	129 ± 1	8 ± 4	1 ± 1
NOR5	132 ± 1	6 ± 1	2 ± 2
S Germany (GER)	**132 ± 7**	**12 ± 4**	**2 ± 1**
GER1	129 ± 8	10 ± 2	1 ± 1
GER2	125 ± 2	8 ± 2	3 ± 1
GER3	133 ± 7	14 ± 3	2 ± 1
GER4	131 ± 1	14 ± 4	1 ± 1
GER5	142 ± 2	12 ± 3	2 ± 1

GDD = Growing degree days >8 °C elapsed in the study year
SE Canada = St. Lawrence region, southeastern Canada
NE USA = Upper New York State, northeastern USA
S Norway = Greater Oslo area, southern Norway
S Germany = Bavaria, southern Germany
See Fig. 9 for a map.

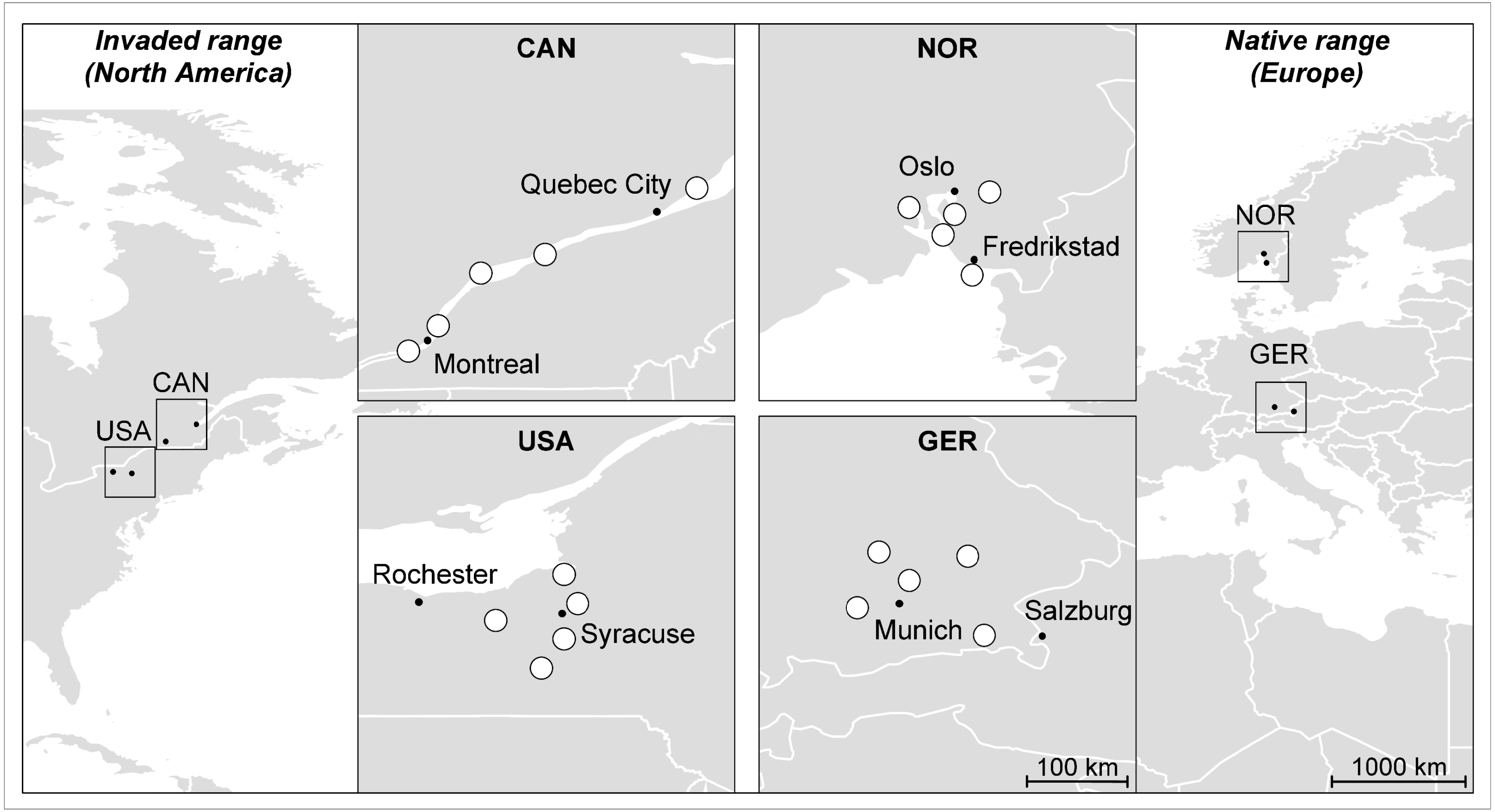


Fig. 9 Location of sampled study sites (open circles) and nearby cities (dots; for orientation), with five populations each, that are situated in two areas within the introduced (CAN: SE Canada, USA: NE USA) and two within the native range (NOR: S Norway, GER: S Germany) of purple loosestrife (*Lythrum salicaria*). The four areas were selected to be comparable with regard to climatic variables irrespective of latitude and the specific geomorphological setting.

Analysis of plant community traits

Plant community traits were assessed based on all vascular plant species present in each subplot. In total, 361 taxa were encountered, of which 323 were identified to the species level (18 taxa to the genus level, 15 to the family level, and five that could not be identified; most frequent species in each study area in Appendix 4). Species number corresponded to the total number of vascular plant species in each subplot. Plant species number was lower in S Norway compared to S Germany (square-rooted, ANOVA, $F_{3,\,96} = 5.15$, $P = 0.002$; Tukey HSD, $P = 0.001$), but did not differ among the other areas.

The cover of each plant species in the subplot was measured with the pin-point frame as described for *Lythrum salicaria.* For each subplot, the maximum height was measured for each species. Other functional traits were compiled from the TRY database (Kattge *et al.*, 2011b), i.e., leaf area, specific leaf area, leaf dry matter content, seed mass, plant growth form, and species reproduction type (see below for original sources of plant trait data). These traits were chosen as they are known to be linked to competition (Table 7). 319 (99%) of the 323 identified species were included in the TRY database. Only traits that were available for at least 60% of all encountered taxa were used for the analysis (see Pywell *et al.*, 2003), i.e., 68% for leaf area, 75% for specific leaf area, 68% for leaf dry matter content, 80% for seed mass, 100% for plant growth form, and 69% for species reproduction type. In case of availability of more than one trait value per trait and species, the median was used for all calculations. Community mean traits (CMTs) where calculated for plant height, leaf area, specific leaf area, leaf dry matter content, and seed mass by weighting the trait values (t_i) of all species i (excluding *Lythrum salicaria* and species with unknown trait values) by their proportional abundance (p_i) in each subplot using the following equation (Garnier *et al.*, 2004; Roscher *et al.*, 2013) where S is the number of species:

$$\mathrm{CMT} = \sum_{i=1}^{S} p_i t_i$$

Relative cover of graminoids, woody species, and those with clonal growth was calculated excluding *Lythrum salicaria.*

Statistical analysis

All statistical analyses were done with R version 3.0.1 (R Core Team, 2013). For all analyses, *Lythrum salicaria* height was square-rooted and shoot length natural logarithm transformed to achieve normality; cover was square-root transformed to enhance normality. Intercontinental patterns in growth and fecundity of *Lythrum salicaria* were evaluated using an analysis of variance (ANOVA) or a Kruskal-Wallis test, as appropriate. For all significant results, post-hoc comparisons were performed using Tukey HSD tests in case of ANOVA and post-hoc multiple comparisons for Kruskal-Wallis tests with the 'pgirmess' package (Giraudoux, 2013).

Additionally, the relationships between *Lythrum salicaria* size as a measure of growth and fecundity (i.e., height, shoot length, cover) and plant community traits (i.e., CMTs for plant height, leaf area, specific leaf area, leaf dry matter content and seed mass, as well as relative cover of graminoids, woody, and clonal species), cumulative cover of all species, species number, and a variable to control for the phenological stage during sampling (GDD), were assessed. We performed multiple linear regressions with the function 'lm' including study area as a dummy variable, i.e., SE Canada was the model default, while NE USA, S Norway, and S Germany were included as dummies. As we did not know if relationships would be the same in the four areas, we included the interaction of each explanatory variable by study area. Model simplification was carried out by step-wise removal of non-significant terms until the minimal adequate model for each response variable was obtained (following Crawley, 2009). All explanatory variables except 'study area' were standardized to make their slopes in each regression model comparable, i.e., the mean was subtracted from each value, and the result was divided by the standard deviation. Model assumptions were checked by reviewing model checking plots for full models.

Results

Variation in plant height, shoot length and cover of **Lythrum salicaria** *among areas*

Plant height, and shoot length of the mean individual, as well as cover of *Lythrum salicaria* in the subplots were significantly different among the study areas. Height was significantly lower in S Germany compared to S Norway (ANOVA, $F_{3,\ 96} = 4.2$, $P = 0.007$; Tukey HSD, $P = 0.004$; Fig. 10A). Shoot length was significantly smaller in S Germany compared to NE USA and S Norway (ANOVA, $F_{3,\ 96} = 10.9$, $P < 0.001$; Tukey HSD, both $P < 0.001$; Fig. 10B), and smaller in SE Canada compared to NE USA (Tukey HSD, $P = 0.031$). *Lythrum salicaria* cover was significantly lower in S Germany compared to the NE USA sites, but showed no difference among the other study areas (Kruskal-Wallis test, $\chi^2 = 14.50$, df = 3, $P = 0.002$; post-hoc multiple comparisons, $P = 0.05$; Fig. 10C). Estimated herbivory was significantly lower in SE Canada, but not different among the other areas (Kruskal-Wallis test, $\chi^2 = 25.3$, df = 3, $P < 0.001$; Table 8), and showed no effect on *Lythrum salicaria* growth (Spearman correlation with *Lythrum salicaria* height; *rho* = –0.02, $P = 0.831$). To sum up, growth and fecundity of *Lythrum salicaria* was generally lowest in S Germany, intermediate in SE Canada, and highest in NE USA and S Norway (Fig. 10).

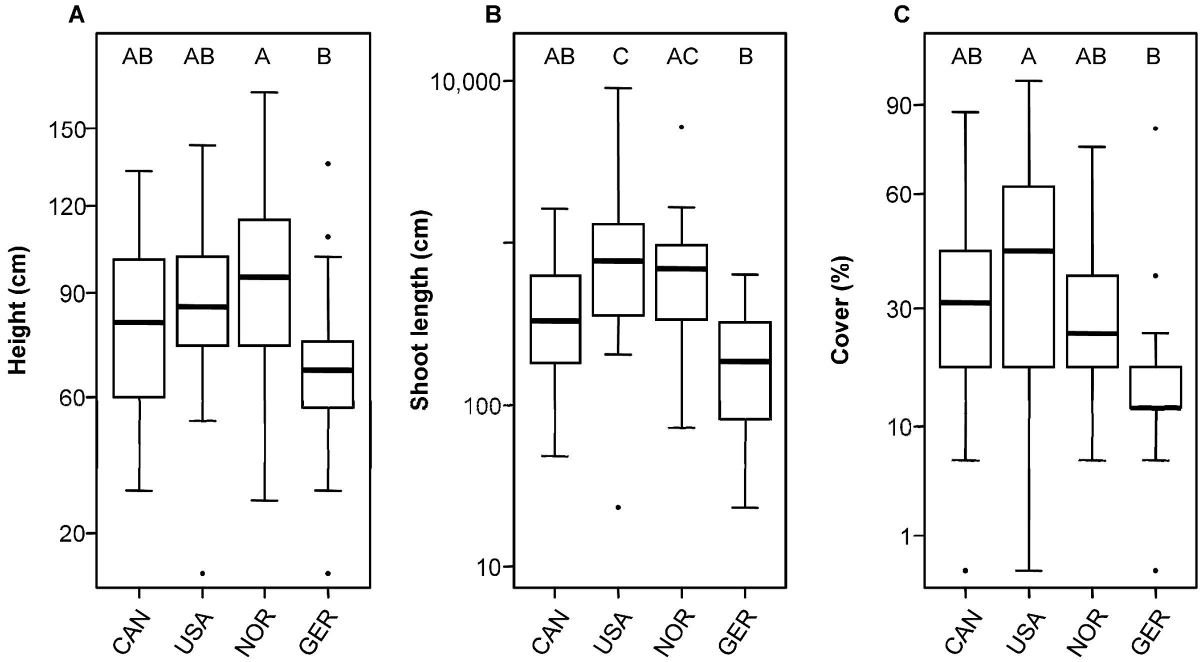


Fig. 10 Patterns in growth and fecundity of *Lythrum salicaria* measured as plant height (A; ANOVA, $F_{3, 96} = 4.2$, $P = 0.007$), shoot length (B; ANOVA, $F_{3, 96} = 10.9$, $P < 0.001$), and cover (C; Kruskal-Wallis test, $\chi^2 = 14.5$, df = 3, $P = 0.002$) in the four study areas (see Table 8; Fig. 9). Letters on top of the boxes indicate significant differences from post-hoc tests ($P < 0.05$).

Community mean traits and **Lythrum salicaria** *height, shoot length and cover*

Variation in height of *Lythrum salicaria* was well explained by community traits ($R^2_{adj.} = 0.64$, $F_{16, 82} = 11.7$, $P < 0.001$; Table 9, Table 10). Height increased considerably with the community means of plant height, leaf area, and specific leaf area (Fig. 11A–C). Relative cover of woody species, species number, and number of growing degree days elapsed (GDD; Fig. 11D–F) had inconsistent effects in the study areas. While *Lythrum salicaria* height decreased strongly with increasing fraction of woody species in S Germany (slope $\beta = -0.17$), the NE USA ($\beta = -0.76$), and especially in the SE Canadian sites ($\beta = -44.9$; Table 10), it increased in S Norway ($\beta = 0.16$). Similarly, *Lythrum salicaria* height decreased slightly with species number in SE Canada, NE USA, and S Norway ($\beta = -0.01$), while it increased in S Norway ($\beta = 0.75$). *Lythrum salicaria* height was strongly negatively influenced by growing degree days in SE Canada ($\beta = -7.34$) and slightly in NE USA ($\beta = -0.36$). In contrast, it was positively influenced in S Norway ($\beta = 1.24$) and S Germany ($\beta = 0.17$). Overall, *Lythrum salicaria* height had positive relationships with community mean plant height, leaf area, and specific leaf area, but the direction of the relationships with other community traits differed among areas.

Table 9 Terms affecting *Lythrum salicaria* height, shoot length and cover in four study areas (SE Canada, USA, NOR, GER; see Table 8) based on linear regressions. All other explanatory variables were standardized to make their influence comparable. The minimal adequate models are presented.

Model	Source of variation	df	Mean Sq.	*F*	*P*
Height	Community mean plant height	1	99.07	98.62	<0.001 ***
$R^2_{adj.} = 0.64$	Community mean leaf area	1	9.95	9.91	0.002 **
$F_{16, 82} = 11.7$	Community mean SLA	1	16.71	16.64	<0.001 ***
$P < 0.001$	Relative cover of woody species	1	0.00	0.00	0.975
	Species number	1	0.73	0.72	0.398
	GDD	1	9.52	9.48	0.002 **
	USA	1	16.87	16.79	<0.001 ***
	NOR	1	0.60	0.59	0.443
	GER	1	0.09	0.09	0.769
	Relative cover of woody species : USA	1	2.65	2.64	0.108
	Relative cover of woody species : NOR	1	4.74	4.72	0.033 *
	Relative cover of woody species : GER	1	3.98	3.96	0.050
	Species number : NOR	1	1.90	1.89	0.173
	GDD : USA	1	0.01	0.01	0.929
	GDD : NOR	1	4.02	4.02	0.048 *
	GDD : GER	1	16.52	16.44	<0.001 ***
	Residuals	82	1.01		
Shoot length	Community mean plant height	1	9.83	14.59	<0.001 ***
$R^2_{adj.} = 0.48$	Community mean leaf area	1	8.24	12.23	<0.001 ***
$F_{6, 92} = 16.2$	Community mean $LDMC^2$		29.56	43.85	<0.001 ***
$P < 0.001$	Relative cover of graminoids	1	1.05	1.56	0.216
	Study area USA	1	13.86	20.56	<0.001 ***
	Relative cover of graminoids : study area USA	1	2.88	4.27	0.042 *
	Residuals	92	0.67		
Cover	Community mean plant height	1	2.03	0.50	0.483
$R^2_{adj.} = 0.17$	Relative cover of graminoids	1	12.18	2.98	0.087
$F_{6, 92} = 4.4$	Cumulative cover of all species	1	22.68	5.56	0.021 *
$P < 0.001$	USA	1	33.93	8.31	0.005 **
	Community mean plant height : USA	1	16.90	4.14	0.045 *
	Relative cover of graminoids : USA	1	20.02	4.91	0.029 *
	Residual	92	4.08		

Study area was included as a dummy variable (see Table 2 for abbreviations), i.e., SE Canada was the model default, USA, NOR and GER were included as dummies.

