The role of evolutionary processes in plant invasions

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Gutachter /in

1. Prof. Dr. Helge Bruelheide, Halle
2. Prof. Dr. Mark van Kleunen, Konstanz
3. Prof. Dr. Petr Pyšek, Průhonice

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By

Alexandra Erfmeier

Institute of Botany – Geobotany and Botanical Garden

Martin Luther University Halle-Wittenberg

Germany

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Preamble

The present thesis is based on a series of published articles and manuscripts currently undergoing peer review and represents the essence of research projects in plant invasion biology conducted, coordinated and supervised by the author since 2005. Results reported here go back to ideas and study designs conceived by the author as an integral part of this habilitation thesis. The results were either achieved in the context of participating in an international research platform, being related to PhD projects supervised by the author or based on data of student qualification theses.

The thesis is organized in two main parts. Part A represents the main corpus: it provides an introduction to the topic of plant invasion ecology and briefly incorporates the outcome of own studies and their contribution to current knowledge. This part will focus on four issues: 1) emphasizing the importance of multi-species approaches, 2) highlighting the role of genetic diversity, 3) introducing the importance of field studies for comparing native and invasive populations and 4) exposing knowledge on experimental evidence of evolutionary shifts in invasions. In addition, it develops a theoretical frame for assessing the evolutionary context in plant invasions that might help with understanding the complex mechanisms involved. This frame summarizes the author's conclusions based on the results gained during her research, highlights gaps of knowledge and suggests further avenues for future research. In particular, this first part introduces the state of knowledge in a review-like summary, identifies inconsistencies and gaps, and arranges the body of knowledge and currently existing hypotheses in a new framework that will be introduced. The implementation of this framework will result in the development of new hypotheses. I will discuss the most promising lines for future research, thus, giving an outline of a research plan that goes beyond the scope of a summarizing habilitation thesis. Studies conducted and/or supervised by the author have contributed to the state of knowledge outlined as well as to the gap identifying process. Their particular importance for developing this framework will be mentioned and references to those studies are earmarked by numbers in squared brackets.

Part B contains details on the studies provided as published work and manuscripts, which are the basis for the frame outlined before. The second part is organized in four chapters summarizing studies according to methodological approaches and theoretical views of investigations conducted, in parallel to the main areas of research addressed in Part A. The first chapter of Part B summarizes studies referring to comparisons at the species level being either classified in native and invasive species or according to functional groups. The second subchapter integrates papers and manuscripts referring to the role of genetic diversity as precondition for successful plant species invasion and for the evolution of invasiveness. The third chapter concentrates on biogeographical comparisons and knowledge gained from field studies. The last chapter, then, summarizes the outcomes of experimental approaches testing explicitly for evolutionary shifts. These different approaches include comparative studies in the field, laboratory and greenhouse, and by the majority, refer to explicit hypothesis-testing experimental manipulations. Each of these four chapters is based on the findings of three to five studies which are briefly outlined for their common basis and motivation and shortly subsumed for their main findings and contribution to overall conclusions. This short summary gives a foretaste on subsequent papers and manuscripts and does not intend to keep the reader from pursuing the publications.

List of publications relevant for the thesis

The publications are thematically ordered and assigned to subchapters addressed in the second part of the thesis. Additional information in brackets specifies the contributions done by A. Erfmeier.

Multi-species approaches testing for functional differences

[1] Bachmann D., Both S., Bruelheide H., Ding B.-Y., Gao M., Härdtle W., Scherer-Lorenzen M. & **Erfmeier A.** (2011): Functional trait similarity of native and invasive herb species in subtropical China – environment-specific differences are the key (unpublished). (BEF-China, DFG ER 371/1-1)
(idea, supervision of data collection, main part of data analysis, large parts of writing and editing of manuscript)

[2] Both S., Fang T., Baruffol M., Schmid B., Bruelheide B. & **Erfmeier A**. (2011): Effects of tree sapling diversity and nutrient addition on herb-layer invasibility in young experimental communities of subtropical species (submitted). (BEF-China, DFG ER 371/1-1)
(large parts of idea, supervision of data collection, parts of data analysis, parts of writing and editing of manuscript)

[3] **Erfmeier A.** (2011): Divergent, but climatic context dependent responses of grasses and herbs following experimental environmental change (submitted).
(idea, supervision of data collection, analysis, manuscript writing)

The evolutionary dimension – The role of genetic diversity

[4] **Erfmeier A.** & Bruelheide H. (2011): Maintenance of high genetic diversity during invasion of in the British Isles. International Journal of Plant Sciences 172 (6): 795-806. DOI: 10.1086/660194.

(parts of the idea, data collection, analysis, large parts of manuscript writing and editing)

[5] **Erfmeier A.**, Tsaliki M., Roß C.A. & Bruelheide H. (2011d): Genetic and phenotypic differentiation between invasive and native *Rhododendron* (Ericaceae) taxa and the role of hybridization. Ecology and Evolution (accepted 24.08.2011).

(parts of the idea and data collection, large parts of analysis and manuscript writing)

[6] Hantsch L., Bruelheide H. & **Erfmeier A.** (2011): High phenotypic variation of seed traits and germination characteristics of an invasive annual weed (submitted).

(large parts of the idea, supervision of data collection, large parts of analysis and manuscript writing)

[7] **Erfmeier A.**, Hantsch L., Bruelheide H. (2011b): The role of propagule pressure, genetic diversity and microsite limitation for *Senecio vernalis* invasion (to be re-submitted following Major Revision).

(idea, supervision of data collection, large parts of analysis, manuscript writing)

Native-invasive populations – Field comparisons

[8] Beckmann M., **Erfmeier A.** & Bruelheide H. (2009): A comparison of native and invasive populations of three clonal plant species in Germany and New Zealand. Journal of Biogeography 36: 865-878. (DAAD grant for M.B.)

(large parts of the idea, supervision of data collection, large parts of analysis and manuscript writing)

[9] Beckmann M., Bruelheide H. & **Erfmeier A.** (2011a): Populations of six clonal invaders compared between native and invasive regions in Germany and New Zealand. (submitted). (DAAD grant for M.B.)

(parts of the idea, supervision of data collection, parts of analysis and manuscript writing)

[10] **Erfmeier A.** & Bruelheide H. (2010): Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive *Rhododendron ponticum* populations. – Biological Invasions 12: 657-676. DOI: 10.1007/s10530-009-9472-x.

(large parts of the idea, data collection, main parts of analysis and manuscript writing)

Experimental evidence for genetic shifts

[11] Beckmann M., Bruelheide H. & **Erfmeier A.** (2011b): Germination responses of three grassland species differ between native and invasive origins. Ecological Research 26: 763-771. DOI: 10.1007/s11284-011-0834-3. (DAAD grant for M.B.)

(parts of the idea, supervision of data collection, parts of analysis, manuscript editing)

[12] Beckmann M., Hock M., Bruelheide H. & **Erfmeier A.** (2011c): The role of UV-B radiation in the invasion of *Hieracium pilosella* - a comparison of German and New Zealand plants. Environmental and Experimental Botany (accepted 16.09.2011). DOI: 10.1016/j.envexpbot.2011.09.010).

(parts of the idea, supervision of data collection, parts of analysis and manuscript editing)

[13] **Erfmeier A.**, Böhnke M. & Bruelheide H. (2011a): Secondary invasion of *Acer negundo* – A shift in strategies from reproduction towards persistence? Biological Invasions 13(7): 1599-1614. DOI: 10.1007/s10530-010-9917-2

(idea, supervision and parts of data collection, analysis and manuscript writing)

[14] Beckmann M., Bruelheide H. & **Erfmeier, A.** (2011d): Reduced tolerance to herbivory on clonal organs in alien genotypes – a multi-species experiment with native and introduced origins. (submitted).

(parts of the idea, supervision of data collection, analysis and manuscript writing)

[15] **Erfmeier A.**, Klein S., Welk E. & Bruelheide H. (2011c): The role of climatic niche shift and study type for phenotypic differentiation – A meta-analysis on native and invasive population comparisons in common environments studies (unpublished).