GDD = Growing degree days >8 °C elapsed in the study year.

Table 10 Slopes and intercepts for terms affecting *Lythrum salicaria* height, shoot length and cover in four study areas (CAN, USA, NOR, GER; see Table 8, linear regressions); see Table 9 for minimal adequate models. Slopes that do not differ among study areas are marked with an asterisk. For further information see Methods.

Model	Intercept/ Slopes	Terms		CAN	USA	NOR	GER
Height	*Intercept* (α)			*-13.26*	*9.48*	*8.06*	*8.66*
	Slopes (*β*)	Community mean plant height	*	1.33	1.33	1.33	1.33
		Community mean leaf area	*	0.41	0.41	0.41	0.41
		Community mean SLA	*	0.45	0.45	0.45	0.45
		Relative cover of woody species		-44.88	-0.76	0.16	-0.17
		Species number		-0.01	-0.01	0.72	-0.01
		GDD		-7.34	-0.36	1.24	0.17
Shoot length	*Intercept* (α)			*5.67*	*6.72*	*5.67*	*5.67*
	Slopes (*β*)	Community mean plant height	*	0.48	0.48	0.48	0.48
		Community mean leaf area	*	0.35	0.35	0.35	0.35
		Community mean LDMC	*	-0.34	-0.34	-0.34	-0.34
		Relative cover of graminoids		-0.04	-0.43	-0.04	-0.04
Cover	*Intercept* (α)			*4.72*	*6.95*	*4.72*	*4.72*
	Slopes (*β*)	Community mean plant height		0.20	1.75	0.20	0.20
		Relative cover of graminoids		-0.12	-1.14	-0.12	-0.12
		Cumulative cover	*	-0.47	-0.47	-0.47	-0.47

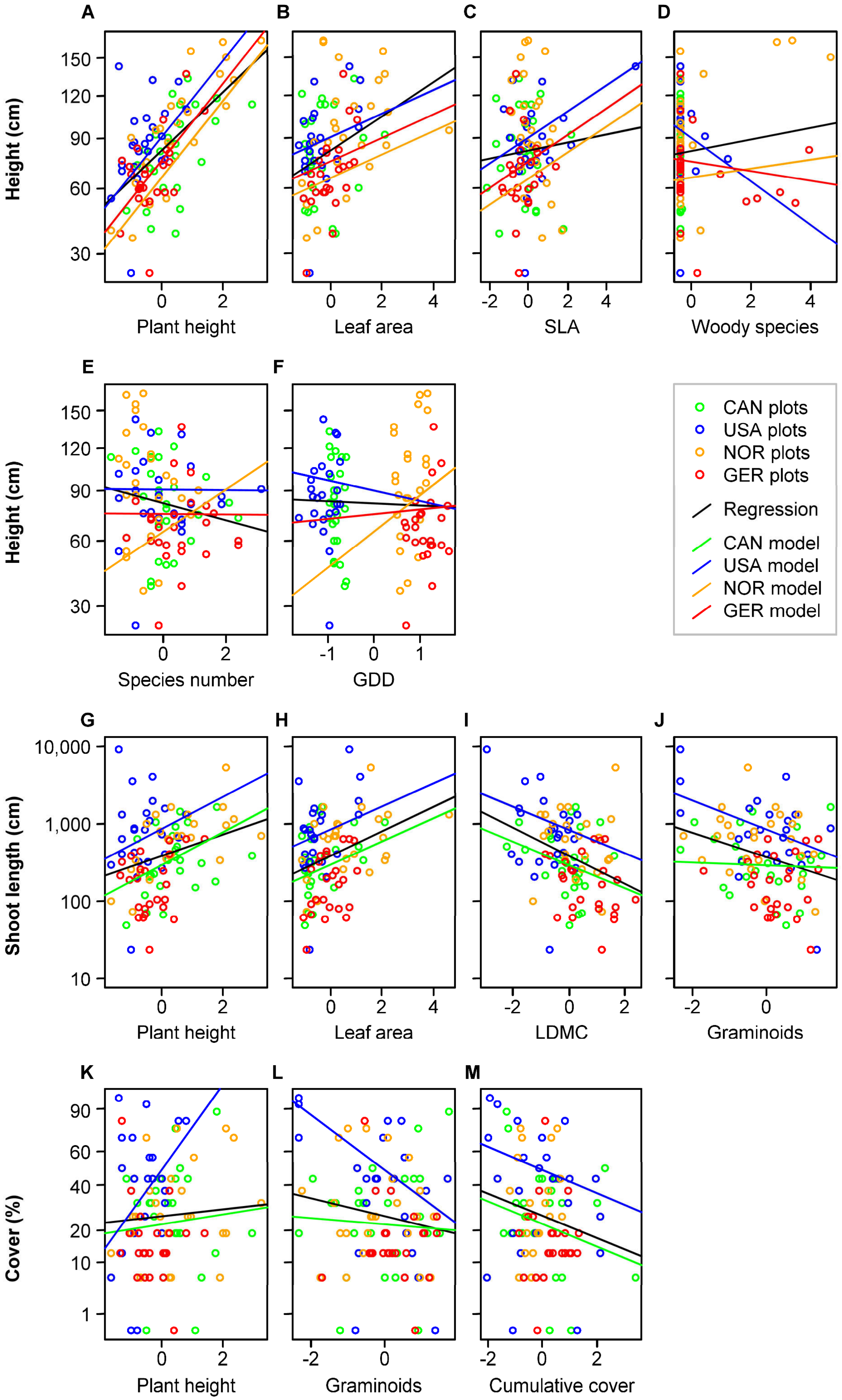
SLA = Specific leaf area.
GDD = Growing degree days >8 °C elapsed in the study year.
LDMC = Leaf dry matter content.

Lythrum salicaria shoot length was explained to an intermediate degree by the selected community traits ($R^2_{\mathrm{adj.}} = 0.48$, $F_{6,\,92} = 16.2$, $P < 0.001$; Table 9, Table 10). Shoot length was longer with increasing community mean plant height and leaf area, but decreased with mean leaf dry matter content and relative cover of graminoids (Fig. 11G–J). The reduction with increasing fraction of grasses and sedges was most pronounced in the NE USA sites ($\beta = –0.43$, compared to $\beta = –0.04$ for the other areas; Table 10). For *Lythrum salicaria* shoot length, the direction of the relationships did not vary among areas.

Lythrum salicaria cover could only be explained to a small degree by the selected community traits ($R^2_{\mathrm{adj.}} = 0.17$, $F_{6,\,92} = 4.4$, $P < 0.001$; Table 9). Cover increased with community mean plant height, but decreased with relative cover of graminoids, and cumulative cover (Fig. 11K–M; Table 9, Table 10). The negative relationship with relative cover of graminoids was especially pronounced in the NE USA sites ($\beta = –1.14$, compared to $\beta = –0.12$ for the other areas; Table 10). The positive influence of community mean plant height was also especially pronounced in the NE USA ($\beta = 1.75$, compared to $\beta = 0.20$ for the other areas; Table 10). Thus, the model on *Lythrum salicaria* cover was the poorest; strength, but not direction, of the detected relationships with community traits differed among study areas.

⟶

Fig. 11 Relationship between *Lythrum salicaria* height (A–F), shoot length (G–J) and cover (K–M) and different community traits, i.e., community mean plant height, leaf area, specific leaf area, relative cover of woody species, species number, growing degree days >8 °C (GDD), leaf dry matter content (LDMC), relative cover of graminoids and cumulative cover of all other species in four areas (green: CAN, blue: USA, orange: NOR, red: GER; see Table 8; Fig. 9). Black lines show simple regressions including all areas. Colored lines show regression slopes and intercepts from the minimum adequate model (Table 9, Table 10) separately for study areas. As the colored lines were calculated for the entire model they do not necessarily fit the points. Green lines (CAN) for height (A–F) are situated outside the plot space. Green lines for shoot length and cover (G–M) include CAN, NOR and GER, as slopes and intercepts were the same for the respective models (Table 10). Explanatory variables were standardized to make their slopes comparable (see Methods).


A
B
C
D
Height (cm)
150
120
90
60
30
0
2
4
-2
Plant height
Leaf area
SLA
Woody species
E
F
Species number
GDD
-1
1
CAN plots
USA plots
NOR plots
GER plots
Regression
CAN model
USA model
NOR model
GER model
G
H
I
J
Shoot length (cm)
10,000
1,000
100
10
LDMC
Graminoids
K
L
M
Cover (%)
90
60
40
20
10
1
Cumulative cover

Discussion

To our knowledge, this is the first study showing correlations between growth and fecundity of a plant species and mean functional traits of plant communities in its native and invaded ranges. We found significant variation in growth and fecundity of *Lythrum salicaria* among four study areas (*Objective A*), and this variation was explained to a considerable degree by community traits representing competition ($R^2_{\mathrm{adj.}} = 0.17$–$0.64$; *Objective B*). Interestingly, not all correlations were consistent among areas (*Objective C*).

Simultaneous high growth and fecundity of **Lythrum salicaria** *and associates*

Growth and fecundity of *Lythrum salicaria* were positively correlated to community means of plant height, leaf area, and specific leaf area. These traits indicate high growth and competitive ability of co-occurring plants (Wang *et al.*, 2010; Craine & Dybzinski, 2013; Marteinsdóttir & Eriksson, 2013). Therefore, the positive correlations suggest high growth and fecundity of the focal species and the other species at the same time. We found mean leaf dry matter content (LDMC) to be negatively correlated with shoot length of the focal species. As LDMC is known to correlate negatively with measures of growth such as specific leaf area and relative growth rate (Cornelissen *et al.*, 2003b), this correlation also suggests simultaneous high growth and fecundity of the focal species and associates. Plants with high values for height, leaf area, and specific leaf area as well as low values for LDMC can also be associated with productive sites (Cornelissen *et al.*, 2003b).

Thus, variation in growth and fecundity of *Lythrum salicaria* could depend on abiotic factors that drive productivity, for example climate, soil moisture or nutrient availability. As one possible scenario, higher nutrient availability at the sampled sites may allow all plants to grow taller and to produce larger and thinner leaves. Higher nutrient availability is known to enhance height (Bastlová *et al.*, 2004) and biomass production in *Lythrum salicaria* (Shamsi & Whitehead, 1977b), which may permit it to grow as quickly as the associated species.

Negative interactions between **Lythrum salicaria** *and associates*

We detected negative correlations between growth and fecundity of *Lythrum salicaria* and the relative cover of graminoids and cumulative cover of other species, indicating negative interactions. Thus, it might be that low vegetation densities and proportions of grasses and sedges enhance *Lythrum salicaria* growth and fecundity, while high vegetation densities and cover of graminoids suppress the species via competition. This is supported by a study that found significant negative correlations between *Lythrum salicaria* biomass and biomass of other species (Farnsworth & Ellis, 2001).

Nevertheless, the negative relationship with cover of graminoids has to be treated with caution as in NE Canadian plots, one of the most frequent graminoid species was *Phalaris arundinacea* L. (Appendix 4) which is invasive in this area (Lavoie *et al.*, 2003; Lavoie *et al.*, 2005).The species was not particularly frequent in the NE USA plots. Nevertheless, our results identify a specific group of plants (graminoids) that may have a competitive advantage over *Lythrum salicaria*. However, manipulative experiments are needed to derive a mechanistic understanding of the relationship. A previous study found competitive ability of *Lythrum salicaria* to be highest among 44 wetland species, but did not find a pattern with regard to graminoid species, although *Phalaris arundinacea* was ranked third (Gaudet & Keddy, 1988). A future study should test the influence of reduced aboveground competition on *Lythrum salicaria* in established graminoid-rich versus herb-dominated wetland communities.

Consistency among study areas in the native and invaded ranges

The correlations discussed above were consistent for all study areas as only slopes or intercepts varied for some of them. However, some relationships had different directions among areas, i.e., some traits had negative effects in some areas, but positive effects in others. This might indicate intercontinental differences in functioning of the competition regime, or in the population genetics of *Lythrum salicaria*.

Relative cover of woody species was negatively connected to *Lythrum salicaria* height in SE Canada, NE USA, and S Germany, but positively in S Norway. Treberg & Husband (1999) found a lower mean number of woody species in plots with than in plots without *Lythrum salicaria*, although not statistically significant. It has been shown that *Lythrum salicaria* is negatively affected by shading (Shamsi & Whitehead, 1974), which should increase during shrub expansion. Nevertheless, woody species could be strong suppressors of *Lythrum salicaria* in some areas, while in S Norway the species appeared to be facilitated by woody species. This raises the question if *Lythrum salicaria* populations sampled in S Norway might have developed higher tolerance to shading than in the other areas. *Lythrum salicaria* height was positively correlated with higher plant species numbers only in the S Norway sites, whereas there was a slightly negative effect in the other areas. In accordance with this, previous field surveys generally found no effect of *Lythrum salicaria* on wetland plant diversity (Lavoie, 2010).

Biodiversity management: application in the context of restoration ecology

Funk *et al.* (2008) suggested the application of plant functional traits in restoration ecology, and first studies showed that functional traits can be used to predict species success in restoration (Roberts *et al.*, 2010; Sandel *et al.*, 2011). This indicates that functional trait data can serve as a basis for decision making and prediction of restoration outcomes (Drenovsky *et* *al.*, 2012). In future restoration projects, species selection should be based on functional traits that correlate negatively with growth and fecundity of invasive species. In this way, species selection could pave the way for invader suppression. To derive new management options following a trait-based method, a survey of the growth and fecundity of the focal species and community composition must first be carried out. Next, selected plant traits related to competition can be used to calculate community mean traits based on species coverage (Roscher *et al.*, 2013). Correlations between community mean traits and growth and fecundity of the focal species indicate which species groups would suppress the focal species. As correlations may vary among areas in the native and invaded ranges of the focal species, more than one area should be considered. In a second step, mechanistic relationships behind the correlational results of the survey must be verified in manipulative experiments. For example, manipulation of aboveground biomass of species groups that inhibit certain traits can prove if the indicated effects are useful for invader suppression.

Our results indicate that the restoration of sites invaded by *Lythrum salicaria* may be improved by using grasses and sedges. After experimental verification of their effects on the invader, these species could be used as part of an invasive species management plan. Especially during restoration, sowing graminoids may limit the establishment of the invader. Although mowing has shown mixed results as a control measure for *Lythrum salicaria* (Gabor & Murkin, 1990; Haworth-Brockman *et al.*, 1991), in some situations it could be useful to increase the cover of graminoids. The choice of graminoid species should reflect the local species pool; invasive aliens like *Phalaris arundinacea* which may have negative effects on rare native species must be avoided.

Community traits and plant invasions

Identifying strong relationships between community mean functional traits related to competition, and the growth and fecundity of alien plants, is a new method for the management of problematic invaders and the conservation of native biodiversity. This approach can be used to derive new management options to control invasive species, and provides a valuable tool for restoration ecologists, because correlations between community mean traits and the growth and fecundity of the focal species indicate which species groups will suppress the focal species. In our case the results indicate that the presence of grasses and sedges may limit the invasion of *Lythrum salicaria* in wetlands.

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Original sources of plant trait data

The original plant trait data (leaf area, specific leaf area, leaf dry matter content, seed mass, plant growth form and species reproduction type) used in our analysis was kindly contributed to the TRY database by several researchers:

Shipley (1989); Shipley & Parent (1991); Shipley (1995); Cornelissen (1996); Cornelissen *et al.* (1996); Atkin *et al.* (1997); Castro-Díez *et al.* (1998); Hickler (1999); Medlyn *et al.* (1999); Meziane & Shipley (1999); Shipley & Lechowicz (2000); White *et al.* (2000); Niinemets (2001); Shipley (2002); Shipley & Vu (2002); Cornelissen *et al.* (2003a); Loveys *et al.* (2003); Ogaya & Peñuelas (2003); Quested *et al.* (2003); Sack *et al.* (2003); Cornelissen *et al.* (2004); Díaz *et al.* (2004); Kühn *et al.* (2004); Sack (2004); Wright *et al.* (2004); Han *et al.* (2005); Moles *et al.* (2005); Vile (2005); Cavender-Bares *et al.* (2006); Kazakou *et al.* (2006); Preston *et al.* (2006); Campbell *et al.* (2007); Garnier *et al.* (2007); Coomes *et al.* (2008); Cornwell *et al.* (2008); Kleyer *et al.* (2008); Reich *et al.* (2008); Royal Botanical Gardens KEW (2008); van Bodegom *et al.* (2008); Craine *et al.* (2009); Green (2009); Kattge *et al.* (2009); Paula *et al.* (2009); Poorter *et al.* (2009); Reich *et al.* (2009); Wirth & Lichstein (2009); Freschet *et al.* (2010); Laughlin *et al.* (2010); Ordoñez *et al.* (2010); Willis *et al.* (2010); Gallagher *et al.* (2011); Onoda *et al.* (2011).