(large parts of the idea, supervision of data collection, parts of analysis and manuscript writing, manuscript editing)

Part A

The frame

1 Introduction

"Nothing in biology makes sense except in light of evolution (Dobzhansky 1973)." This paradigm has guided researchers in invasion biology during the last decades. In particular, the question if evolution of invasiveness occurs has become a central motivation for research approaches. The concept of invasiveness was initially introduced by Baker (1965, 1974) to describe increased size and vigour of successful colonizers and aims to identify 'invasive' traits and to predict the invasion potential of species. Contemporary biological invasions induced by human intervention represent a breaking out of natural barriers and a translocation to new situations where species encounter a different set of conditions controlling their abundance than at their home site (Mack et al. 2000, Hierro et al. 2005). Plant species that expand their distribution ranges have been studied for a long time from an ecological and biogeographical perspective in response to the community where exotic species have been introduced to (Pyšek & Richardson 2006). Accordingly, many of the hypotheses raised to explain the success of introduced species have an explicit ecological background, many of them postulating that certain traits of species or certain features of the habitat and community favour invasions (see Table 1 for listing of some of some of the most frequently consulted hypotheses). Historically, such approaches have been coined studying invasiveness (Rejmánek 1995, Williamson & Fitter 1996) or invasibility (Crawley 1987, Noble 1989), although awareness has risen that these view represent two sides of the same coin (Pyšek & Richardson 2006). Many of the hypotheses listed in Table 1 are based on such ecological mechanisms and mostly refer to the species level. While these hypotheses to some degree rely on assumptions of species sorting, other hypotheses focus more explicitly on the within-species level and refer to differentiation between parts of (native and invasive) ranges (see lower part of Table 1 for some examples). Although having a common mechanistic background, they are loosely arranged to each other, overlapping in some parts and, in turn, leaving other fields of evolutionary dimensions open. Addressing the evolutionary background of plant species invasions is the central topic of this thesis. Inferring knowledge from species comparisons in the beginning, the main subsequent objectives are related to evolutionary questions: as such they highlight the preconditions that need to be fulfilled for contemporary evolution in invasions at the within-species level and focus on both observational and experimental research approaches. As a synthesis, the present thesis aims at suggesting a framework to integrate the hypotheses raised so far.

Table 1: Overview on current hypotheses suggested for explaining invasion success of exotic plant species.
The upper part lists some of the hypotheses related to ecological explanations and mostly referring to the species level. The lower part compiles hypotheses with a more explicit evolutionary background, thus referring to within-species differentiation between native and invasive ranges.

Abbreviation	Hypothesis	Explanation	Mechanism	Reference
Ideal weed	Ideal weed	Traits and life-history characteristics of invasive species facilitate invasion	ecological	Elton 1958, Baker1965, Baker 1974
Empty Niche	Occupation of empty niches, Niche opportunity	Invasive species utilize unused resources by the local community	ecological	MacArthur 1970, Shea & Chesson 2002, Hierro et al. 2005
Biotic resistance	Biotic resistance hypothesis / Diversity barrier	Habitats with higher diversity are more resistant against invasions	ecological	Elton 1958, Stohlgren et al. 1999, Maron & Vilà 2001, Kennedy et al. 2002
REH	Resource enrichment hypothesis, Fluctuating resource hypothesis	Resource availability favours invasive species	ecological	Davis et al. 2000, Davis and Pelsor 2001
PP	Propagule pressure	Differences in the number of invasive propagules arriving in a new community explain different levels of invasion	ecological	Williamson 1996, Lonsdale 1999, Lockwood et al. 2005
ERH	Enemy release Hypothesis	Release from natural enemies in the invasive range	ecological	Darwin 1859, Crawley 1987, Keane & Crawley 2002, Mitchell & Power 2003
Habitat filtering Climate match	Habitat match / Climate match	Succesful invaders are pre-adapted to habitat conditions	ecological/ evolutionary	Facon et al. 2005 Kriticos et al. 2005, Maron et al. 2006
Filters	Filters at different stages	Abiotic and biotic resistance, propagule pressure and human intervention	ecological	Theoharides & Dukes 2007
EEH	Enemy of my enemy hypothesis	Co-introduced enemies promote invasion by attacking native competitors	ecological	Colautti et al. 2004
	Invasional meltdown	Facilitation of invasion by previously released organisms		Simberloff & Von Holle 1999, Richardson et al. 2000
Hybrid	Hybridization, (neo-)polyploidy	Increased vigour due to novel genetic constitution	evolutionary	Ellstrand & Schierenbeck 2000
GPG	General purpose genotype hypothesis	Successful invaders are a genetic subset of native populations that have evolved invasiveness	evolutionary	Baker 1965, Parker et al. 2003
RERH	Resource-enemy release hypothesis	Invasion will be enhanced if increased resources co-occur with release from natural enemies	ecological/ evolutionary	Blumenthal 2005, 2006
EIH	Enemy inversion hypothesis	Co-introduced enemies have a reduced or reversed effect on their hosts	ecological/ evolutionary	Colautti et al. 2004
Novel weapons	Novel weapons	Alien species bring novel negative biochemical interactions (allelopathy) to recipient communities	ecological/ evolutionary	Hierro & Callaway 2003, Callaway & Ridenour 2004
EICA	Evolution of increased competitive ability	Increased vigour following release from natural enemies in the invasive range at the expense of reduced defences	evolutionary	Blossey & Nötzold 1995, Bossdorf et al. 2005
ERCA	Evolution of reduced competitive ability	Reduced competitive strength following reduced competition levels	evolutionary	Bossdorf et al. 2004

2 Multispecies approaches testing for functional differences

There have been numerous attempts to identify traits that differentiate native and invasive species with a focus on size-related variables such as relative growth rates or on leaf- related characteristics such as specific leaf area (Pattison et al. 1998, Grotkopp et al. 2002, Violle et al. 2007). This research field has obtained large acceptance and the number of studies measuring traits on invasive plant species under common environmental conditions has notably increased during the last 30 years (Pyšek & Richardson 2007). However, these studies are heterogeneous with respect to the types of traits considered and design of the study. More generalizing approaches to identify differences by means of large multi-species experiments and datasets concluded that invasive species tend to share certain characteristics, for example short life cycles, effective dispersal strategies, large native range sizes and presence of organs of clonal growth, but native species of comparable habitats were not necessarily significantly different by the majority of the traits studied (Cadotte et al. 2006, Küster et al. 2008, Tecco et al. 2010, Scharfy et al. 2011). In contrast, if invasive species actually grew faster, produced more seeds or germinated faster, in particular, in nutrient rich environments, they would share the same characteristics with a subset of most successful native plants in the world (Thompson & Davis 2011). In their meta-analysis of field and common environment studies between native and invasive species, van Kleunen et al. (2010a) found higher values for invasive species in performance-related traits. However, in their analysis, heterogeneity in effect sizes of compared species groups was largely attributable to differences in study types, the fact that native species are invasive elsewhere or not, their phylogenetic non-independence or their growth form. In addition, inferences drawn from comparisons between native and invasive species might also depend on the type of comparison made (van Kleunen et al. 2010b). Accordingly, comparing invasive alien species, non-invasive alien species and native species yields different outcomes depending on the groups contrasted and, therefore, requires different conclusions (van Kleunen et al. 2010b). Moreover, the importance of particular plant traits is known to vary with the environmental conditions (Thompson et al. 1995, Küster et al. 2008, Tecco et al. 2010) which might severely affect the generalisability of findings when comparing groups of species. For example, results of repeated field-site - common garden comparison conducted for grasses and herbs of dry grassland situations have displayed large effects of interannual climatic differences on the outcome of the experimental comparisons (Erfmeier 2011 [3]). In this, study, it was shown that the interpretation of functionality of species groups largely depended on the precipitation and temperature context of the respective study year in addition to the environmental treatment, i.e. the diagnostic value of differentiation in traits between species groups might interact with the climatic settings (Erfmeier 2011 [3]). When further factors, such as habitat type, are considered, the magnitude of differentiation encountered between native and invasive species might be affected. Testing for consistency of traits conferring invasiveness, thus, requires experimental multi-species comparisons (Grotkopp & Rejmánek 2007, van Kleunen et al. 2010a). We conducted such an experimental multi-species study of 15 native and 15 invasive Chinese herb species of comparable ruderal habitats and growth form (Bachmann et al. 2011 [1]). Therein, we found similarities in fundamental abiotic niches between the species groups. Additionally, differences in fundamental niches were detectable and effective, in particular, under high light conditions, and therefore under favourable environmental conditions only (Bachmann et al. 2011 [1]). This strategy can be summarized as an opportunistic one (Richards et al. 2006) and was, subsequently confirmed to be of importance in experimental early successional forest plots at Chinese field sites (Both et al. 2011).