CHAPTER 4

NO EVIDENCE FOR LOCAL ADAPTATION IN AN INVASIVE ALIEN PLANT: FIELD AND GREENHOUSE EXPERIMENTS TRACING A COLONIZATION SEQUENCE

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Abstract

• *Background and Aims* Local adaptation enables plant species to persist under different environmental conditions. Evolutionary change can occur rapidly in invasive annual species and has been shown to lead to local adaptation. However, the patterns and mechanisms of local adaptation in invasive species along colonization sequences are not yet understood. Thus, we used the alien annual *Impatiens glandulifera* to investigate local adaptation to distinct habitats that were consecutively invaded in central Europe.

• *Methods* We performed a reciprocal transplant experiment using 15 populations from alluvial deciduous forests, fallow meadows and coniferous upland forests, and a greenhouse experiment growing plants from these habitats under treatments reflecting the main habitat differentiators (shade, soil acidity, competition).

• *Key Results* Biomass production, specific leaf area, plant height and relative growth rate differed between habitats in the field experiment and between treatments in the greenhouse, but not between seed origins. Overall, there was no indication of local adaptation in either experiment.

• *Conclusions* Since *Impatiens glandulifera* is a successful invader in many habitats without showing local adaptation, we suggest that the species is coping with environmental variation by means of high phenotypic plasticity. The species seems to follow a 'Jack-and-master' strategy, i.e., it is able to maintain high fitness under a wide range of environmental conditions, but performs particularly well in favorable habitats. Therefore, the proposed colonization sequence is likely to be based primarily on changes in propagule pressure. We conclude that invasive alien plants can become dominant in distinct habitats without local adaptation.

Keywords

biological invasions • colonization history • general-purpose genotype • greenhouse experiment • home site advantage • invasive alien plant • *Impatiens glandulifera* • Jack-and-master strategy • local adaptation • phenotypic plasticity • propagule pressure • reciprocal transplant experiment

Introduction

Environmental variability causes opposing selection pressures and therefore favors genetic adaptation of plant species. Adaptation, in turn, enables plant species to persist in a set of different environmental conditions (Leimu & Fischer, 2008). If adaptation has taken place, resident genotypes will have a higher relative fitness than foreign ones ('local vs. foreign' criterion; Kawecki & Ebert, 2004). While at large scales climatic differences are important for adaptation (Macel *et al.*, 2007), at local scales distinct habitat characteristics might be more relevant (Hereford & Winn, 2008), e.g., soil conditions (Raabová *et al.*, 2011), shade (Godoy *et al.*, 2011b) or biotic interactions (Grøndahl & Ehlers, 2008). Many studies have found evidence for adaptation in plant species (e.g., Becker *et al.*, 2008; Hufford *et al.*, 2008; see meta-analysis by Leimu & Fischer, 2008; Hereford, 2009), but others did not (e.g., Leiss & Müller-Schärer, 2001; Hereford & Winn, 2008; Ebeling *et al.*, 2011; Garrido *et al.*, 2012). Recently, progress has been made in explaining the mechanisms influencing local adaptation (e.g., Leimu & Fischer, 2008; Hereford, 2009; Lopez *et al.*, 2009), but it is still a challenge to understand the underlying patterns and drivers of adaptation in plants.

In invasive alien species, evolutionary change can occur rapidly (Maron *et al.*, 2004; Bossdorf *et al.*, 2005). Although there are several mechanisms that are believed to inhibit adaptation, e.g., low genetic variability (see Taylor & Keller, 2007), local adaptation of invasive alien plants to distinct habitat types has been proven repeatedly (e.g., Scott *et al.*, 2010; Godoy *et al.*, 2011b). Sax *et al.* (2007) suggested that invasive alien species can be used as 'model organisms' for studying ecological and evolutionary processes in real time. Therefore, invasive alien species are a suitable study system to investigate the evolution of local adaptation.

Local adaptation can broaden species' ecological niches. This is particularly important in secondary invasions (Dietz & Edwards, 2006). According to Dietz and Edwards (2006) plant invasions occur in two stages. During the primary invasion, alien species establish in habitats with the highest propagule pressure, e.g., along transport corridors, while in the secondary invasion additional habitats with distinct environmental conditions are colonized. These two stages do not have to be entered consecutively, but in many plant invasions the most accessible habitats are colonized first before secondary invasion to new habitat conditions takes place. We expect local adaptation in the secondary invasion to be more pronounced for early invaded habitats due to longer residence time. When different habitats have been colonized consecutively, a sequence of local adaptation can be studied along this colonization sequence. For example, Erfmeier *et al.* (2011) found a shift in life history strategy during secondary invasion of a deciduous tree suggesting on-going adaptation to less favorable habitats. However, there are two possible alternative explanations for secondary invasion in invasive alien plants. First, the species' ecological niche can also be broadened by high phenotypic plasticity (Dietz & Edwards, 2006; Moloney *et al.*, 2009). Invasive plants can profit from high phenotypic plasticity in morphological and physiological traits by two main strategies (Richards *et al.*, 2006): The 'Jack-of-all-trades' strategy is able to maintain high fitness in a set of distinct habitats (general-purpose genotype; Baker, 1965), while the 'master-of-some' can increase fitness in especially favorable habitats (e.g., Sultan, 2001). Second, changing patterns of local propagule pressure may also contribute to secondary invasion. Propagule pressure depends mainly on the distance to (Rouget & Richardson, 2003) and the size of donor populations (Richardson & Pyšek, 2006), i.e., older, larger populations are more likely to donate propagules to other sites. Land use alteration can further change temporal patterns in propagule pressure through alterations of disturbance regimes and transport pathways.

A prominent invasive alien plant species that has colonized distinct habitats in Europe over a long time period is *Impatiens glandulifera*. In the invaded range, this species frequently occurs in near-natural habitats, primarily in riparian habitats, fenland, mesotrophic grassland and deciduous woodland (Andrews *et al.*, 2005). *I. glandulifera* is a suitable species to study local adaptation to different habitats because it is an outcrossing annual with potentially fast evolution (Beerling & Perrins, 1993). Previous work showed that *I. glandulifera* exhibits latitudinal trends in growth which might reflect an adaptation to the length of the growing season (Kollmann & Bañuelos, 2004). In the congeneric *I. capensis* potential to develop local adaptation was shown, especially with regard to shade (Dudley & Schmitt, 1995) and density (Donohue *et al.*, 2001). Additionally, Walker *et al.* (2009) found substantial genetic variation in *I. glandulifera* in northeast England using microsatellite analysis, and Zybartaite *et al.* (2011) revealed four major genetic groups of populations in Lithuania using randomly amplified polymorphic DNA.

Historical reconstructions suggest that *I. glandulifera* colonized different near-natural habitats consecutively in the past 100 years starting from settlements and riparian habitats (Pyšek & Prach, 1995). In the Czech Republic, for example, the species was first recorded in riparian habitats in 1900, in fallow meadows in 1934, and in forests in 1941 (Pyšek & Prach, 1995). Rivers act as dispersal corridors and it took about 20 years from the first occurrence of the species on main rivers until invasion proceeded upstream along tributaries and laterally away from the rivers (Malíková & Prach, 2010). Invasion in the Czech Republic is still in progress and expected to continue (Malíková & Prach, 2010). Accordingly, first records from southern Germany date to the first two decades of the 20th century (Hegi, 1925–1965) and it can be assumed that habitat colonization in Germany has progressed in a similar way as in the Czech Republic. Deciduous forests along rivers were most probably invaded first, while fallow meadows and coniferous upland forests are spatially separated from riverine habitats, and thus, colonization started later. These three habitats differ mainly with regard to shade, soil acidity and competition. Forest habitats are characterized by moderate to high shade, while fallow meadows are mainly open. Soils in coniferous forests are usually more acid compared to alluvial deciduous forests and fallow meadows. Competition among herbs is more intense in fallow meadows and alluvial deciduous forests compared to coniferous forests with sparse herb layers. These contrasting habitat conditions should favor local adaptation.

We conducted a reciprocal transplant experiment in southern Germany to test for local adaptation in *I. glandulifera* to three habitat types along a colonization sequence consisting of alluvial deciduous forests, fallow meadows and coniferous upland forests. Additionally, we manipulated shade, soil acidity and competition as main habitat differentiators in a factorial greenhouse experiment to extract the ecological factors that are likely to lead to local adaptation. Our main aim was to test for local adaptation in *I. glandulifera*. More specifically we hypothesized (1) higher fitness of local origins when reciprocally sown in the three habitats in the field ('home habitat advantage'). Based on habitat characteristics, we expected in the greenhouse (2a) under high shade, low soil acidity and high competition, plants originating from alluvial deciduous forests have higher fitness compared with other origins, (2b) under low shade, low soil acidity and high competition, plants from fallow meadows have highest fitness, and (2c) under high shade, high soil acidity and without competition, plants from coniferous upland forests have the highest fitness. (3) We further predicted local adaptation to be most pronounced in origins from alluvial deciduous forests, followed by those from fallow meadows and by those from coniferous upland forests.

Materials and methods

Study species

Impatiens glandulifera (Balsaminaceae) is a herbaceous annual species that was introduced from the Himalaya to Europe as an ornamental plant in the 19th century (Beerling & Perrins, 1993), and has become abundant with considerable impact in 19 European countries within latitudes 30–64° N (Kollmann & Bañuelos, 2004). It is common in open and shaded habitats in lowland and lower montane areas (<800 m a.s.l.), but occurs in the Alps up to 1550 m altitude (Kollmann & Bañuelos, 2004). *I. glandulifera* grows up to 3 m tall, and the basal diameter of the stem can reach 5 cm (Beerling & Perrins, 1993). Germination takes place from February to April. The flowering period is from July to October, and the seeds disperse by dehiscent seed-capsules between August and October (Ammer *et al.*, 2011). They are transported over long distances through human activities and water dispersal (Hartmann *et al.*, 1995). The species has no clonal growth and a short-lived seed bank (Beerling & Perrins, 1993).

Study area and source populations

Seeds of *I. glandulifera* were collected in the region of Freising, southern Germany (study area: 48.39–48.45° N, 11.65–11.88° E, ca. 140 km², 366–506 m a.s.l.) in three different habitats, i.e., alluvial deciduous forests, fallow meadows and coniferous forests on nearby hills, each with five replicate populations to cover variability within habitats (hereafter 'source populations'). The alluvial deciduous forests were located in the floodplain of the River Isar. *I. glandulifera* populations in this habitat were rather continuous and situated close to the main river channel as well as along forest roads. The tree layer was dominated by *Fraxinus excelsior* mixed with *Acer pseudoplatanus* and *Salix alba* (height 20–30 m), leading to deep shade (canopy cover 70–90%). The understory had 60–80% cover of herbs and shrubs, mainly *Aegopodium podagraria* and *Rubus caesius*. The soil was moderately moist with neutral reaction. The fallow meadows occurred at plane to slightly inclined locations on loamy and moist soils with neutral reaction. *I. glandulifera* populations in this habitat were rather separated by more intense land use around the patches. The vegetation was characterized by tall herbs and grasses, including *Arrhenatherum elatius*, *Galium mollugo* and *Phalaris arundinacea* (cover 80–100%) with little shade from trees or shrubs. The coniferous upland forests were old-grown spruce plantations on sandy and less moist soils with slightly acidic reaction in the tertiary hills around Freising, with modest slopes under variable orientation. *I. glandulifera* populations in this habitat were less dense than in the other two habitats, and patches were mostly continuous with small gaps in between. The canopy consisted of 20–30 m tall *Picea abies* leading to moderate shade (cover 60–80%). The herb layer was sparser than in the other habitats (cover 30–50%), including mosses, *Oxalis acetosella, Rubus fruticosus* agg., and young plants of *Quercus robur* and *Acer pseudoplatanus*. The three habitats were all relatively nutrient-rich, while there was a pronounced gradient in soil acidity (see Appendix 5 for further information).

The first specimen from the greater study region stored in the two most important herbaria of the federal state is dated to 1909 (Munich) and originates from a riverine site approx. 85 km upstream to the study area, situated at River Isar which runs through the study area. It is assumed that invasion in the study area first covered habitats along River Isar and tributary River Amper before it proceeded to habitats outside the floodplains. Small tributaries as well as roads are most likely to have served as secondary colonization corridors. From Rivers Isar and Amper, colonization most probably first reached fallow wet meadow habitats, often situated close to tributaries, while colonization of upland coniferous forests began later and is still in progress. The distances between source populations were 5.7 ± 2.9 km (mean ± s.d., accordingly throughout the study) for deciduous forests, 5.3 ± 2.2 km for fallow meadows and 7.5 ± 4.1 km for coniferous forests, and did not differ within habitats (Anova, $F = 1.19$, $P = 0.32$; see Appendix 5 for distances to the closest source population overall and within each habitat).

Annual average temperature in the study region is 7.5 ºC, and annual precipitation 788 mm (Weihenstephan 1961–1990; Bayerische Landesanstalt für Landwirtschaft, 2012). Monthly mean temperature during the experiment (March–August 2012) was 2 ºC higher than long-term average (1961–1990). Precipitation from March to May 2012 was 54 mm, i.e., 29% less than normal, while from June to August 2012 precipitation amounted to 125 mm (42% more than normal in 1961–1990).

Seed material

In each population in the three habitat types we took 2–5 ripe capsules from 75 randomly chosen plants in September 2011 and again in October 2011 to account for possible temporal differences in seed quality. Seeds were dried at room temperature for 3 weeks and stored at 5 °C for 2 months prior to seed mass determination and stratification. Average seed mass of the used plant material was 13.6 ± 0.9 mg for populations in the deciduous forest, 12.8 ± 0.9 mg in the fallow meadows, and 11.8 ± 1.3 mg in coniferous forest (*n* = 5 x 500 seeds per source population, and *n* = 5 populations per habitat). Seeds were cold-wet stratified on filter paper in Petri dishes and stored at 3 °C. Seed germination rate after 3 weeks (5/15 °C, 12:12 h, without light) was 73 ± 11% for populations from deciduous forests, 93 ± 4% for fallow meadows, and 79 ± 12% for coniferous forests (*n* = 5 x 50 seeds per source population, and *n* = 5 populations per habitat).

Reciprocal seed transplant experiment

In mid-March 2012, we established one experimental plot (0.8 m x 1.6 m) in close proximity to each of the 15 source populations (see Appendix 7A for the experimental design). The 15 plot sites were chosen to be similar to the source populations, but free of *I. glandulifera* with a buffer zone of >2 m. The distances between plot and source population ranged from 34 to 962 m with values of 279 ± 358 m for deciduous forests, 69 ± 39 m for fallow meadows and 379 ± 226 m for coniferous forests. Distances were not different within habitats (Kruskal-Wallis test, *P* = 0.075; Appendix 6).

In one half of each plot (0.8 m x 0.8 m) soil remained untreated ('undisturbed soil'). In the other half all aboveground litter and vegetation were removed and the soil was disturbed with a rake (10 cm deep) one week before sowing ('disturbed soil'). This treatment was included to cover variability within habitats and meant to simulate disturbance by wild animals, e.g., boars. Each half of a plot was divided into 16 subplots. The subplot size (0.2 m x 0.2 m) was chosen based on observed plant densities in the source populations and experiences from a preliminary study in 2011. While one of them remained as a control, 20 seeds of each of the source populations were sown into the other subplots. Subplots were equipped with plastic rings (diameter 10 cm, height 3 cm) that were gently pushed into the soil to prevent seed losses. Nevertheless, we found germination in 7% of the control subplots which we consider to be caused by accidental dispersal from the other subplots. After 7 weeks, seedlings were thinned to a maximum of five per subplot to avoid bias due to intraspecific competition. In deciduous forests, 4 ± 4 seedlings per subplot (across all subplots within the habitat, but excluding controls) were removed, 6 ± 4 in fallow meadows and 1 ± 2 in coniferous forests. The removed seedlings were used to determine aboveground dry biomass per plant (after 3 days drying at 70 °C).