In conclusion, these results point towards a context-dependency of invasiveness. Many of the different results gained from comparisons of native and invasive species might be reconciled when taking the circumstances under which the data were obtained into consideration. This applies to comparisons between species, but also when referring to within-species differentiation and evolution.

3 The evolutionary dimension: the role of genetic diversity

A key consideration for studying evolution in biological invasions is a shift in focus from across-taxa comparisons to the population level. On the one hand, the population level does not suffer from pitfalls of phylogenetic comparability. On the other hand, evidence of contemporary evolution should play out at first at this level. A plethora of studies on invasive plants and animals has suggested that invading populations have experienced evolutionary shifts that allow them to cope with biotic and abiotic environmental changes encountered in new environments (Lee 2002, Stockwell et al. 2003, Kawecki & Ebert 2004, Lambrinos 2004, Maron et al. 2004, Strauss et al. 2006, Buswell et al. 2011). There are some notable exceptions to this pattern, most of which are successfully invading clonal plant species that manage to maintain their seemingly appropriate genetic constitution via asexual reproduction (Allendorf & Lundquist 2003, Bailey et al. 2009, Zhang et al. 2010). Plant invasions with evidence of evolutionary adjustments to altered selection pressures comprise examples of increased sexual reproductive output in respect of numbers of fruits and seeds (Ridley & Ellstrand 2009), enhanced vegetative reproduction (Lavergne & Molofsky 2007) and shifts towards increased plant size (Siemann & Rogers 2001, Bossdorf et al. 2004) in invasive populations when compared to native ones.

While such population comparisons naturally have an evolutionary perspective (Lee 2002, Cox 2004, Lambrinos 2004), the mechanisms that drive the evolution of invasiveness in the introduced range have been less satisfactorily addressed (Ellstrand & Schierenbeck 2000, Sax et al. 2007). Several preconditions need to be fulfilled to allow for adaptive evolution during invasion, but in general, genetic principles that act during invasions are the same as those identified in the field of conservation biology when studying populations threatened with extinction, i.e. genetic drift and Allee effects of small populations, gene flow and hybridization (Allendorf & Lundquist 2003). High levels of genetic variation are a precondition for selection to act on (Hedrick 2005) and, thus, represent a common challenge founder populations have to meet. Based on neutral genetic markers, a wide range of studies on invasive plant species have shown that founder populations actually have lower levels of genetic variation compared to ancestral populations (e.g. Amsellem et al. 2000, DeWalt & Hamrick 2004, Dlugosch & Parker 2008, Henry et al. 2009, Zimmermann et al. 2010). In contrast, other studies found no evidence of such loss in genetic variation within populations of introduced/invasive plants and animals (Wares et al. 2005, Marrs et al. 2008, Chun et al. 2009, Doorduin et al. 2010, Lachmuth et al. 2010, Pairon et al. 2010). Addressing the role of genetic diversity as a precondition for successful invasion has also been of vital importance for the present thesis. Referring to *Rhododendron ponticum* as long-lived and insect-pollinated and woody plant invader in Atlantic Western Europe, this species served exemplarily to study the amount of changes in neutral genetic diversity and differentiation from native to invasive ranges (Erfmeier & Bruelheide 2011 [4]). One main conclusion drawn from this study was the evidence of maintained high genetic diversity and a lack of within-country differentiation in the invasive range, in Ireland, which can most probably be ascribed to high gene flow among populations as well as to repeated intentional introduction and naturalization of this species for reasons of horticultural interest (Dehnen-Schmutz & Williamson 2006). Multiple introductions into a new range or region are a common feature of invasions (Ellstrand & Schierenbeck 2000, Lockwood et al. 2005, Lavergne & Molofsky 2007). They contribute to increasing genetic variation in founder populations and, thus, to augmenting levels of allelic variation and diversity (Novak 2007, Dlugosch & Parker 2008). Multiple introductions into a new territory might allow for new genetic recombinations of hitherto separated genotypes and may result in reshuffling genetic variation, thus, providing the raw material for further adaptation. Additionally, mechanisms of evolutionary change at the molecular level include examples of polyploidization or novel allele combinations following hybridizations (Abbott 1992, Ellstrand & Schierenbeck 2000, Milne & Abbott 2000, Blum et al. 2007, Rieseberg et al. 2007, Vellend et al. 2007, Prentis et al. 2008; Table 1). The mechanistic explanation of hybridization contributing to the maintenance of genetic diversity was explicitly tested for *Rhododendron ponticum* in the present thesis (Erfmeier et al. 2011d [5]). However, hybridization has not proven to be evident in *R. ponticum* in the part of the invasive range studied, neither in molecular markers nor in a set of quantitative traits studied on North American conspecifics and native and invasive provenances of *R. ponticum*. For invasive *R. ponticum*, it could be assumed that irrespective of inter-specific hybridization, a fitness boost in newly admixed populations alone might have contributed to an increased colonization success. Verhoeven et al. (2011) recently underlined that the benefit of new admixtures in relation to the costs induced by the risk of maladaptations is presumably higher in the new range because of an altered selection regime compared to the home sites. Therefore, increased intra-specific genetic exchange might not only sustain patterns of genetic diversity, but also allow for increased fitness of invasive populations compared to native ones, which might be a coherent explanation for the invasion of *R. ponticum* (Erfmeier et al. 2011d [5]).

The maintenance of high genetic diversity supports the maintenance of phenotypic variation in morphological, physiological or ecological traits, which has often been found to be indispensable for successful plant establishment (Richards et al. 2006, Funk 2008, Hulme 2008), in particular under heterogeneous environmental conditions (Thompson et al. 2001, Durka et al. 2005, Fumanal et al. 2007, Monty & Mahy 2010). The species' biology being characterised by traits supporting high gene flow among populations, e.g. small and light seeds that are easily dispersed, also contribute to keep high levels of genetic diversity and phenotypic variation in the invasive range (Colautti et al. 2006). In addition, a high number of propagules arriving in a community increases the probability of subsequent establishment (Lockwood et al. 2005, Table 1). Studying invasive *Senecio vernalis* populations as part of the present thesis, highest variation in seed traits and in genetic diversity were found within populations and did not reflect differentiation in reproductive traits between habitat types (Hantsch et al. 2011 [6]). High gene flow among populations can impede differentiation (Slatkin 1985). However, experimental testing provided evidence that propagule pressure and genetic diversity might differentially affect specific life stages of individuals (Erfmeier et al. 2011b [7]): High propagule pressure in particular increased emergence and establishment of *Senecio vernalis* but did not translate into increased individual performance. In contrast, sampling effects associated with diversity seemed to affect later demographic life stages.

This experiment displayed a shift from density dependence to impact of genetic diversity across life stages of *S. vernalis* (Erfmeier et al. 2011b [7]). Recent investigations indicate that impacts of different genotypes are similar to those of different species (Hughes et al. 2008, Vellend et al. 2010). For *S. vernalis*, the outcome of experimental testing correspondingly suggests that effects of diversity on colonization success might be caused by genotype identity effects (Erfmeier et al. 2011b [7]).

In summary, own findings and those of other studies provide convincing evidence of effective mechanisms that maintain high genetic and phenotypic diversity in invaded ranges for several invasive plant species. These mechnisms directly influence the performance of populations and thus, set the stage for contemporary evolution during invasions.

4 Native-invasive populations - field comparisons

Taking the biogeographical approach of field comparisons is a key to understanding exotic plant invasions; however, inferences on the evolutionary dimension strongly depend on the nature of approaches for intraspecific comparisons between ranges (van Kleunen et al. 2010b). Descriptive, observational field approaches are useful tools to assess the degree of differentiation in densities and distribution patterns between ranges and can already constrain the number of putative hypothesis on invasions that might apply (Hierro et al. 2005). Biogeographical comparisons, for example, might allow for conclusions on the role of enemy release or empty niches (Table 1) or suggest mechanistic hypotheses that need to be tested experimentally. In this way, when comparing three clonal plant species in the invaded range in New Zealand and in the native range in Germany, e.g. Beckmann et al. (2009, [8]) suggested a weakened trade-off between individual growth and sexual reproduction for *Achillea millefolium* in the invaded range, whereas *Hieracium pilosella*, in contrast, displayed an overall increased sexual reproduction in the invaded range.In addition, a multi-species field comparison on six clonal plant species in native and invasive ranges revealed that the detection of increased abundances in the invaded range strongly depends on the scale of observation applied, ranging from the individual, the neighbourhood and the population scale (Beckmann et al. 2011 [9]). For *Rhododendron ponticum*, such field analyses suggested that a combination of favourable abiotic conditions at invaded Irish sites and climatic suitability (i.e. diminished temperature amplitude) has contributed to the invasion success (Erfmeier & Bruelheide 2010 [10]). These findings relate to a combination of the climate match hypothesis and/or habitat match hypotheses (Table 1) that might apply including the possibility that the new environments provide more beneficial conditions than the home sites. However, additional transplant experiments experiments suggested that evolution can occur in response to relaxed selection pressure provided by beneficial conditions (Erfmeier & Bruelheide 2010 [10]). This would indicate that the “habitat match” might also be of adaptive value.