All plants were harvested after 20 weeks in August 2012. Biomass was used as a proxy for fitness since aboveground biomass and seed production of annual species are often correlated (e.g., Thompson *et al.*, 1991; Shipley & Dion, 1992). In addition, specific leaf area (SLA), plant height and relative growth rate (RGR) were measured, to detect plastic plant responses to the main habitat differentiators, i.e., shade, soil acidity and competition. One individual per subplot was chosen randomly to measure height. Three fully developed leaves of the same plant were photographed to determine SLA with the software ImageJ 1.46 (Schneider *et al.*, 2012), and dried afterwards. SLA was calculated as $\mathrm{SLA} = A\, W_{\mathrm{L}}^{-1}$, where A means area and

W_L dry mass of the selected three leaves (Cornelissen *et al.*, 2003b). We harvested aboveground biomass of all *I. glandulifera* individuals and determined dry biomass per plant. Mean RGR per subplot was calculated as $\mathrm{RGR} = (\ln(W_2)\, n_2^{-1} - \ln(W_1)\, n_1^{-1})\, (t_2 - t_1)^{-1}$, where W_1 and W_2 are the aboveground dry biomass of n individuals harvested at times t_1 (week 7) and t_2 (week 20) in each subplot. As suggested by Hoffmann and Poorter (2002), biomass was natural logarithm-transformed before averaging.

Greenhouse experiment

In the same time period a greenhouse experiment was conducted in the *Dürnast Research Center* (located within the study area; www.wzw.tum.de/ghl/) to identify the environmental factors potentially leading to local adaptation. Treatments included shade, soil acidity and competition, giving a full-factorial design with a total of eight treatments including all 15 source populations.

For the shade treatment, plants were grown under a single or a double layer of green fabric, resulting in approx. 10% and 5%, respectively, photosynthetic active radiation (PAR) in relation to full sunlight, which corresponds to moderate to deep shade, for example in coniferous forests (8.7 ± 4.9 % PAR) and deciduous forests (2.5 ± 1.9% PAR; Appendix 5). As the shade treatment was expected to alter not only light availability but also air humidity and temperature, we performed two shade treatments rather than comparing shade to no shade.

To manipulate soil acidity, commercial peat (Floragard Floratorf; $\mathrm{pH_{CaCl_2}}$ 3.0–4.0; nitrogen, phosphate and potassium oxide <0.05 kg $\mathrm{m^{-3}}$ each) was mixed with fertilizer (FERTY® 2; nitrogen 0.15 kg $\mathrm{m^{-3}}$, phosphate 0.05 kg $\mathrm{m^{-3}}$, potassium oxide 0.25 kg $\mathrm{m^{-3}}$, magnesium oxide 0.02 kg $\mathrm{m^{-3}}$) and different concentrations of lime. To achieve a moderately low pH treatment, 6 kg $\mathrm{m^{-3}}$ pelleted lime (concentration 50%) was applied, resulting in $\mathrm{pH_{CaCl_2}}$ 5.1. For neutral substrate, 14.5 kg $\mathrm{m^{-3}}$ pelleted lime (50%) and 10 kg $\mathrm{m^{-3}}$ fine lime (95%) were used. Additionally, $\mathrm{Ca(OH)_2}$ (0.3%) was added with watering to achieve $\mathrm{pH_{CaCl_2}}$ 6.5; the $\mathrm{pH_{CaCl_2}}$ in both treatments increased during the experiment to 6.4 and 7.2, respectively. The high pH treatment was comparable to the considered alluvial deciduous forests, where $\mathrm{pH_{H_2O}}$ was around 7.3 (Appendix 5) which corresponds to a $\mathrm{pH_{CaCl_2}}$ of approx. 6.8 (after Sillanpää equation: $\mathrm{pH_{CaCl_2}} = 1.044,\ \mathrm{pH_{H_2O}} - 0.808$; Budoi *et al.*, 2003). The low pH treatment was comparable to fallow meadows with $\mathrm{pH_{H_2O}}$ 6.9 which corresponds to a $\mathrm{pH_{CaCl_2}}$ of approx. 6.4. Plot sites had comparable soil reactions (Appendix 6).

For the competition treatment *I. glandulifera* seedlings were planted alone or together with five individuals of *Arrhenatherum elatius*. This grass species is known to be a good competitor and has been used in competition experiments for a long time (e.g., Mahmoud & Grime, 1976). Additionally, it grows in one of the considered habitats, i.e., fallow meadows.

The grass seedlings were germinated from regional seed material (Rieger-Hofmann GmbH), and introduced 21 days before the target plants to create sufficient competition.

Seeds of *I. glandulifera* were pre-germinated on a standard growing substrate in multipots. In March 2012, cotyledon length of all seedlings was measured. 40 seedlings of each of the source populations were selected at random and potted individually (pot diameter 19 cm, volume 0.003 m^3). Remaining seedlings (minimum of 35 per habitat) were used to determine starting aboveground biomass. Plants were exposed to the eight treatments with five replicates, giving a total of 600 plants. The pots were arranged in five rows (see Appendix 7B for the experimental design). Half of each row was covered with a double layer of green fabric ('high shade'), the other half with a single layer ('low shade'). Each row contained eight blocks. All blocks contained one plant of each source population. Within the two shade levels, the soil acidity and competition treatments were randomized, i.e., each row contained a randomized arrangement of one block per treatment with only the light levels being grouped together. To avoid edge effects, pots were randomized and rotated within the blocks, and blocks of the same shade treatment were rotated within rows once.

After 8 weeks (May 2012), three plants per source population were randomly selected from each treatment; the others were kept for further experiments. Aboveground biomass, plant height and SLA were determined as in the field experiment. To calculate RGR plant dry mass W_1 was estimated based on the correlation between cotyledon length (x) and starting aboveground biomass of remaining seedlings at the beginning of the experiment (for deciduous forest populations, Pearson correlation, $W_1 = 0.10\,x + 0.04$, $r = 0.41$, $P = 0.004$; for fallow meadows, $W_1 = 0.12\,x - 0.06$, $r = 0.70$, $P < 0.001$; and coniferous forest, $W_1 = 0.24\,x - 0.38$, $r = 0.60$, $P < 0.001$). Additionally, aboveground dry biomass of *Arrhenatherum elatius* per pot was determined in the competition treatment.

Statistical data analysis

All statistical analyses were performed with R 2.15.1 (R Core Team, 2012), using the packages 'lme4' (Bates *et al.*, 2012) and 'multcomp' (Hothorn *et al.*, 2009). For the reciprocal transplant experiment we fitted linear mixed effects models using maximum likelihood (ML) separately for both treatments (undisturbed soil, disturbed soil) and the different response variables (biomass, SLA, plant height and RGR of *I. glandulifera*). Full models contained seed origin, habitat and their interaction. A significant interaction between seed origin and habitat would indicate an adaptation of *I. glandulifera* to the local environmental conditions (see Van Groenendael, 1985; Leiss & Müller-Schärer, 2001). Seed mass and seedling emergence were included as covariates to partially control for maternal effects and varying intraspecific competition before the thinning to five seedlings per subplot after 7 weeks. We added source population nested in habitat and plot nested in habitat as crossed random factors to account for the spatial structure of seed sources and the experimental plot design.

To analyze the effects of seed origin and the eight treatments in the greenhouse on biomass, SLA, plant height and RGR of *I. glandulifera,* we also used linear mixed effects models fitted with maximum likelihood. We included seed origin, shade, soil acidity and competition with *Arrhenatherum elatius*, and all possible two-way and three-way interactions as fixed factors. Seed mass and grass biomass (competition treatment) were included as covariates to partially control for maternal effects and variation in competition. Source population nested in habitat, and block nested in rows within the shade treatment were included as crossed random factors to reflect the spatial component of seed origin and experimental design.

We simplified all models (field and greenhouse experiment) stepwise backwards based on likelihood ratio tests and removed non-significant fixed factors. Model checking plots were inspected to ensure that model assumptions were met. Biomass was natural logarithm-transformed to improve model fitting. No further transformations were necessary. Finally, we calculated post-hoc Tukey contrasts for all significant factors with more than two levels in the minimum adequate models.

Results

Plant performance in the field

We could not detect any influence of seed origin on aboveground biomass, SLA, plant height and RGR of transplanted *I. glandulifera* in the field experiment (Table 11). The response of all origins was very similar within each habitat (Fig. 12A–D; Appendix 8A–D).

In the undisturbed soil treatment, SLA was the only measured trait that was affected significantly by habitat (Table 11): transplants in deciduous forests revealed highest SLA (Tukey contrasts against both fallow meadows and coniferous forests $P < 0.001$), followed by those in coniferous forests (against fallow meadows $P = 0.002$) and fallow meadows (Fig. 12C). In the disturbed soil treatment, plant performance varied considerably across habitats and the influence of habitat was significant for all measured traits (Table 11). Plants transplanted to fallow meadows produced significantly more aboveground biomass than those in the two forest habitats (Tukey contrasts against deciduous forest $P = 0.004$, against coniferous forests $P > 0.001$) and did not differ between deciduous and coniferous forests ($P = 0.107$; Fig. 12B). SLA was similarly high in deciduous and coniferous forests ($P = 0.864$) and significantly lower in fallow meadows (Tukey contrast against both forest habitats $P < 0.001$; Fig. 12D). Height of plants in coniferous forests was significantly lower (Tukey contrasts against deciduous forests $P = 0.006$, against fallow meadows $P < 0.001$), but comparable between deciduous forests and fallow meadows ($P = 0.614$; Appendix 8B). RGR was significantly higher in fallow meadows than in deciduous forests (Tukey contrast $P < 0.001$; Appendix 8D).

Seedling emergence in the plots was 44 ± 29% in deciduous forests (for all subplots together, but excluding the controls), 54 ± 26% in fallow meadows and 14 ± 21% in coniferous forests. The response of all five source populations of the same origin was similar for each habitat and treatment, and in all models the population factor within origin explained less than 5% of the variance of the random factors. The plot site within a habitat explained some of the variance in most models (0–47%), but most variance of the random factors remained unexplained.

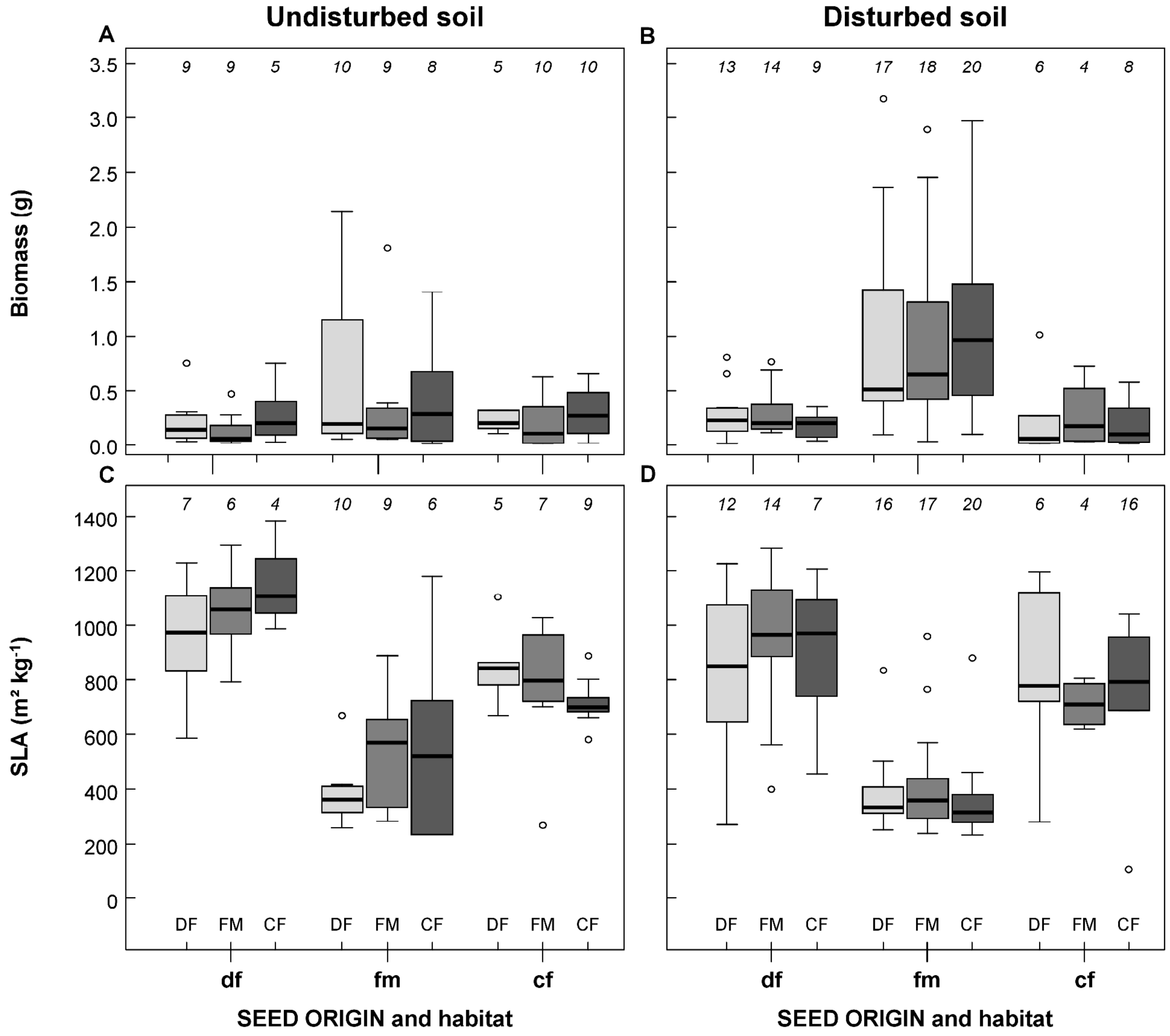

Fig. 12 Aboveground biomass (A, B) and specific leaf area (C, D) of the invasive alien *Impatiens glandulifera* when reciprocally transplanted between alluvial deciduous forests (df/DF), fallow meadows (fm/FM) und coniferous forests (cf/CF) in the invaded range. Seed origins are indicated with capital letters, plot habitats with small letters. Plots remained either untreated (A, C) or were experimentally disturbed before planting (B, D). The number of plant individuals in each group is given in small italic numbers above the boxplots.[6]

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[6] Included here with kind permission from Oxford University Press (original copyright). Figure 1 in Pahl et al. (2013, *Annals of Botany* 112: 1921-1930; slightly modified).

Table 11 Influence of seed origin, habitat and their interaction on aboveground biomass, specific leaf area (SLA), plant height and relative growth rate (RGR) of the invasive alien *Impatiens glandulifera* in a reciprocal transplant experiment in the invaded range in central Europe.[7]

	Biomass		SLA		Height		RGR	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Undisturbed soil								
Origin	3.73	0.155	2.04	0.362	1.56	0.459	0.60	0.741
Habitat	1.41	0.493	**9.58**	**0.008**	3.34	0.188	2.82	0.245
Origin x habitat	2.77	0.596	7.17	0.127	2.97	0.563	7.58	0.108
Disturbed soil								
Origin	0.63	0.729	1.29	0.525	1.59	0.452	3.70	0.157
Habitat	**9.30**	**0.010**	**8.95**	**0.011**	**8.35**	**0.015**	**4.47**	**0.035**
Origin x habitat	1.95	0.745	7.36	0.118	1.14	0.887	0.97	0.617

χ^2- and P-values are based on maximum likelihood ratio tests for linear mixed effects models.

χ^2-square- and P-values of non-significant factors refer to the respective step of the model simplification procedure. Significant terms were tested against the minimum adequate model.

See Methods section for information on random factors and covariates. For sample size see Fig. 12 and Appendix 8.

Significant values ($P < 0.05$) are printed in bold.

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[7] Included here with kind permission from Oxford University Press (original copyright). Table 1 in Pahl et al. (2013, *Annals of Botany* 112: 1921-1930).

Plant performance in the greenhouse

In the greenhouse experiment, seed origin had a significant influence on biomass production (Table 12). Nevertheless, there was no clear pattern and no better performance of each origin in the treatment reflecting its original habitat conditions (Fig. 13A, B). Including all treatments, biomass was highest for plants from coniferous forests (6.5 ± 4.0 g) and lowest for those from fallow meadows (5.6 ± 3.9 g; Tukey contrast, $P = 0.001$). However, the maximum value for biomass was achieved by plants from fallow meadows (17.4 g). Biomass of plants from deciduous forests ranged in between (6.0 ± 3.3 g) and was not significantly different from either fallow meadows ($P = 0.086$) or coniferous forests ($P = 0.385$). Biomass was additionally affected by soil acidity and the interaction of shade and competition (Table 12). Plants produced little biomass under high shade also in the absence of competitors, while plants grown under low shade produced remarkably more biomass when released from competition (Fig. 13A, B).