5 Experimental evidence for genetic shifts

The most straightforward approach to spot evolution at the phenotypic level in plant invasions is to study native and invasive populations in a common environment, in which displayed genetic differences might reflect either adaptive or non-adaptive evolutionary changes. To identify as to which degree genotypic shifts in traits during range expansion have resulted in adaptations is only detectable by reciprocal transplant experiments in native and invasive ranges (Parker et al. 2003, Maron et al. 2004, Moloney et al. 2009b). Nevertheless, within-one-habitat comparisons of native and invasive provenances, to some degree, might be diagnostic for local adaptation (Kawecki & Ebert 2004). For plant species, appropriate tools that allow to quantify the amount of phenotypic shift reflecting evidence of evolution during invasions are common garden experiments with distinct native and invasive genotypes. During the last decade, a multitude of such comparisons were conducted and support the idea of adaptive evolution of invasiveness, providing evidence for increases in plant size, relative growth rates, allocation to reproduction and plasticity (Siemann & Rogers 2001, Leger & Rice 2003, Brown & Eckert 2005, Erfmeier & Bruelheide 2005, Caño et al. 2008). In particular, as part of the present thesis, several approaches were explored, including growth chamber, germination cabinet, common garden and reciprocal transplant experiments as well asmeta-analysis. As main result of germination experiments with multiple species and provenances, for example, we found early life stages to be affected by post-introduction evolution. Several of these studies indicate that shifts in germination patterns across ranges in different invasive species occurred and contributed to increased invasiveness of introduced populations (Erfmeier et al. 2011a,d [13, 5], Beckmann et al. 2011 [11]). While there is some evidence that rapid adaptation in germination strategies might contribute to the invasion success in such across-range tests (see also Kudoh et al. 2007 , Hierro et al. 2009), germination might also be subjected to differentiation within the invaded range as was shown for invasive *Acer negundo* populations from secondarily colonized dryer habitats (Erfmeier et al. 2011a [13]). While, initially, invasive occurrences of *Acer negundo* in Germany were restricted to moist habitats, preferably along rivers, the species has increased in abundance also in dry habitats of industrial wastelands and ruderal sites during the last decades. Reciprocal transplant experiments across moist and dry habitat type have shown, that post-introduction evolution, as displayed in increased leaf life span, seems to have contributed to secondary invasion of *Acer negundo* into more constrained habitats (Erfmeier & al. 2011a [13]).

In contrast, other studies contradict explicit theories of evolution during invasions (see Bossdorf et al. 2004, 2005, Franks et al. 2008). Summarizing attempts at the vote count level, accordingly, found no unequivocal pattern (Hinz & Schwarzländer 2004, Bossdorf et al. 2005). Experimental multispecies approaches with pairs of 14 plant species suggested that increased plant size of invasive provenances might reflect adaptation to non-competitive environments (Blumenthal & Hufbauer 2007). Thus, biotic factors like competition, but also trophic interactions can exert a covarying influence on the interpretation of putative differentiation between origins. This hypothesis was explicitly tested in one study conducted with native and invasive provenances of six clonal plant species from Germany and New Zealand in a common garden experiment (Beckmann et al. 2011d [14]). Combining treatments of simulated herbivory on clonal organs with different spatial availability of nutrients, we found consistent evidence of increased clonal growth in invasive genotypes, thus adaptive differentiation. Moreover, the number of clonal organs in invasive provenances compared to native ones was significantly increased in combined treatments of absent herbivory and heterogeneous availability of nutrients supplied. These results indirectly suggest an adaptive adjustment of the nutrient foraging strategy in invasive clonal plants being advantageous in the face of heterogeneous abiotic conditions of nutrient availability under situations of enemy release (Beckmann et al. 2011d [14]). Such examples of interacting factors highlight that some evidence of evolutionary shift might only be encountered when controlling for interacting factors.

The unknown covariance

Many of the results encountered in the studies mentioned above remain idiosyncratic and the attempt to find generalizing patterns on the role of evolutionary shifts during invasions has not yet been satisfactorily rewarded (see also summary in Maron et al. 2004). This circumstance is largely attributable to co-varying effects that hamper generalizations. Common garden conditions e.g. might provide less beneficial situations compared to those situations populations encounter at their home sites. In consequence, adaptation to more efficient resource-use would not pay-off and might remain undetected. In statistical terms, such situations reflect interactions between the location of common gardens, representing local environmental factors (both abiotic and biotic) outside the control of the experiment, and the genetic provenance of the plants (Moloney et al. 2009a), which suggests that different common garden locations might provide different results (Maron et al. 2004, Williams et al. 2008). Mechanistically, adaptation is influenced by the strength of local selection, the amount of genetic variance, the demographic cost of maladaptation, but also by the spatial scale of gene flow and the amount of habitat heterogeneity (Hanski et al. 2011). The strength of local adaptation is often related to geographical distance between compared sites of plant origin, which depends on its association with actual environmental differences and, accordingly, acts as additional selective agent behind (Joshi et al. 2001, Leimu & Fischer 2008). In consequence, one can expect abiotic factors, including large scale climatic factors (for convenience in the following referred to as climate) and small scale abiotic environmental factors related to resources and microclimate (in the following referred to as abiotic factors in the narrow sense), and biotic factors, including both competitive as well as trophic interactions, to considerably affect the degree of adaptations encountered during plant invasions. Some of these factors have already found their way into synthesizing frameworks. In their meta-analysis on comparisons of native and invasive populations, Colautti et al. (2009) aimed at seizing the nature and effect of co-varying factors and detected a relationship between trait performances in populations and the latitude of the respective sampling locations, including different climatic signatures. Such type of confounding might result in mistaking environmental effects as invasive-native contrasts (Erfmeier et al. 2011c [15]). In this recent meta-analysis on 37 common environment studies with native and invasive provenances of 27 species, we explicitly addressed the influence of study type, common garden location and climatic niche shift on the magnitude of native-invasive trait shift (Erfmeier et al. 2011c [15]). The study confirmed previous findings of increased growth of invasive populations and elucidated that results of native-invasive comparison could be affected by study type (greenhouse vs. common garden) but not by the location of common garden (native vs. invaded range). A clear recommendation of this study was to test hypotheses on interactions in evolutionary processes, e.g. explicitly for species with evidenced climatic niche shifts, in combination with further abiotic and/or biotic environmental changes to account for the context-dependency.

With regard to abiotic environmental conditions, Daehler (2003) was one of the first to explicitly point at the context-dependency of traits promoting invasions. He emphasised the role of environmental conditions related to resource availability to differentially increase the performance of invaders over that of native species. In the following, several attempts to grasp such context-dependency in theories of invasions have included environmental heterogeneity and community characteristics (Melbourne et al. 2007) or incorporated intrinsic and extrinsic factors, i.e. propagule pressure, growth rates, feedback relationships in resource competition and spatial scale (Eppstein & Molofsky 2007). Biotic interactions also modify the degree as to which adaptations can become evident. Only few comprehensive frameworks of invasion have taken the context-dependency of the evolutionary background explicitly into account. In particular, this is the case for process-oriented frameworks that link subsequent stages of invasion to patterns of plant invasions (Dietz & Edwards 2006, Theoharides & Dukes 2007). Dietz & Edwards (2006), suggested that invasion processes can be more generalizable by subdividing the invasion phase into a primary phase when exotic species increase rapidly in abundance, presumably in resource-rich habitats by pre-adapted genotypes, and into a secondary phase, which requires plastic responses or genetic adaptations to new ecological circumstances. The authors pointed out that adaptability of plant invaders in the secondary phase can follow either abrupt transitions with regard to a switch of contrasting habitats or the experiencing of gradual changes (e.g. climatic gradients). Theoharides & Dukes (2007), in turn, identified geographic, abiotic, biotic and landscape filters to primarily act during stages of transport, colonization, establishment and geographic spread.