For all origins, SLA was significantly higher in the high shade treatment irrespective of additional treatments and origin (Table 12; Fig. 13C, D). Plants grown without competitors were generally taller than those grown under competition (Table 12; Appendix 9A, B). Additionally, height was significantly increased under low shade, especially for plants from coniferous forests (significant origin-by-shade-interaction, Table 12)). Plants from coniferous forests and fallow meadows grew taller under low compared to high pH, while plants from alluvial deciduous forests were taller under high pH (Fig. 14; significant origin-by-soil acidity-interaction, Table 12). In all treatments, RGR of plants originating from fallow meadows and coniferous forests did not differ ($P = 0.503$), but RGR was smaller for deciduous forest origins compared to fallow meadows ($P < 0.001$) and coniferous forests ($P = 0.027$; Appendix 9C, D). RGR was significantly higher for plants grown under low shade or high soil acidity (Table 12; Appendix 9C, D).

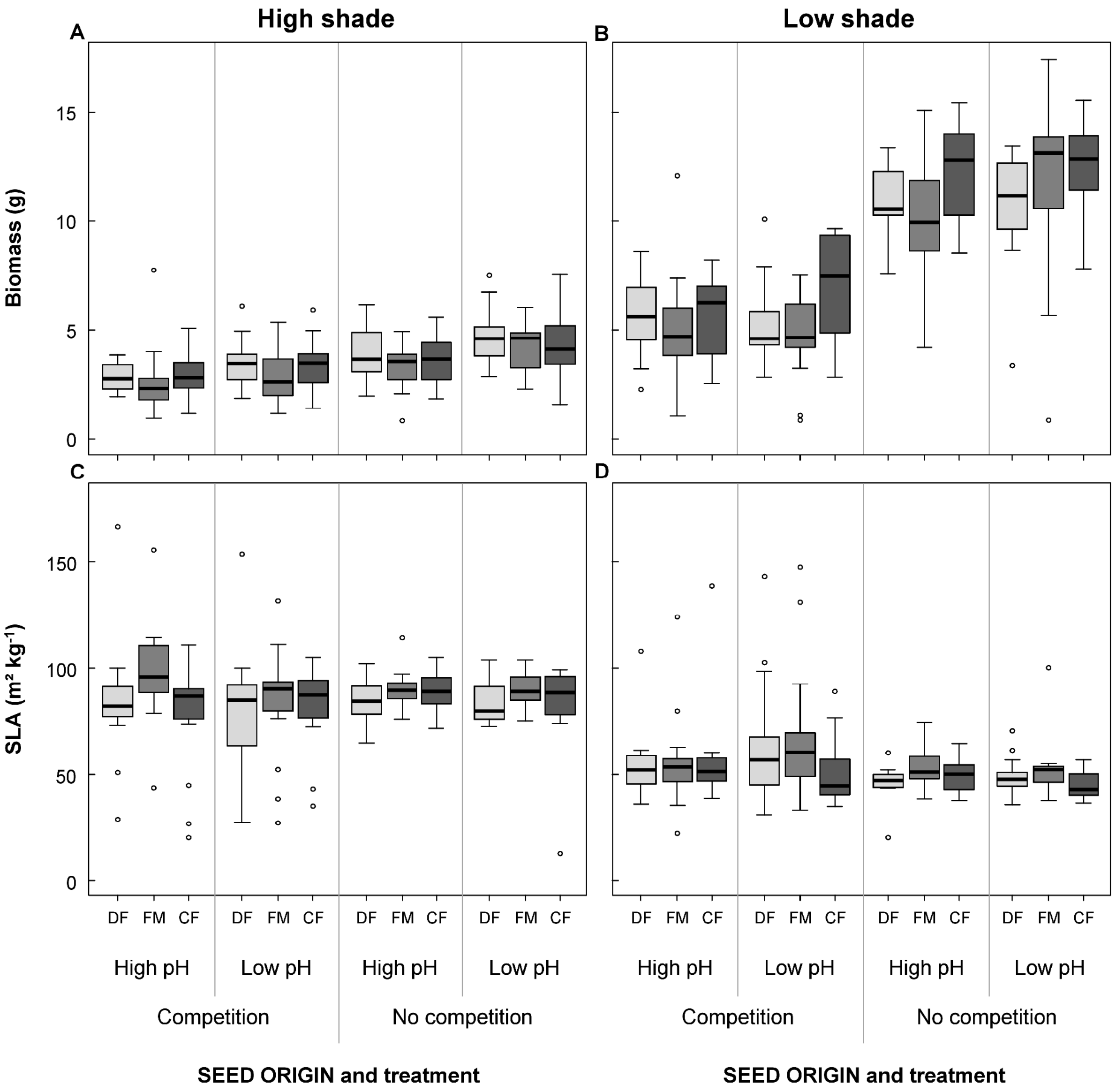

Fig. 13 Aboveground biomass (A, B) and specific leaf area (C, D) of invasive populations of *Impatiens glandulifera* in a greenhouse experiment. Plants were exposed to eight treatments in a full-factorial design, including high and low shade, competition by a common grass species (Arrhenatherum elatius) and no competition, as well as low and high soil acidity. Plant material originated from three habitat types, i.e., alluvial deciduous forests (DF), fallow meadows (FM) und coniferous forests (CF). Most groups represent 15 replicates, except five cases where only 14 replicates were available.[8]

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[8] Included here with kind permission from Oxford University Press (original copyright). Figure 2 in Pahl et al. (2013, *Annals of Botany* 112: 1921-1930; slightly modified).

Table 12 Effects of seed origin, shade, soil acidity, competition and their pairwise interactions on aboveground biomass, specific leaf area (SLA), plant height and relative growth rate (RGR) of the invasive *Impatiens glandulifera* in a greenhouse experiment.[9]

	Biomass		SLA		Height		RGR	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Origin	**6.74**	**0.034**	3.46	0.177	n.a.	n.a.	**7.84**	**0.020**
Shade	n.a.	n.a.	**14.11**	**<0.001**	n.a.	n.a.	**37.56**	**<0.001**
Soil acidity	**4.04**	**0.045**	1.24	0.265	n.a.	n.a.	**6.43**	**0.011**
Competition	n.a.	n.a.	0.30	0.585	**9.80**	**0.002**	1.03	0.310
Origin x shade	4.70	0.096	4.79	0.091	**6.03**	**0.049**	4.69	0.096
Origin x soil acidity	1.17	0.558	0.86	0.650	**8.42**	**0.015**	1.60	0.450
Origin x competition	2.19	0.335	1.15	0.562	0.38	0.829	0.58	0.750
Shade x soil acidity	3.07	0.080	0.07	0.796	1.30	0.255	0.17	0.300
Shade x competition	**5.73**	**0.017**	1.09	0.296	0.34	0.560	0.93	0.334
Soil acidity x competition	0.01	0.912	0.20	0.652	2.25	0.134	0.02	0.891

χ^2-square- and *P*-values are based on maximum likelihood ratio tests for linear mixed effects models. χ^2-square- and *P*-values of non-significant factors refer to the respective step of the model simplification procedure. Significant terms were tested against the minimum adequate model. See Methods section for information on model simplification, random factors and covariates. $N = 15$, except five cases where only 14 replicates were available. Main factors included in a significant interaction were not further explored (n.a. = not assessed). All three-way interactions were not significant (not shown). Significant values ($P < 0.05$) are printed in bold.

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[9] Included here with kind permission from Oxford University Press (original copyright). Table 2 in Pahl et al. (2013, *Annals of Botany* 112: 1921-1930).

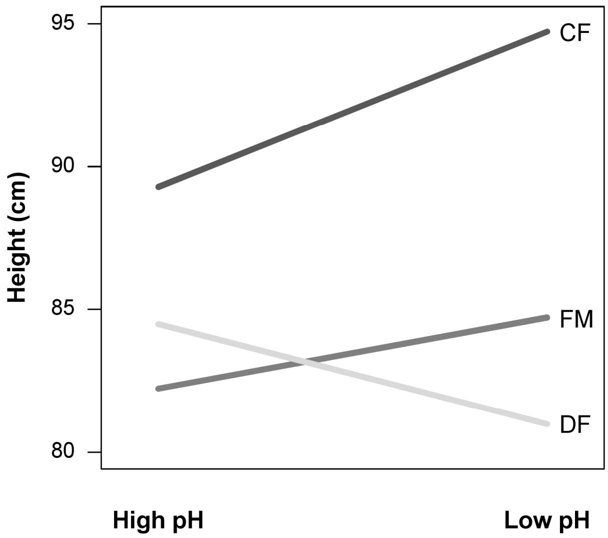

Fig. 14 Plant height of invasive populations of *Impatiens glandulifera* in a greenhouse experiment affected by a significant interaction ($\chi^2 = 8.42$, $P = 0.015$, for methods see text) between pH and seed origin, i.e., alluvial deciduous forests (DF), fallow meadows (FM) und coniferous forests (CF). Graphs were computed pooling all treatments.[10]

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[10] Included here with kind permission from Oxford University Press (original copyright). Figure 3 in Pahl et al. (2013, *Annals of Botany* 112: 1921-1930).

Discussion

Explaining the lack of local adaptation

We could not find any indication for local adaptation of the invasive alien *I. glandulifera* to three distinct habitats, i.e., alluvial deciduous forests, fallow meadows and coniferous forests. Neither an interaction between origin and habitat nor higher fitness of local origins emerged when reciprocally sown to the three habitats in the field (*Hypothesis 1*), nor did the experimental treatments reflecting the three habitat types in the greenhouse favor the respective provenances (*Hypotheses 2a-c*). Thus, we could not explain the proposed colonization sequence by different degrees of local adaptation (*Hypothesis 3*). The lack of local adaptation found in adult plants seems to be consistent for other phases of the study species' life cycle. Our results support the observations by Skálová *et al.* (2012) who found least local differentiation in seedling traits of *I. glandulifera* when compared to congeneric *I. parviflora, I. capensis* and *I. noli-tangere* under controlled climate chamber conditions.

Performance of *I. glandulifera* in the reciprocal field experiment was overall rather poor. Aboveground biomass in fallow meadow plots with disturbed soil treatment reached comparable values to a field study conducted in Czech Republic (Skálová & Pyšek, 2009), while most other values actually were lower. SLA was comparable to values observed in a field study in England (approx. 370–1000 $cm^2 g^{-1}$; Andrews *et al.*, 2009), slightly exceeding them in deciduous forests and slightly falling below them in fallow meadows. Plant height was at the lower margin of values reported from England (Andrews *et al.*, 2005). In the greenhouse experiment, values of biomass and plant height were smaller than in a previous common garden experiment (Kollmann & Bañuelos, 2004).

There are several reasons why an invasive alien species may lack local adaptation. Based on the results of our study, three lines of arguments seem to be relevant. First, residence time in the new range might have been too short (Ross *et al.*, 2009; Haider *et al.*, 2010; Ebeling *et al.*, 2011). *I. glandulifera* was introduced to England as early as 1839 (Beerling & Perrins, 1993), and the first herbarium specimen from a river approx. 85 km upstream from the study area dates back to the beginning of the 20th Century. Other studies, however, found adaptation in annual invasive species over comparable time scales, e.g., in *Eschscholzia californica* with a residence time in the invaded range of 110–150 years (Leger & Rice, 2007). Still, we cannot exclude that residence time may have been too short until now and local adaptation might evolve in future. Second, it is commonly assumed that high gene flow prevents the evolution of locally adapted genotypes (Haider *et al.*, 2011; Haider *et al.*, 2012). *I. glandulifera* is self-compatible, but protandrous and thus frequently cross-pollinated by several species of bumblebees, honeybees and wasps (Bartomeus *et al.*, 2010). Pollinators are capable of transferring pollen over several kilometers (Walker *et al.*, 2009), thus, enabling long-distance gene flow. Beside pollination, effective seed dispersal can increase gene flow. At the local scale seeds of *I. glandulifera* are dispersed up to 6 m by exploding fruits (Chapman & Gray, 2012), but long-distance dispersal via waterways (max. 20 km; Wadsworth *et al.*, 2000), vehicles and contaminated soil is also common (Hartmann *et al.*, 1995). Long distance pollen transfer and seed dispersal suggest effective gene flow in *I. glandulifera* which probably counteracts local adaptation. Third, strong spatial and temporal fluctuations in populations can act against local adaptation. Although we have no data on persistence of *I. glandulifera* populations in our study area, this idea is supported by molecular studies in northeast England that suggest frequent local extinction, re-colonization and repeated anthropogenic dispersal in populations of *I. glandulifera* (Walker *et al.*, 2009).

Reasons for the success of **I. glandulifera** *in distinct habitats*

Despite the observed lack of local adaptation*, I. glandulifera* was performing well in all studied habitats (see Appendix 5 for plant height in the source populations). The most likely reason why the species is able to cope with distinct habitats without showing local adaptation is high phenotypic plasticity (Pigliucci, 2001), which might enable the species to expand its ecological niche (Richards *et al.*, 2006). It has been shown recently that *I. glandulifera* exhibits higher plasticity in seedling biomass, height and root-shoot ratio than the less invasive congeners *I. parviflora* and *I. capensis* (Skálová *et al.*, 2012). We found plasticity in the morphological traits SLA and height which are particularly plastic (e.g., Flory *et al.*, 2011; Godoy *et al.*, 2011b). SLA was larger in shaded habitats (i.e., deciduous and coniferous forests) compared to fallow meadows. Similarly, SLA increased under high shade compared to low shade in the greenhouse. Higher SLA allows plant species to better capture light under shaded conditions and thereby increases fitness (Grotkopp & Rejmánek, 2007). Plant height was comparable in the deciduous forests and fallow meadows, but lower in coniferous forests in the undisturbed soil treatment in the field experiment. In the greenhouse experiment, plants were taller under low shade and in the absence of the competing grass. Plant height is known to be linked to competitive ability with larger species generally being able to suppress the growth of smaller species (Wang *et al.*, 2010) which in turn is a fitness advantage. As a result, plasticity in SLA and height can generally affect fitness.

From our study we have some indication for both the ‘Jack-of-all-trades’ and ‘master-of-some’ strategies (Richards *et al.*, 2006). On the one hand, there are no significant fitness differences (measured as biomass) of transplanted *I. glandulifera* in the undisturbed soil treatment between habitats suggesting a ‘Jack-of-all-trades’ strategy with high fitness in a set of distinct habitats. On the other hand, some of our results suggest a ‘master-of-some’ strategy with increased fitness under favorable conditions. In the disturbed soil treatment fitness was higher in fallow meadow habitats compared to both forest habitats. In the greenhouse low shade similarly led to increased biomass, particularly in absence of the competing grass. Thus, there are indications for both a good fitness in all considered habitats and an increased fitness under especially favorable conditions. This suggests that *I. glandulifera* may follow a ‘Jack-and-master’ strategy (Richards *et al.*, 2006).

Alternative factors determining the colonization sequence

As we could not detect local adaptation in *I. glandulifera,* this mechanism cannot explain the consecutive colonization of different habitats in the invaded range. Therefore, there must be other reasons explaining the colonization sequence. If *I. glandulifera* is capable of colonizing distinct habitats due to high phenotypic plasticity as suggested above, the species will be able to cope with a broad range of environmental conditions. Then, the colonization sequence must be related to landscape and land use characteristics that govern propagule pressure (e.g., Lockwood *et al.*, 2005; Colautti *et al.*, 2006). If propagule pressure instead of adaptation to environmental conditions is the main driver of the proposed colonization sequence, then *I. glandulifera* will colonize further habitats in the coming decades when propagule pressure continues to increase.

We conclude that invasive alien plants can become dominant in a set of distinct habitat types in the same region without local adaptation. These species may show high degrees of phenotypic plasticity following a ‘Jack-and-master’ strategy. Additionally, in these species the significance of propagule pressure and land use patterns will be high.

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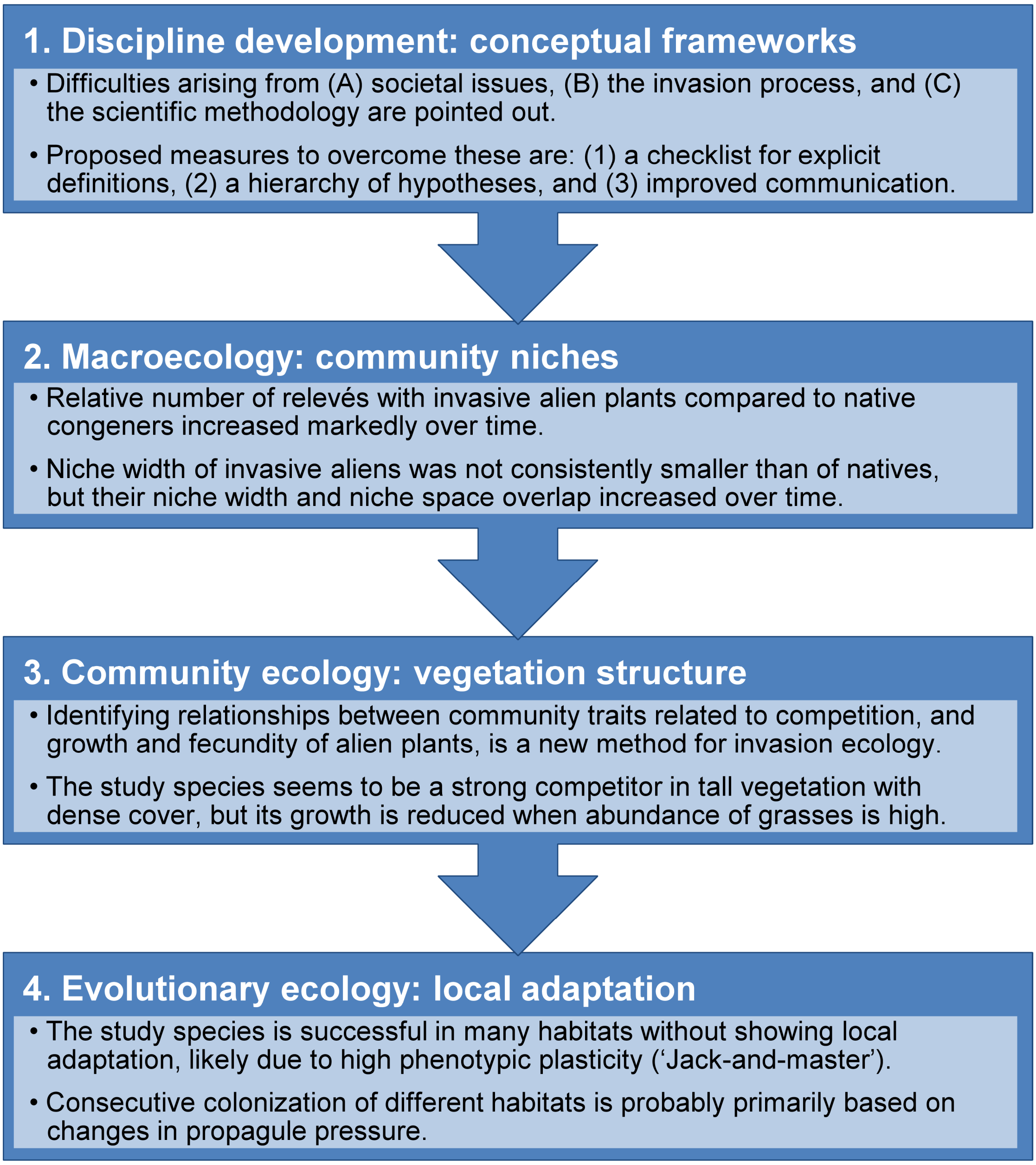
SYNOPSIS

The main aim of this dissertation was to contribute to four current research fields within invasion ecology. Theoretical invasion ecology, macroecology, community ecology, and evolutionary ecology were chosen as these disciplines are flourishing lately. Explanation and prediction of biological invasions is difficult, and additionally challenged by global change. Each discipline allows asking different questions on different scales. While it was intended to further develop the scientific field by pointing on current difficulties and presenting measures to overcome them the first chapter, a diverse array of methods was used to look at factors controlling plant invasions in three different research fields in the other three chapters. In the field of macroecology, related native and invasive species were studied in a single range on a national scale; questions in community ecology were addressed in native and introduced populations of a single species in four areas on an intercontinental scale; and in the field of evolutionary ecology populations of one invasive alien species in different habitats were studied on a local scale. Only taken together, the four current research fields enhance the overall understanding of factors that control plant invasions.

The main conclusions of each chapter are briefly summarized in Fig. 15. In the field of theoretical invasion ecology (Chapter 1) difficulties in invasion ecology arising from (A) societal issues, (B) the peculiarity of the invasion process, and (C) the scientific methodology used in invasion ecology were pointed out. Three key measures to overcome difficulties were presented, i.e., (1) a checklist for definitions that encourages explicit definition, (2) a hierarchy of hypotheses where general hypotheses branch into explicitly testable hypotheses, and (3) platforms for improved communication among scientists of different disciplines and with other societal groups. In the field of macroecology (Chapter 2) a consideration of community niches of invasive alien plants and native congeners, their width and changes over time was performed. It was shown that the relative number of relevés with invasive alien plants compared to natives as well as niche width of the invaders (β-diversity) increased markedly over time indicating increased abundance in invasive plants. The niche width of invasive alien plants was not consistently smaller than that of natives suggesting that niche width of invaders has reached a similar extend for the study species which started spreading ca. 70–130 years ago. One very interesting finding in the macroecological work was that niche overlap increased over time in all study species pairs. This might be attributed to biotic homogenization. In the realm of community ecology (Chapter 3) a study on correlations between vegetation structure, and growth and fecundity of a perennial plant in its native and invaded range was done. It was shown that mean community traits related to competition can well explain variation in growth and fecundity of the study species. The used approach may serve as a new option for future selection of plants in restoration of invaded communities. In the studied case, results indicate that the species may be a good competitor in tall vegetation with dense cover, but its growth and fecundity can be reduced if abundance of grasses and sedges is high. In the field of evolutionary ecology (Chapter 4), potential local adaptation of



1. Discipline development: conceptual frameworks

- Difficulties arising from (A) societal issues, (B) the invasion process, and (C) the scientific methodology are pointed out.
- Proposed measures to overcome these are: (1) a checklist for explicit definitions, (2) a hierarchy of hypotheses, and (3) improved communication.

2. Macroecology: community niches

- Relative number of relevés with invasive alien plants compared to native congeners increased markedly over time.
- Niche width of invasive aliens was not consistently smaller than of natives, but their niche width and niche space overlap increased over time.

3. Community ecology: vegetation structure

- Identifying relationships between community traits related to competition, and growth and fecundity of alien plants, is a new method for invasion ecology.
- The study species seems to be a strong competitor in tall vegetation with dense cover, but its growth is reduced when abundance of grasses is high.

4. Evolutionary ecology: local adaptation

- The study species is successful in many habitats without showing local adaptation, likely due to high phenotypic plasticity (‘Jack-and-master’).
- Consecutive colonization of different habitats is probably primarily based on changes in propagule pressure.

Fig. 15 Main conclusions from each of the four chapters.

an annual invasive alien plant to three different habitats along a colonization sequence was addressed. Although the habitats differed markedly with regard to shade, soil acidity, and competition, no evidence of local adaptation was found. This suggests that invasive aliens may be successful in many habitats without showing local adaptation, likely due to high phenotypic plasticity that allows them to keep fitness high in many habitats, and further increase it under especially favorable conditions. As local adaptation did not play a role, the consecutive colonization of different habitats was probably a consequence of changing patterns in propagule pressure.

As described above, the different fields within invasion ecology and the different objectives for each field required the use of a diverse set of methods. Each methodology had its strengths and weaknesses. Conceptual work (Chapter 1) is relatively free, and hard data play a minor role. Nevertheless, the conceptual work has to be supported by the research community. In the present case, this was achieved as the difficulties in invasion ecology and measures to overcome them were developed in group discussions during a workshop in which researchers from different nations took part and gave their opinions. Broad scale work in the field of macroecology (Chapter 2) can identify large patterns and helps to address overarching questions. However this approach has also its weaknesses as collecting comparable data on big scales is very difficult. Therefore, vegetation data from databases was used. As this data was not produced for the study question itself, special care had to be taken such as using a random subsample weighted by geography. Vegetation surveys on intercontinental scales (Chapter 3) require intense logistics and precise planning. Large scale field surveys enhance relevance of the results, but often do not allow mechanistic explanations. A mechanistic understanding in ecology can only be achieved by performing manipulative experiments. This approach was used in the field of evolutionary ecology (Chapter 4). Experiments in the field are more reliable as they mirror field conditions, but also bare a higher risk than more artificial settings in a greenhouse. Of course, experiments may fail and results may be trivial. The complementary use of these different methods allowed a relatively high scientific diversity within this dissertation. Additionally, it was attributed to the focus of four up-to-date research fields within invasion ecology. Focusing on current trends allows capturing recent developments and contributing to the overall field.

To conclude, invasion ecology has advanced considerably since its beginning, but there are still roads to travel. My results indicate that plant invasion success in the studied cases mainly depended on time since introduction (Chapter 2), vegetation structure and competition in plant communities (Chapter 3), phenotypic plasticity, and propagule pressure (Chapter 4). This further strengthens the idea that the interplay of invasiveness and invasibility has to be addressed as a whole.

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Fig. 16 Some of the people who contributed and helped me to complete this dissertation.

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APPENDIX

Chapter 2
Changes in the community context of native and invasive non-native plant species in Germany

Chapter 3
Plant community traits as correlates of plant growth and fecundity: the case of *Lythrum salicaria* (Lythraceae) in its native and invaded ranges

Chapter 4
No evidence for local adaptation in an invasive alien plant: Field and greenhouse experiments tracing a colonization sequence

Appendix 1 Vascular plant species with especially high and low scores on DCA axis 1 and 2 for *Impatiens*, *Solidago* and *Prunus*. Species in between are left out (…). Nomenclature follows GermanSL Version 1.1 (Jansen & Dengler 2008, *Tuexenia* **28**: 239-253).

	Axis 1		**Axis 2**	
Impatiens	**Score**	**Species**	**Score**	**Species**
	4.30	*Euphorbia exigua*	5.21	*Senecio sylvaticus*
	4.24	*Euphorbia helioscopia*	5.21	*Sedum telephium* agg.
	4.24	*Erechtites hieraciifolius*	5.02	*Anthericum liliago*
	4.22	*Silene noctiflora*	4.68	*Orthilia secunda*
	4.22	*Chaenorhinum minus*	4.68	*Amelanchier spicata*
	…	…	…	…
	-3.70	*Galium saxatile*	-3.48	*Sisymbrium officinale*
	-3.70	*Luzula sylvatica*	-3.55	*Stellaria alsine*
	-4.27	*Luzula luzulina*	-4.07	*Rumex hydrolapathum*
	-4.47	*Festuca altissima*	-4.54	*Berula erecta*
	-4.72	*Larix decidua*	-7.65	*Poa chaixii*
Solidago	**Score**	**Species**	**Score**	**Species**
	4.74	*Veronica urticifolia*	3.75	*Persicaria amphibia*
	4.74	*Veratrum album*	3.72	*Viola palustris*
	4.74	*Valeriana montana*	3.72	*Stellaria palustris*
	4.74	*Tofieldia calyculata*	3.72	*Scutellaria galericulata*
	4.74	*Primula auricula*	3.72	*Potentilla palustris*
	…	…	…	…
	-3.21	*Persicaria lapathifolia*	-4.62	*Lathyrus niger*
	-3.22	*Erechtites hieraciifolius*	-4.62	*Taxus baccata*
	-3.25	*Persicaria minor*	-4.71	*Actaea spicata*
	-3.30	*Solanum nigrum*	-4.71	*Vicia sepium*
	-3.31	*Lamium maculatum*	-4.72	*Festuca heterophylla*
Prunus	**Score**	**Species**	**Score**	**Species**
	3.90	*Linaria vulgaris* agg.	3.73	*Origanum vulgare* agg.
	3.87	*Salix repens* agg.	3.73	*Leymus arenarius*
	3.58	*Anthericum ramosum*	3.73	*Elymus farctus*
	3.55	*Polygonatum odoratum*	3.44	*Vicia sativa* agg.
	3.55	*Viscum album*	3.44	*Trifolium arvense*
	…	…	…	…
	-4.40	*Allium scorodoprasum* agg.	-3.96	*Rubus plicatus*
	-4.48	*Platanthera bifolia*	-3.96	*Rubus pyramidalis*
	-4.60	*Alisma plantago-aquatica* agg.	-3.96	*Teucrium scorodonia*
	-4.68	*Carex strigosa*	-4.46	*Ceratocapnos claviculata*
	-4.79	*Lamium maculatum*	-4.70	*Ilex aquifolium*

Appendix 2 Five of the most frequent species in relevés with selected native, invasive or both species of the genera *Impatiens*, *Solidago* and *Prunus* from three time periods. Nomenclature follows GermanSL Version 1.1 (Jansen & Dengler 2008, *Tuexenia* **28**: 239-253).

	1950–1969		**1970–1989**	
	Species	**%**	**Species**	**%**
Impatiens				
native	*Urtica dioica*	73	*Fagus sylvatica*	55
	Fraxinus excelsior	64	*Fraxinus excelsior*	53
	Deschampsia cespitosa	58	*Urtica dioica*	53
	Alnus glutinosa	55	*Circaea lutetiana*	49
	Circaea lutetiana	53	*Deschampsia cespitosa*	49
invasive	*Fagus sylvatica*	62	*Quercus robur*	66
	Milium effusum	56	*Urtica dioica*	47
	Oxalis acetosella	52	*Brachypodium sylvaticum*	43
	Galium odoratum	48	*Fraxinus excelsior*	43
	Urtica dioica	43	*Fagus sylvatica*	41
both	*Fraxinus excelsior*	83	*Fraxinus excelsior*	64
	Galium odoratum	83	*Urtica dioica*	64
	Milium effusum	83	*Deschampsia cespitosa*	57
	Fagus sylvatica	67	*Circaea lutetiana*	54
	Urtica dioica	67	*Alnus glutinosa*	50
Solidago				
native	*Fagus sylvatica*	54	*Festuca ovina* agg.	65
	Carex digitata	40	*Thymus pulegioides* agg.	52
	Sorbus aucuparia	39	*Pinus sylvestris*	44
	Deschampsia flexuosa	38	*Quercus robur*	40
	Hieracium murorum	37	*Achillea millefolium* agg.	39
invasive	*Plantago major*	100	*Poa trivialis*	99
	Poa annua agg.	100	*Taraxacum* sect. A., H. et R.	99
	Sonchus oleraceus	100	*Cirsium arvense*	97
	Stellaria media agg.	100	*Picris hieracioides*	95
	Taraxacum sect. A., H. et R.	100	*Equisetum arvense*	94
both	(no relevés)		*Dactylis glomerata* agg.	100
			Equisetum arvense	100
			Fraxinus excelsior	100
			Poa trivialis	100
			Taraxacum sect. A., H. et R.	100