6 The challenge: ‘constraint’ vs. ‘release’

Here, I suggest that all these hierarchical factors that affect invasions do not only act as environmental filters but also as agents of selection for differentiation. While awareness is rising for the need to more appropriately quantify the complexity of confounding co-varying conditions in hierarchical factors across scales (Milbau et al. 2009, Gurevitch et al. 2011), this complexity has to be combined with a consistent evolutionary perspective to uncover mechanistic relationships in adaptive processes during invasions.

In the following, I will show how such a hierarchical frame of evolutionary processes brings new insights into so far unconnected fields of study and, thus, might lead to a more differentiated mechanistic understanding of invasion ecology.

6.1. Within hierarchical factors

Conceiving invasions as a match between a species and the respective recipient ecosystem (Facon et al. 2006), exotic species can encounter more beneficial or more stressful conditions relative to their habitat of origin. This alternative, yet not appreciated view is also reflected in some of the hypotheses raised in Table 1: while some terms imply such a “match” (e.g. empty niche, fluctuating resources, habitat match, enemy release), a few enunciate the perspective of more constrained situations, such as in the biotic resistance hypothesis. Accordingly, associated selection pressures display either increased constraints or increased releases (Fig. 1). Along an environmental gradient, as depicted by the horizontal axis in Fig. 1, the change from native to exotic situations can differ in direction and quality, and thus, differentially affect the extent of necessary subsequent adaptations.

While the lower part of the figure represents situations of release, where the relative comparison of native to exotic populations (transitions a) and b) in Fig. 1) implies shifts towards more favourable situations with regard to the focal environmental factor, the upper part describes the inverse scenario of shifts along environments with increasing constraints (transitions c) and d) in Fig. 1).

Less favourable conditions (c, d) imply shifts in traits leading to specialization with respect to those factors of constraints. Conversely, under conditions of release (a, b), adaptations in these traits include the abandonment of specialization, normally involving costs of construction, which may be allocated elsewhere, e.g. in increased growth and vigour of individuals. However, depending on the relative position of the starting point (Fig. 1), introductions into a new range can occur from relaxed, intermediate situations to more severe or more constrained conditions or can come from particularly favourable or unfavourable environments at home sites.

The direction and the degree of the relative change along this gradient will be translated into graduated levels of genetic shifts, and thus, lead to inconsistent outcomes on different examples of plant invasions. This perception of constraint vs. release can be consistently applied across hierarchical level of filters of climate, abiotic and biotic environment as presented in Fig. 2.

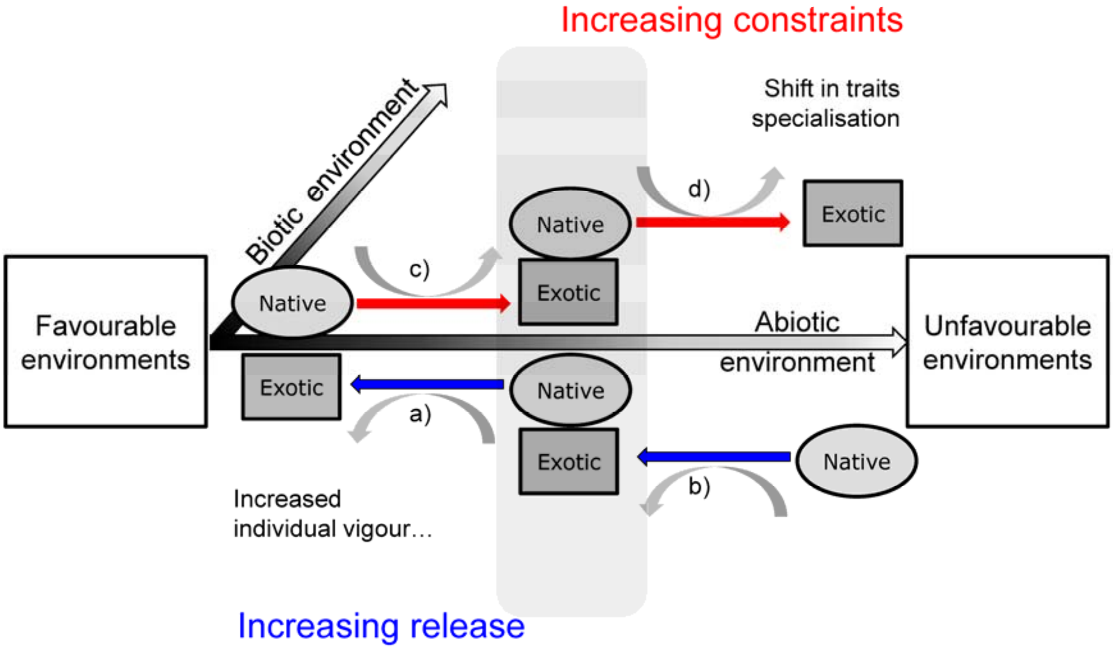

Fig. 1: Model on the directional and qualitative role of environmental changes during invasions and associated changes in selection pressures. Native populations are given in light grey ovals, exotic populations in dark grey boxes. The horizontal axis displays an environmental gradient with decreasing favourability. The grey shaded area depicts conditions of intermediate environmental conditions. Environmental changes during plant invasions might imply translocations from unfavourable environments to more favourable environments (lower part, a) and b)), thus being connected with release, or vice-versa, translocations from favourable environments at their home sites to less favourable environments at their new sites (upper part, c) and d)), thus, experiencing increasing constraints. In both directions, the quality of environmental change is additionally influenced by the relative position of change along the environmental gradient, depending on whether increasing release is experienced from intermediate to more favourable (a) or from unfavourable to intermediate (b) conditions, and on whether increasing constraints start from favourable to intermediate (c) or from intermediate to unfavourable (d) conditions.

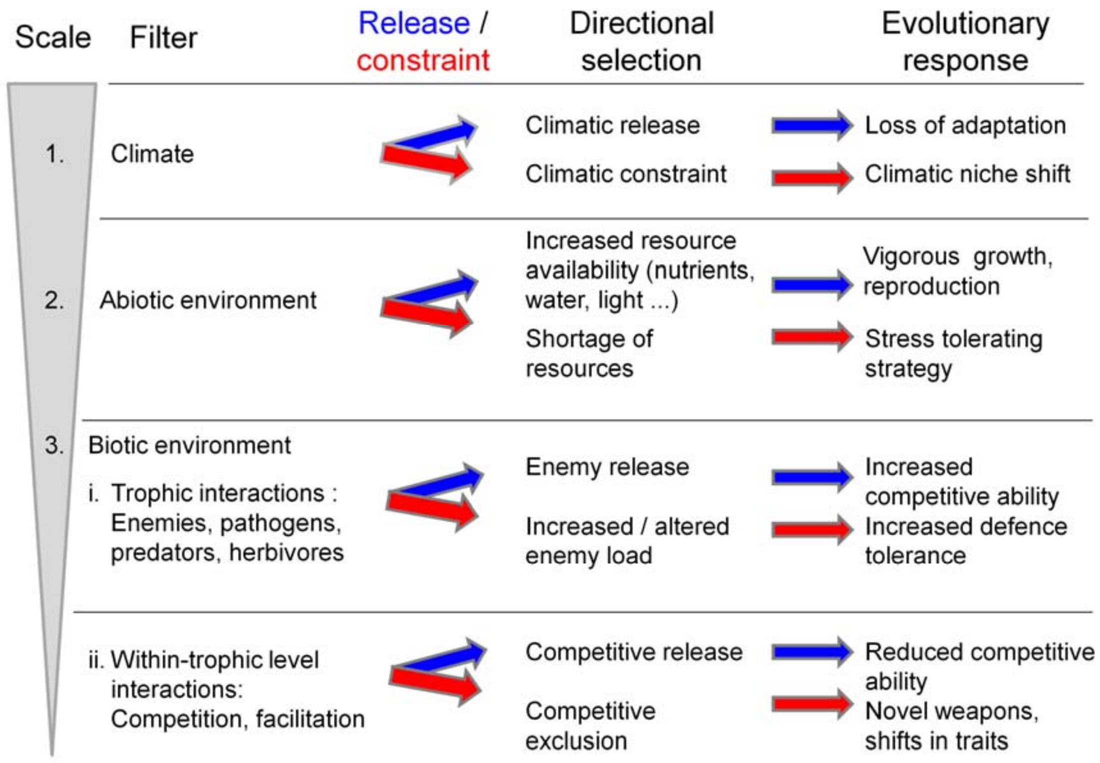

Fig. 2: Summary of potential directional paths of release and constraints encountered during range expansion in plant invasions across hierarchical factors and subsequent evolutionary responses.