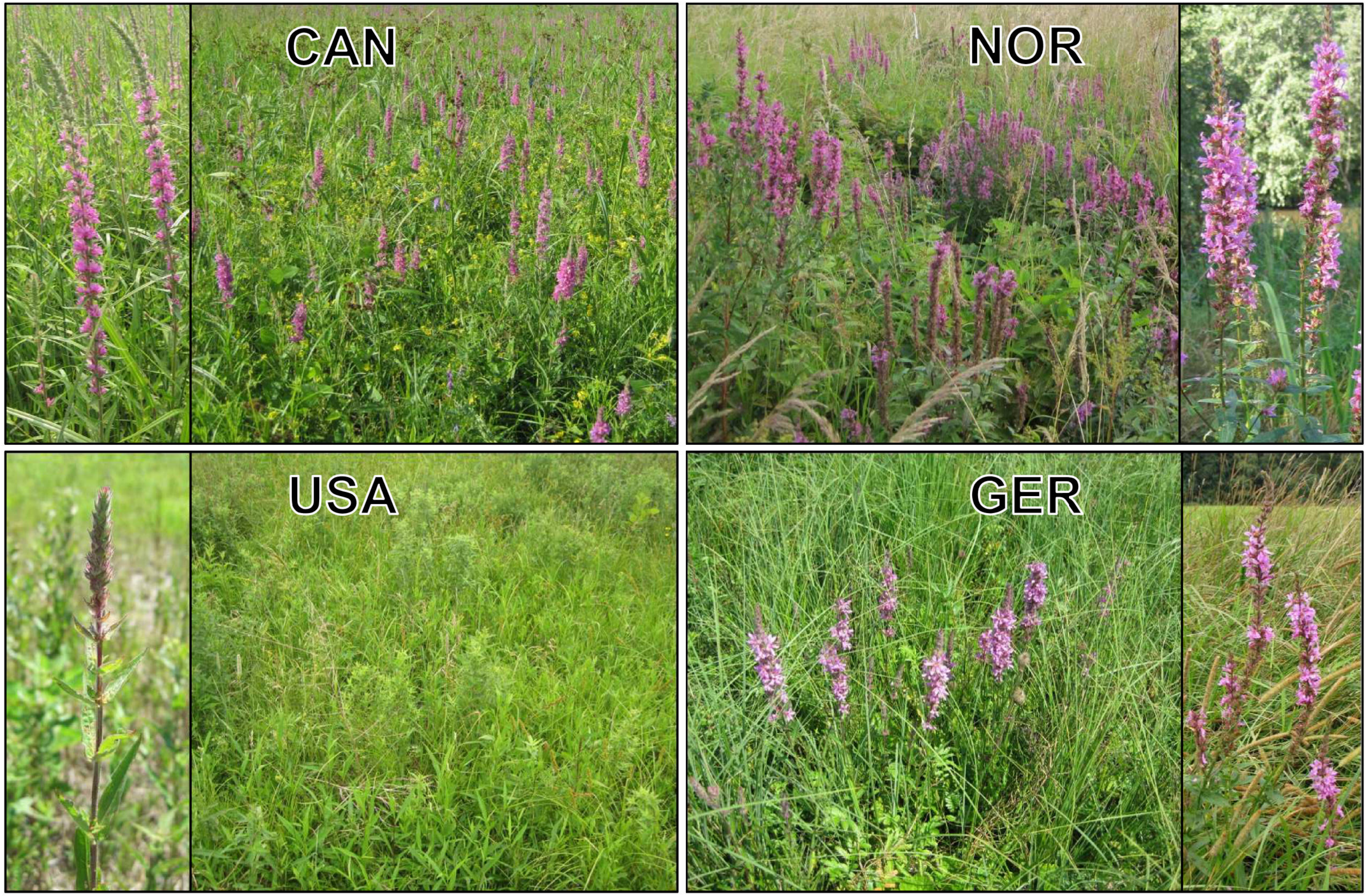
	1990–2009	
	Species	**%**
Impatiens		
native	*Urtica dioica*	52
	Fraxinus excelsior	49
	Fagus sylvatica	47
	Oxalis acetosella	42
	Deschampsia cespitosa	41
invasive	*Fagus sylvatia*	70
	Oxalis acetosella	59
	Rubus idaeus	36
	Quercus robur	32
	Urtica dioica	30
both	*Cicaea lutetiana*	73
	Urtica dioica	73
	Fraxinus excelsior	66
	Alnus glutinosa	65
	Poa trivialis	63
Solidago		
native	*Dactylis glomerata* agg.	61
	Achillea millefolium agg.	48
	Hyperiucum perforatum	44
	Plantago lanceolata	40
	Galium mollugo agg.	39
invasive	*Calamagrostis epigejos*	88
	Achillea millefolium agg.	75
	Picris hieracioides	72
	Taraxacum sect. A., H. et R.	69
	Cirsium arvense	60
both	*Arrhenatherum elatius*	77
	Taraxacum sect. A., H. et R.	77
	Achillea millefolium agg.	62
	Calamagrostis epigejos	62
	Populus tremula	54

Taraxacum sect. A., H. et R. = *Taraxacum* sect. Alpina, Hamata et Ruderalia.

Appendix 2 (continued).

	1950–1969		1970–1989	
	Species	**%**	**Species**	**%**
Prunus				
native	*Deschampsia cespitosa*	82	*Fraxinus excelsior*	78
	Urtica dioica	74	*Deschampsia cespitosa*	75
	Fraxinus excelsior	73	*Fagus sylvatica*	51
	Rubus idaeus	70	*Galium aparine*	45
	Alnus glutinosa	67	*Milium effusum*	45
invasive	*Deschampsia flexuosa*	96	*Quercus robur*	83
	Sorbus aucuparia	93	*Sorbus aucuparia*	67
	Pinus sylvestris	81	*Pinus sylvestris*	67
	Quercus petrae agg.	81	*Deschampsia flexuosa*	60
	Hieracium lachenalii	70	*Fagus sylvatica*	59
both	(no relevés)		*Deschampsia cespitosa*	100
			Acer pseudoplatanus	86
			Euonymus europaea	86
			Fraxinus excelsior	86
			Sambucus nigra	86

	1990–2009	
	Species	**%**
Prunus		
native	*Deschampsia cespitosa*	64
	Fraxinus excelsior	63
	Alnus glutinosa	58
	Quercus robur	52
	Urtica dioica	50
invasive	*Sorbus aucuparia*	59
	Pinus sylvestris	56
	Deschampsia flexuosa	55
	Quercus robur	49
	Betula pendula	44
both	*Quercus robur*	93
	Betula pendula	79
	Sorbus aucuparia	79
	Calamagrostis epigejos	71
	Pinus sylvestris	57



Appendix 3 Typical aspects of the *Lythrum salicaria* populations sampled in two areas that have been invaded for a relatively long time, i.e., St. Lawrence region, southeastern Canada (CAN); and Upper New York State, northeastern USA (USA), and two within the native range, i.e., Greater Oslo area, southern Norway (NOR); and Bavaria, southern Germany (GER) in June–August 2010/2011 during the early to peak flowering season.

Appendix 4 The ten most frequent species from 25 relevés (0.5 x 0.5 m²) with *Lythrum salicaria* for each of the four study areas ordered by frequency (see main text for area abbreviations). Species names follow The Plant List (2010; *Version 1. Published on the Internet*; http://www.theplantlist.org/; accessed 29 October 2013).

SE Canada	**S Norway**
Vicia cracca L.	*Filipendula ulmaria* (L.) Maxim.
Poa pratensis L.	*Lysimachia vulgaris* L.
Equisetum arvense L.	*Agrostis stolonifera* L.
Phalaris arundinacea L.	*Cirsium arvense* (L.) Scop.
Galium palustre L.	*Poa pratensis* L.
Carex vulpinoidea Michx.	*Urtica dioica* L.
Agrostis gigantea Roth	*Potentilla anserina* L.
Solidago gigantea Aiton	*Vicia cracca* L.
Taraxacum officinale Webb	*Festuca arundinacea* Schreb.
Stellaria graminea L.	*Phragmites australis* (Cav.) Trin. ex Steud.
NE USA	**S Germany**
Poa pratensis L.	*Filipendula ulmaria* (L.) Maxim.
Asteraceae	*Lysimachia vulgaris* L.
Festuca arundinacea Schreb.	*Molinia caerulea* (L.) Moench
Juncus tenuis Willd.	*Mentha aquatica* L.
Ranunculus acris L.	*Sanguisorba officinalis* L.
Galium palustre L.	*Phragmites australis* (Cav.) Trin. ex Steud.
Taraxacum officinale Webb	*Galium mollugo* L.
Equisetum arvense L.	*Equisetum palustre* L.
Carex tribuloides Wahlenb.	*Deschampsia cespitosa* (L.) P. Beauv.
Symphyotrichum puniceum (L.) Á.Löve & D.Löve	*Agrostis stolonifera* L.

Appendix 5 Main characteristics of the source populations and their sites, especially soil conditions.

		Site		**Distance to closest population**	
		Latitude/ Longitude	**Altitude** (m)	**Overall** (km)	**Within habitat** (km)
Deciduous forest	1	48.423/11.878	425	2.3	2.5
	2	48.402/11.760	493	2.1	2.2
	3	48.403/11.791	493	2.3	2.3
	4	48.385/11.744	493	2.2	2.2
	5[6]	48.413/11.848	426	0.9	2.5
Mean ± s.d.			*466 ± 33*	*1.9 ± 0.5*	*2.3 ± 0.2*
Fallow meadow	1	48.440/11.625	366	2.6	2.6
	2	48.443/11.660	438	2.6	2.6
	3	48.451/11.706	429	2.5	3.5
	4	48.403/11.711	452	0.9	0.9[7]
	5	48.395/11.713	461	0.9	0.9[7]
Mean ± s.d.			*429 ± 33*	*1.9 ± 0.8*	*2.1 ± 1.1*
Coniferous forest	1	48.429/11.700	477	2.5	2.5
	2	48.411/11.679	469	2.5	2.5
	3	48.414/11.640	504	2.9	2.9
	4	48.421/11.847	479	0.9	6.6
	5	48.420/11.758	489	2.1	4.4
Mean ± s.d.			*484 ± 12*	*2.2 ± 0.7*	*3.8 ± 1.6*

		Soil conditions[4]				
		pH_{H_2O}	**Moisture**[5]	**N** (%)	**C** (%)	**C/N**
Deciduous forest	1	7.5	15.7	0.4	7.7	28
	2	7.5	12.6	0.3	7.3	38
	3	6.5	12.6	0.2	4.1	32
	4	7.6	10.6	0.2	6.9	72
	5[6]	n.a.	n.a.	n.a.	n.a.	n.a.
Mean ± s.d.		*7.3 ± 0.4*	*12.9 ± 1.8*	*0.2 ± 0.1*	*6.5 ± 1.4*	*42 ± 18*
Fallow meadow	1	6.8	11.3	0.6	6.3	14
	2	7.3	19.7	0.3	2.8	12
	3	6.4	30.2	0.3	3.7	17
	4	7.2	18.5	0.2	2.1	12
	5	6.7	25.4	0.4	3.7	10
Mean ± s.d.		*6.9 ± 0.3*	*21.0 ± 6.4*	*0.4 ± 0.1*	*3.7 ± 1.5*	*13 ± 2*
Coniferous forest	1	6.9	10.2	0.5	7.6	22
	2	4.2	32.2	0.3	5.6	17
	3	4.1	4.5	0.8	13.8	20
	4	4.7	6.2	0.5	6.4	16
	5	5.7	14.8	0.3	4.9	18
Mean ± s.d.		*5.1 ± 1.1*	*13.6 ± 10.0*	*0.5 ± 0.2*	*7.7 ± 3.2*	*19 ± 2*

		Population		
		Plant height[1] (cm)	**Seed mass**[2] (mg)	**Germination**[3] (%)
Deciduous forest	1	185	13	72
	2	125	14	72
	3	148	14	92
	4	96	13	57
	5[6]	n.a.	15	73
Mean ± s.d.		*138 ± 32*	*14 ± 1*	*73 ± 11*
Fallow meadow	1	n.a.	14	94
	2	193	13	86
	3	146	13	97
	4	180	11	96
	5	128	13	93
Mean ± s.d.		*162 ± 26*	*13 ± 1*	*93 ± 4*
Coniferous forest	1	156	11	84
	2	155	12	83
	3	91	11	77
	4	149	14	93
	5	139	11	58
Mean ± s.d.		*138 ± 24*	*12 ± 1*	*79 ± 12*

n.a. = not available

[1] *Impatiens glandulifera*, mean plant height of four measurements per population at full development (August 2012)

[2] Weighted as $n = 5 \times 500$ seeds per population

[3] $N = 5 \times 50$ stratified seeds germinated on wet filter paper in Petri dishes at 5/15 °C, 12:12 h, without light, for 3 weeks

[4] Mixed soil sample from five cores, diameter 1.5 cm, 0–14 cm depth (for all soil characteristics but moisture)

[5] Mean of five measurements per population in August 2012

[6] Site became disturbed after seed collection in autumn 2011

[7] Distance between fallow meadows 4 and 5 below 2 km was considered not to cause problems because sites are separated by a ridge and belong to different watersheds.

*Below detection limit

		Soil conditions[4] (continued)					
		Ammonium (mg/kg)	**Nitrate** (mg/kg)	**Phosphate** (mg/kg)	**Potassium** (mg/kg)	**Magnesium** (mg/kg)	**Calcium** (mg/kg)
Deciduous forest	1	38.8	366	20	59.7	47.1	888
	2	23.6	112	29	63.4	38.9	722
	3	*	129	19	37.8	24.4	137
	4	29.9	84	19	62.0	25.0	616
	5[6]	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Mean ± s.d.		*30.8 ± 6.2*	*172 ± 133*	*22 ± 4*	*55.7 ± 10.5*	*33.8 ± 9.6*	*591 ± 280*
Fallow meadow	1	48.9	558	148	549.0	67.2	693
	2	0.0	134	14	7.1	31.9	77
	3	28.5	288	23	102.0	39.6	576
	4	10.2	241	76	131.9	27.7	256
	5	7.6	301	22	21.2	44.3	376
Mean ± s.d.		*19.0 ± 17.6*	*305 ± 140*	*57 ± 51*	*162.2 ± 199.0*	*42.1 ± 13.8*	*396 ± 220*
Coniferous forest	1	38.8	391	27	57.7	70.9	1127
	2	32.1	n.a.	n.a.	63.9	37.1	79
	3	65.4	200	93	128.7	26.0	243
	4	35.0	83	21	105.1	22.6	176
	5	20.1	85	*	35.1	32.6	254
Mean ± s.d.		*38.3 ± 14.9*	*190 ± 125*	*47 ± 32*	*78.1 ± 33.9*	*37.8 ± 17.3*	*376 ± 381*

Appendix 6 Main characteristics of the plot sites in the reciprocal transplant experiment and their soil conditions.

		Site			
		Latitude/ Longitude	**Distance to source pop.** (m)	**Altitude** (m)	**PAR**[1] (%)
Deciduous forest	1	48.423/11.878	48	432	0.8
	2	48.404/11.762	314	448	2.7
	3	48.403/11.791	35	445	5.9
	4	48.385/11.744	36	460	2.2
	5[6]	48.410/11.836	962	437	0.9
Mean ± s.d.			*279 ± 358*	*444 ± 10*	*2.5 ± 1.9*
Fallow meadow	1	48.441/11.626	118	438	88.0
	2	48.443/11.660	37	450	3.2
	3	48.451/11.706	42	439	42.5
	4	48.403/11.709	116	465	47.1
	5	48.395/11.713	34	450	85.5
Mean ± s.d.			*69 ± 39*	*448 ± 10*	*53.2 ± 31.3*
Coniferous forest	1	48.431/11.689	792	487	6.7
	2	48.408/11.679	407	481	16.8
	3	48.414/11.641	119	506	3.4
	4	48.420/11.844	310	492	11.5
	5	48.418/11.760	269	493	5.0
Mean ± s.d.			*379 ± 226*	*492 ± 8*	*8.7 ± 4.9*

		Soil conditions[4]				
		pH$_{H_2O}$	**Moisture**[5]	**N** (%)	**C** (%)	**C/N**
Deciduous forest	1	7.5	22.6	0.4	8.4	31
	2	7.5	11.7	0.3	7.9	41
	3	7.5	20.0	0.3	8.5	36
	4	7.6	9.3	0.1	6.8	142
	5[6]	7.6	16.2	0.3	8.3	36
Mean ± s.d.		*7.5 ± 0.0*	*16 ± 4.9*	*0.3 ± 0.1*	*8.0 ± 0.6*	*57 ± 43*
Fallow meadow	1	6.6	12.4	0.2	3.0	18
	2	6.0	10.7	0.3	3.2	12
	3	6.0	17.4	0.3	3.4	18
	4	5.8	24.2	0.3	2.6	10
	5	6.3	37.9	0.3	2.8	10
Mean ± s.d.		*6.1 ± 0.3*	*20.5 ± 9.9*	*0.3 ± 0.0*	*3.0 ± 0.3*	*14 ± 4*
Coniferous forest	1	4.0	10.6	0.4	7.1	20
	2	4.1	18.4	0.4	7.5	19
	3	4.0	11.0	0.3	7.1	24
	4	3.9	6.9	0.3	5.1	18
	5	3.8	18.4	0.2	4.0	18
Mean ± s.d.		*4.0 ± 0.1*	*13.1 ± 4.6*	*0.3 ± 0.1*	*6.2 ± 1.4*	*20 ± 2*