In the following, this view will be exemplarily used to suggest that gains and losses of adaptations act similarly under more constrained and more alleviated conditions for most hierarchical factors. In accordance with the idea of species sorting in response to environmental filtering (Leibold et al. 2004), these filters include 1) climate at large scale, 2) abiotic environmental factors at small scale and 3) biotic factors at increasingly finer scales. Acknowledging that the term "biotic factors" comprises a multitude of conditions, interactions and processes evoking different consequences for invasions, this filter level requires additional differentiation, distinguishing between trophic interactions (including herbivore-plant, predator-prey and pathogen-host relationships) and within-trophic level interactions (comprising facilitation, mutualism and competition) to appropriately address its complexity.

6.1.1 Climate

Climate is the most constraining factor for plant species distribution (Woodward 1987). Accordingly, climatic match between native and exotic ranges is a precondition for successful colonization (Thuiller et al. 2005, Theoharides & Dukes 2007, Table 1). In contrast, encountering more severe climatic conditions in a novel range can require the evolution of more specialized ecotypes (Sexton et al. 2009). Evidence of climatic adjustment during invasions has historically been adduced by latitudinal matching. Sexton et al. (2002) found northern ecotypes of introduced *Tamarix ramosissima* (saltcedar) to invest more into roots under cold conditions, which increased the survival over the first winter. In particular, hybridization seems to have contributed to the evolution of cold hardiness in introduced saltcedar (Friedman et al. 2008). The cline concept as a continuous form of climatic adjustment, including latitudinal and altitudinal differentiation can be fully transferred to biological invasions. Accordingly, there is evidence of differentiation in invasive ranges of exotic plant species (Weber & Schmid 1998, Maron et al. 2004, 2007, Etterson et al. 2008, Alexander et al. 2009, Alexander & Edwards 2010). More recently, climatic space relationships between native and exotic populations have been used to identify realized climatic niche shifts (Gallagher et al. 2010). Apart from the climate match hypothesis that assumes that invasive species conserve their climatic niche in the invaded ranges, climatic niche shift between ranges can also reflect evolutionary responses in terms of adaptation to novel climatic conditions (Broennimann et al. 2007). For example, climate models of *Centaurea maculosa* fitted for Europe failed to predict the distribution range in western North American where the species is invasive (Broennimann et al. 2007). High levels of precipitation and, thus, high water availability in the native range, were identified as major factors of climate niche differentiation. A similar pattern of differentiation was recently provided on the basis of a multi-species comparison for a set of several invasive plant species (Erfmeier et al. 2011c [15]). In this approach, we explicitly linked climatic niche shift and the magnitude of native-invasive trait differentiations, which applied for some examples of successful invasions, but not for others. Admittedly, climate niche shifts between native and invasive ranges cannot unequivocally be interpreted as adaptations, since differentiation may result from changes in the realized or fundamental niche or both. Thus, it could be brought about by biotic constraints (Bruelheide & Scheidel 1999) or be limited by the introduction history (Bucharova & van Kleunen 2009). The mechanism of adaptation to a more constrained climate has been well documented for *Centaurea stoebe* (Henery et al. 2010). After an initial colonization of genotypes that matched the more continental climatic conditions in the new range, the invasive tetraploid populations have, additionally, undergone post-introduction adaptation supporting subsequent invasive spread (Henery et al. 2010). For these populations, a shift in tetraploid biology from monocarpic towards polycarpic life cycle and increased carbon investment to leaves has contributed to exotic range expansion into dryer habitats of a more continental climate compared to those that had been initially colonized. In contrast, range shifts into more benign climatic conditions might imply losses of adaptations, given that adaptations incur fitness costs, such as the formation of traits of drought resistance or frost tolerance. In consequence, there should be an increase of investments either in other constraints or in overall variability in traits. For invasive *Rhododendron ponticum* populations in Ireland, it has been suggested that mild temperatures and high precipitation levels evoked a genetic shift from restricted, precautious germination in the native range to increased germination and, thus, reproduction and establishment in the new range (Erfmeier & Bruelheide 2005, 2010 [10]). The idea of climatically induced losses of adaptations in terms of frost hardiness was pursued by Ebeling et al. (2008) who studied frost resistance in invasive *Buddleja davidii* depending on the origin of populations. Although, in this case, the authors failed to demonstrate differentiation in frost hardiness, this attempt is an example of how to relate effects of climatic constraints or releases to trait performances.

6.1.2 Abiotic context related to microclimate and resources

With regard to the abiotic context, there is some evidence that exotic species make better use of increased resource levels, e.g. in light and nutrient supply (Pattison et al. 1998, Davis et al. 2000). Along this line, Davis et al. (2000) put forward the resource enrichment hypothesis (REH, Table 1), stating that invasive species can become particularly successful in resource-rich habitats or in those with (temporarily) increased resources (Daehler 2003, Blumenthal 2006, Blumenthal et al. 2009, Bachmann et al. 2011[1]). This hypothesis is supported by the finding that, in comparisons of native and invasive provenances, invasive populations can use soil resources and light more efficiently than native populations (Zou et al. 2007). This underlines the adaptive nature of increased resource use efficiency, which finally results in more vigorous growth and reproduction under relaxed selection pressure. For *Helianthus exilis*, Sambatti & Rice (2007) demonstrated adaptation in invasive riparian provenances and in origins from serpentine soil as a classical trade-off: while most of the populations encountered in the US are adapted to serpentine habitats and display high investment in root biomass and mechanisms to exclude high leaf Mg contents, riparian provenances show increased aboveground growth. Thus, higher vigour seems to be provided at more beneficial sites.

In contrast, shifts towards attributes of resource conservation are needed when invasions occur in resource-poor or pristine habitats (Funk & Vitousek 2007, Tecco et al. 2010). Some few examples of invasions into abiotically more severe habitats indicate post-introduction adaptation to edaphic stress and can be regarded as secondary shifts (Dietz & Edwards 2006). *Lythrum salicaria*, e.g. displayed shifts in responses to reduced water availability with smaller growth and increased longevity in dry habitats compared to wet ones (Moloney et al. 2009b). Accordingly, the above mentioned example of secondary invasion of *Acer negundo* displays evidence of post- introduction adaptation in leaf life span as response to more severe abiotic habitat conditions (Erfmeier et al. 2011a [13]). However, the relative position on the resource gradient in Fig. 1, i.e. the magnitude and quality of changes in resource supply, can equally be responsible for different findings: invasive *Hypochoeris radicata* at N-limited sites at Mount St. Helens displayed rapid uptake and utilization of N, once nitrogen inputs are available (Schoenfelder et al. 2010); whereas in invasive occurrences of *H. radicata* in Hawaii, higher resource use efficiency seemed to contribute to the invasion success (Funk & Vitousek 2007). Therefore, different strategies can be the result of different N-availability at these two sites, with *H. radicata* being subjected to repeated brief N pulses at Mount St Helens, which might not occur in Hawaii (Schoenfelder et al. 2010). This example of different mechanisms under different abiotic environmental conditions suggests that multiple-region studies integrating examples of exotic species that expand into different regions can be very valuable in order to quantify the role of differential qualitative abiotic changes on evolutionary shifts. Future studies should include such multiple-region and multiple-habitat comparisons on invasive species and should link these to changes in habitat favourability as outlined in Fig. 1.

6.1.3 Biotic context: Between-trophic level interactions

One of the most frequently consulted hypotheses in invasion biology is related to the loss of biotic interactions in the new range: the enemy release hypothesis (ERH, Table 1, Fig. 3) implies the escape from natural antagonists (pathogens, insect herbivores, soil biota) and thus, the disappearance of previous selection pressures (Crawley 1987, Keane & Crawley 2002, van Kleunen & Fischer 2009). However, while enemy release seems to be important in some invasions, it turned out to be ineffective in others despite evidence that levels of antagonists differ between native and invasive ranges. Thus, inconclusive results hamper generalizations (Beckstead & Parker 2003, Colautti et al. 2004, Mitchell et al. 2006, Siemann et al. 2006, Chun et al. 2010, Dormontt et al. 2011). Potentially, the release from constraints as to one type of enemy is replaced by constraints in form of other enemies, thus, requiring altered strategies of defence and/or compensatory growth (Joshi & Vrieling 2005). Two opposing mechanisms that occur simultaneously might outbalance each other and reflect a trade-off in types of defences (Orians & Ward 2010). This seems to apply to to several *Senecio* species (Caño et al. 2009, Rapo et al. 2010) and also to invasive *Triadica sebifera* (=*Sapium sebiferum*), which experienced a decrease in resistance to specialist herbivores and an increase in tolerance to generalist herbivores (Huang et al. 2010).

Conversely, biotic interactions in species invasions can be related to less comfortable situations in the new range. Exotic *Hypericum perforatum* populations, e.g., displayed a reduction of mycorrhizal dependency; however, this loss combined with shifts in biomass allocation did not seem to restrain the species from invading the new range (Seifert et al. 2009). In particular, invasive species involved in obligate mycorrhizal associations or requiring specific pollinators are predicted to experience strong barriers to invasion in the absence of their mutualist, whereas generalists can associate with a diverse array of symbionts (Richardson et al. 2000, Pringle et al. 2009). Studying examples of such specialists' invasion should be related to hypotheses that evolutionary adaptations and/or shifts to biotic constraints might be involved to overcome this obligate shortage.

6.1.4 Biotic context: Within-trophic level interactions

Within communities, direct interactions among native recipient and exotic invading species mostly act via competition for resources. Reduced competition in the invasive range has been invoked as biotic explanation for invasions (Shea & Chesson 2002). In continuation, this might lead to the evolution of reduced competitive ability (ERCA, Bossdorf et al. 2004, Table 1, Fig. 3), a theory acknowledging that the maintenance of traits conferring competitive ability, such as large height and biomass, generates fitness cost and that directional selection will favour reduced competitive strength.

Conversely, competition intensity might also be increased in the new range. Evolution in direction of increased competitive ability is described by novel weapon hypothesis (Table 1, Fig. 3, Callaway & Aschehoug 2000, Reinhart et al. 2003, Callaway & Ridenour 2004). This theory implies that exudation of allelochemicals by invaders that are ineffective against neighbours in natural communities due to their historical co-evolution, can have strong inhibitory effects to plants in invaded communities, thus leading to rapid evolution of those weapons. Biogeographical differences in the effects of allelopathic chemicals suggest that these chemicals are under selection pressure (Thorpe et al. 2011). Mechanisms of (resource-related) competitive constraints are based on niche similarities and complementary in multispecies coexistence. To avoid competitive exclusion, adaptive niche divergence among coexisting plants will favour differentiation (Silvertown 2004). In consequence, invaders with niches distinct from those of the native flora should be able to coexist in invaded communities (Emery 2007, Funk et al. 2008), whereas invaders that are similar to established abundant species should experience greater competitive inhibition (Fargione et al. 2003). Accordingly, diversity decreases invasion via both sampling and complementarity effects (Fargione & Tilman 2005). Species diversity and functional diversity repel invasions and mitigate impacts of invasions (Elton 1958, Kennedy et al. 2002, Fargione et al. 2003, Maron & Marler 2007). In particular, functional diversity expressed as phenotypic divergence between native and invasive species contributes to the success of alien species (Ordonez et al. 2010). However, to the best of my knowledge it has not yet been explicitly addressed yet whether responses of invaders towards functionally diverse communities go beyond simple phenomenological "matches", but might also include evolutionary adaptations. Thus, addressing the hypothesis of the evolution of increased diversity compatibility is a conclusive implication for future research.

6.2 Multifactor considerations: The interaction approach

The framework presented so far has already put many of the so far-proposed hypotheses and mechanisms into a common perspective. However, the scheme suggested here has a much larger potential by identifying numerous, yet unrecognized hypotheses. In addition to the evolutionary shifts within the four main hierarchical levels mentioned in the previous chapters (Fig. 2), interactions across these main levels have to be introduced in the scheme to fully reach this potential. Naturally, this will turn the simple framework into one with considerable complexity. From an evolutionary point of view, all shifts from more favourable to less favourable environments or vice versa can only be expressed as trade-offs. These trade-offs can also be formulated across hierarchies, i.e. as long as they include the opposing directions as exemplarily depicted by arrow-headed lines in Fig. 3. Favourable conditions within one hierarchical level might be traded-off by unfavourable conditions within another level, and these relationships could be inversed. High resource levels, e.g., can, in theory, compensate for high enemy loads and support the evolution of defence structures, whereas low resource levels, in turn, need to be alleviated by lower impact of enemy load to allow for invasions. Invasions into more stressful situations, in consequence, need to be purchased at the expense of adaptations to released situations at another level. Following Silvertown (2005, p. 147), "[...] every organism is subject to trade-offs that prevent it from excelling in every way in every environment.". Many of such trade-offs have been accounted for in appropriate hypotheses and theories in invasion biology, in particular those related to biotic interactions, but not all of them have been addressed so far.

6.2.1 Interactions with climate

Situations of climatic mismatch between simulated and observed distributions often gave rise to the assumption that other than climatic factors are involved (Pearson & Dawson 2003). Indeed, hypotheses on climate-resource interactions (CR-IA, Fig. 3) have rarely been proposed. Some few examples borrowed from global change experiments in the context of plant invasions might hint at trade-offs between climatic scenarios and the level of biotic interactions.

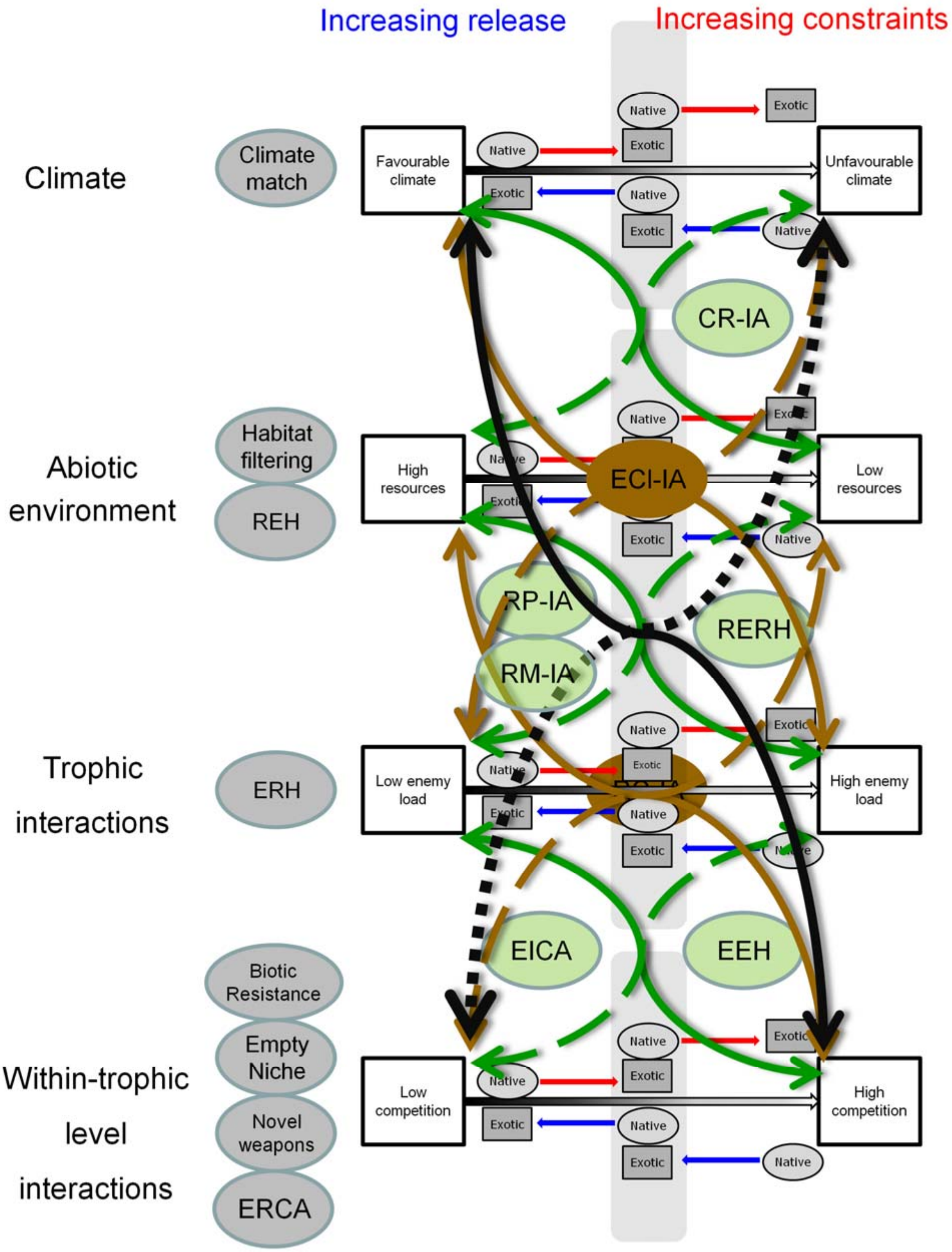

Fig. 3: Model on trade-off relationships across hierarchical levels of changing selection factors during invasions.