n.a. = not available

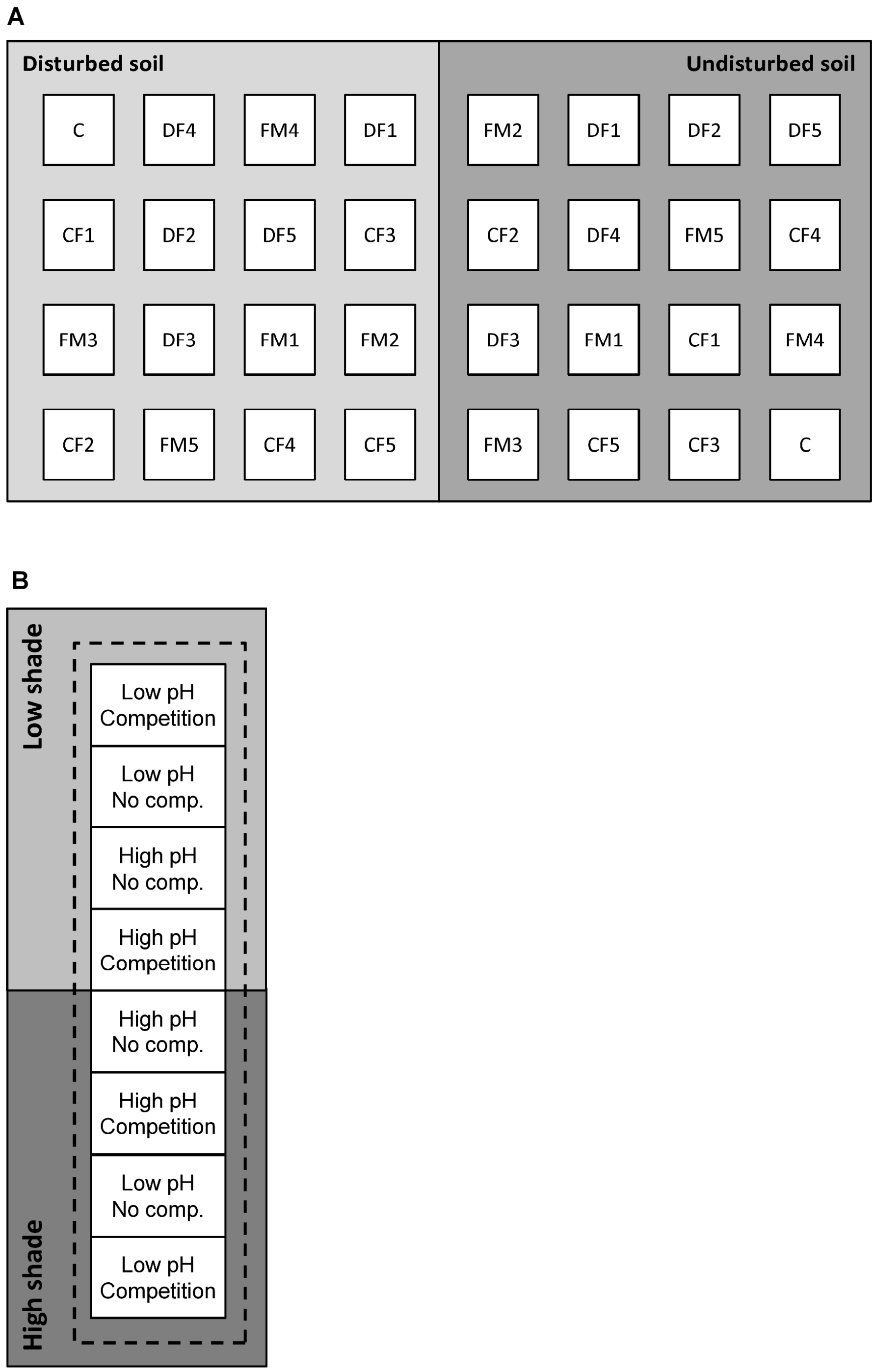
[1] Photosynthetically active radiation above *Impatiens glandulifera* canopy in the control treatment, n = four measurements per plot (August 2012)

[2] Mixed soil sample from five cores, diameter 1.5 cm, 0–14 cm depth (for all soil characteristics but moisture)

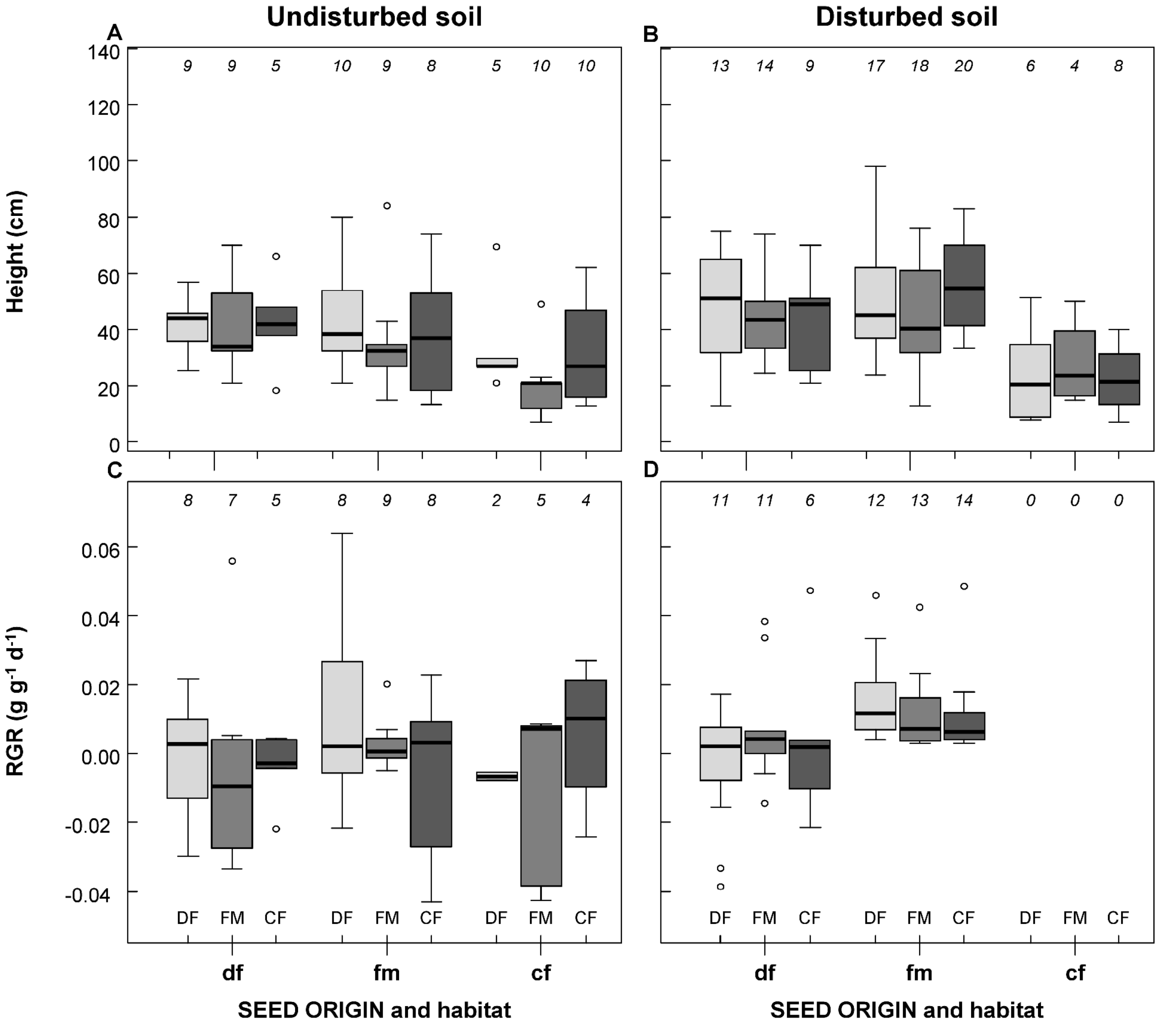
[3] Mean of five measurements per population in August 2012

*Below detection limit

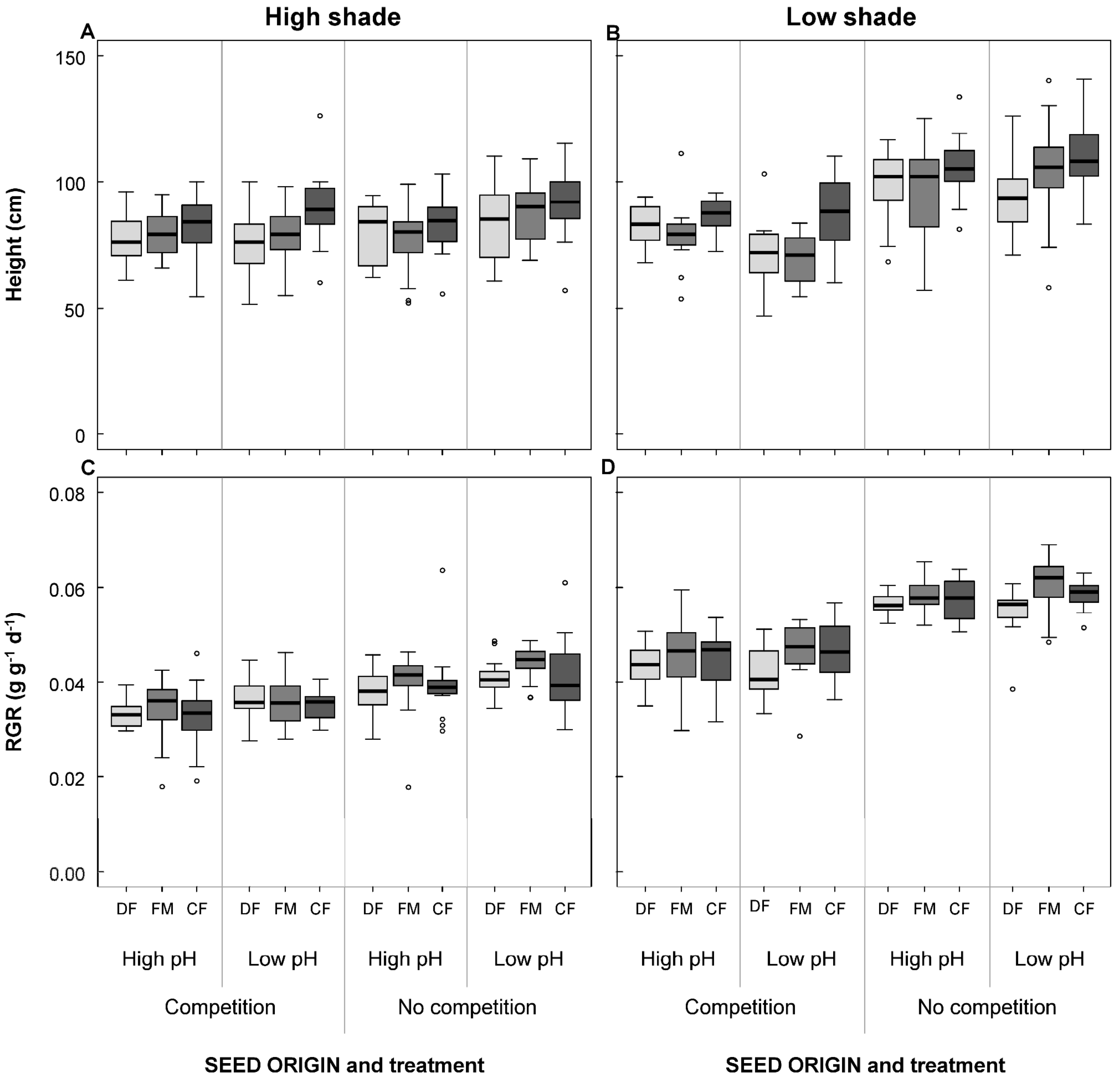
		Soil conditions[4] (continued)					
		Ammonium (mg/kg)	**Nitrate** (mg/kg)	**Phosphate** (mg/kg)	**Potassium** (mg/kg)	**Magnesium** (mg/kg)	**Calcium** (mg/kg)
Deciduous forest	1	32.3	407	*	76.3	50.3	915
	2	27.9	161	15	88.3	42.4	784
	3	2.3	194	27	42.1	15.5	128
	4	20.1	50	*	53.6	24.1	621
	5[6]	32.5	406	19	87.9	53.8	834
Mean ± s.d.		*23.0 ± 11.3*	*244 ± 141*	*20 ± 5*	*69.6 ± 18.7*	*37.2 ± 15.0*	*656 ± 281*
Fallow meadow	1	11.7	156	11	20.5	27.7	616
	2	15.2	33	16	26.0	18.1	37
	3	34.4	136	42	65,6	31.0	789
	4	10.3	232	33	28.4	21.6	235
	5	13.8	360	17	23.3	31.9	293
Mean ± s.d.		*17.1 ± 8.8*	*183 ± 107*	*24 ± 12*	*32,8 ± 16.6*	*26.1 ± 5.4*	*394 ± 271*
Coniferous forest	1	44.1	55	25	65.3	15.6	86
	2	15.0	53	59	24.9	8.6	20
	3	42.9	76	*	48.2	13.5	84
	4	36.9	16	*	61.4	7.9	54
	5	30.9	69	*	37.0	14.5	74
Mean ± s.d.		*33.9 ± 10.6*	*54 ± 21*	*n.a.*	*47.4 ± 15.0*	*12.0 ± 3.2*	*64 ± 25*



Appendix 7 Experimental design. The transplant experiment (A) included 15 plots (one is shown), five in each of three habitat types. In one half of each plot (0.8 m x 0.8 m) the soil remained untreated ('undisturbed soil'); in the other half all aboveground litter and vegetation were removed and the soil was disturbed with a rake ('disturbed soil'). Each half of the plot contained 16 subplots (0.2 m x 0.2 m). One remained as a control (C) and seeds of each source populations were sown into the other subplots (DF = deciduous alluvial forest; FM = fallow meadow; CF = coniferous upland forest). The greenhouse experiment (B) included five replicated rows of eight blocks (one row is shown). Half of each row was exposed to high shade (5% PAR), the other half to low shade (10% PAR). Each block contained one plant from each for the source populations, leading to 15 pots per block.



Appendix 8 Plant height (A, B) and relative growth rate (C, D) of the invasive alien *Impatiens glandulifera* when reciprocally transplanted between deciduous forests (df/DF), fallow meadows (fm/FM) und coniferous upland forest (cf/CF) in the invaded range. Seed origins are indicated with capital letters, plot habitats with small letters. Soil remained either undisturbed (A, C) or was experimentally disturbed before planting (B, D). The number of plant individuals in each group is given in small italic numbers above the boxplots.



Appendix 9 Plant height (A, B) and relative growth rate (C, D) of invasive populations of *Impatiens glandulifera* in a greenhouse experiment. Plants were exposed to eight treatments in a full-factorial design, including high and low shade, competition by a common grass species (*Arrhenatherum elatius*) and no competition, as well as low and high soil acidity. Plant material originated from three habitat types, i.e., alluvial deciduous forests (DF), fallow meadows (FM) und coniferous upland forests (CF). Most groups represent 15 replicates, except five cases where only 14 replicates were available.

AUFLISTUNG DER VORVERÖFFENTLICHUNGEN

Veröffentlichungen in Zeitschriften mit Peer-Review-Verfahren

(1) Heger, T., **Pahl, A.T.**, Botta-Dukát, Z., Gherardi, F., Hoppe, C., Hoste, I., Jax, K., Lindström, L., Boets, P., Haider, S., Kollmann, J., Wittmann, M.J. & Jeschke, J.M. (2013): Conceptual frameworks and methods for advancing invasion ecology. *Ambio* **42**: 527–540. DOI 10.1007/s13280-012-0379-x.

(2) **Pahl, A.T.**, Kollmann, J., Mayer, A. & Haider, S. (2013): No evidence for local adaptation in an invasive alien plant: field and greenhouse experiments tracing a colonization sequence. *Annals of Botany* **112**: 1921-1930. DOI 10.1093/aob/mct246.

Einreichungen bei Zeitschriften mit Peer-Review-Verfahren

(1) **Pahl, A.T.**, Heger, T., Lavoie, C., Kattge, J. & Kollmann, J.: Plant community traits as correlates of plant growth and fecundity: the case of *Lythrum salicaria* (Lythraceae) in its native and invaded ranges. *American Journal of Botany.*

(2) **Pahl, A.T.**, & Kollmann, J.: Changes in the community context of native and invasive non-native plant species in Germany. *Preslia.*

Andere Veröffentlichungen

(1) **Pahl, A.T.** (2013): Invasive Pflanzen erobern neue Standorte: Lokale Anpassung des Drüsigen Springkrauts? *Nodium. Die Zeitschrift des Alumni-Clubs Landschaft, Absolventenvereinigung der Studienfakultät Landschaftsarchitektur und Landschaftsplanung an der TU München* **5**.

Vorträge auf internationalen Konferenzen

(1) **Pahl, A.T.**, Kollmann, J., Mayer, A. & Haider, S. (2013): Limited evidence for local adaptation in an invasive alien plant: field and greenhouse experiments tracing a colonization sequence. *Plant Population Biology Conference 2013*, Tartu, Estonia, 9.-11.05.2013.

Poster-Präsentationen

(1) **Liebaug, A.T.**, Haider, S. & Kollmann, J. (2012): Local adaptation of invasive alien *Impatiens glandulifera* to contrasting habitats?
European Conference on Biological Invasions NEOBIOTA 2012, Pontevedra, Spain, 12.-14.09.2012.

(2) **Liebaug, A.T.**, Lavoie, C., Heger, T. & Kollmann, J. (2012): Variation in vegetation structure and biodiversity in sites with native or invasive *Lythrum salicaria* populations.
Plant Population Biology Conference 2012, Zürich, Switzerland, 17.-19.05.2012.

(3) **Liebaug, A.T.**, Heger, T. & Kollmann, J. (2011): Community context of native and invasive alien species – large scale vegetation analysis using databases.
Workshop of the Working Group on Vegetation Databases „Vegetation databases and spatial analysis“, Freising, Germany, 19.-21.09.2011.