Fig. 3 (cont.): The basic setting within hierarchical level is equivalent to the one given in Fig. 1. Green lines describe interacting trade-offs between two adjacent hierarchical levels, brown lines relate trade-off relationships across two hierarchical levels, and black lines interrelate trade-offs across three hierarchical levels. Solid and dotted lines represent the direction of environmental differences in the invasion, i.e. towards more favourable and unfavourable conditions, respectively. Oval text forms represent assignment of current invasion hypotheses raised to their respective position in the present model. Grey ovals indicate within-level hypotheses; green ovals indicate hypotheses related to trade-offs between neighbouring hierarchical levels, brown ovals depict hypothesis related to trade-offs across two hierarchical levels. CR-IA = Climate-Resource-Interaction, ECl-IA = Enemy Release – Climate Interactions, EEH = Enemy-of-my-Enemy Hypothesis, EICA = Evolution of Increased Competitive Ability, ERCA = Evolution of Reduced Competitive Ability, ERH = Enemy Release Hypothesis, RC-IA = Resource-Competition-Interaction, REH = Resource Enrichment Hypothesis, RERH = Resource-Enemy Release Hypothesis, RM-IA = Resource-Mutualist Interaction, RP-IA = Resource-Pathogen-Interaction.

Blumenthal et al. (2008) simulated increased snowfall scenarios at different nutrient levels in North American mixed grass prairie. The authors found increased abundance of invasive forbs with increasing winter precipitation through increased recruitment, still being positively reinforced by increased nutrient availability, thus reflecting combinations confined to the left hand side of Fig. 3. Combining levels in opposite directions would allow testing for compensating effects of more beneficial climatic conditions with severed resource situations at the same time, something which has not been done yet to my knowledge. Similarly, the extent as to which more beneficial nutrient conditions in a new range might allow to afford adaptation to less favourable climatic conditions would be a promising hypothesis to be tested.

Further examples of climate-related interactions are provided for climate x biotic relationships. As summarized by Mitchell et al. (2006), introduction to a new region may influence a plant’s biotic interactions not only directly through the gain and the loss of enemies, mutualists and competitors, but also indirectly by putting interactions with the same species in a different environmental context. For example, the release from herbivores and pathogens might be related to latitude effects during range expansions. While low latitude plant provenances are supposed to be adapted to experiencing higher consumer pressure and, thus, to invest more into defence, high latitude regions are generally characterised by lower consumer loads. Increased invasiveness following the predictions of the enemy release hypothesis (ERH, Table 1) can, thus, additionally have a macroclimatic background. This idea was recently discussed as key feature of intracontinental range expansion in the context of climate warming (Morriën et al. 2010; Fig. 3, ECl-IA: enemy release-climate interaction). In her meta-analysis on the role of co-evolution on divergent selection, Laine (2009) emphasised that the variability in a co-evolving interaction could be induced by abiotic factors that determine the extent of co-evolutionary processes. Thereby, selection trajectories may be reversed from high to low temperatures. As an example of such a trophic co-evolution the pollinating long-tongued fly (*Prosoeca ganglbaeri*) and its floral host plant (*Zaluzianskya microsiphon*) may serve. The relationship between these two organisms is constrained by climate as the development of the fly's proboscis is retarded at low temperatures and strong winds impede flight activities at high altitudes (Anderson & Johnson 2008). However, such co-evolution of trophic interactions with climate are worth being studied in an evolutionary invasion context.

As known from climate change research, temperature changes can modify host physiology and resistance, where increased temperature stress increases pathogen susceptibility of host plants (Coakley et al. 1999). Accordingly, most host-parasite systems are predicted to experience more intensive disease impacts with warming or, alternatively, when transferred to warmer climatic settings during invasions. However, release from disease will also occur for some hosts with warming (Harvell et al. 2002; Fig. 3, ECl-IA). These types of opposing directions of climate-pathogen interactions can be predicted to allow shifts in allocation patterns that support invasive spread.

6.2.2 Interactions with abiotic factors

A couple of theories have already addressed the trade-offs between abiotic factors and counteracting biotic factors, and those related to resource-enemy load are among the most often tested ones. In an experimental approach, DeWalt et al. (2004) reduced enemy densities in the native and in the invasive range of *Clidemia hirta* and tested for differential effects of both high and low light environments on establishment success. The results suggested that fungal pathogens limit the growth of *C. hirta* in its native range, and that this effect strongly relies on habitat characteristics, as it is expressed only under conditions of reduced light environments (DeWalt et al. 2004; Fig. 3, RP-IA: Resource-Pathogen interaction). Double constraints in form of low-resources combined with high enemy load control the spread of *C. hirta* in the native range, while, reduced enemy load in the new range seems to have triggered the colonization of unfavourable low light resource habitats. Blumenthal (2005) was among the first who suggested that resource availability and enemy release may interact in successful invasions and accordingly formulated the resource-enemy release hypothesis (RERH) (Blumenthal 2006; Fig. 3). In his review, Blumenthal (2006) summarized that invasive species adapted to high resource levels in their native range may be those species that gain most from a putative enemy release in the new range. The author predicted that exotic species would have a greater advantage over native species in high- compared to low-resource environments. In that context, the evolution of increased invasiveness would be most important for species with manifold constraints, i.e. those that are simultaneously well defended and adapted to low resource levels. Accordingly, combined effects of high resource supply and loss of pathogens, viruses and fungi, can be expected (Blumenthal et al. 2009; Fig. 3), since plants adapted to high resource levels are particularly susceptible to pathogens. For example, Mitchell et al. (2003)

found elevated CO_2 and nitrogen addition (i.e. an increase in abiotic resources), to increase foliar nitrogen concentration and, in return, to enhance pathogen infection. Accordingly, Blumenthal et al. (2009) predicted plants adapted to high resource levels in their native range likewise to experience above average release effects in the new range.

Abiotic-biotic interactions with evolutionary dimensions are also related to resource-mutualist interactions (Fig. 3, RM-IA). One possibility to overcome the loss of mycorrhizal dependency in the above cited example of *Hypericum perforatum* invasion (Seifert et al. 2009), includes the idea that higher soil nutrient availability in the new range has acted as a selective force in facilitating nutrient acquisition via fungi, accompanied by a shift in root morphology.

Abiotic-biotic interactions can also be conceived to affect the role of plant diversity on invasion resistance of a community. Despite some examples of co-varying influence of the environment on invasibility and community performance (Davies et al. 2007, Maron & Marler 2007), there is no evidence on whether evolutionary aspects are involved. Wardle et al. (2008) particularly underlined the importance of context-dependency when studying invasion resistance as a function of plant diversity. The authors found effects of functional group loss at the plot level to be largely dependent on the ecosystem studied, which, in their example, differed in soil fertility and productivity. In their field study with local colonizing species, removal of shrubs increased invasibility on islands with more productive habitats more than on islands with less productive ones, whereas the loss of mosses increased colonization at less productive sites. Similar effects have been shown for native competitor identity experiments displaying interacting effects with resource availability on invasion resistance of communities (Thomsen & D'Antonio 2007, Going et al. 2009).

Many of these examples provide evidence of enforced invasion resistance in situations with simultaneous shortages in resource availability and intensity in competition. However, experimental settings that allow for conclusions on trade-off situations are missing. Testing for differential effects of functional group or competitor presence or absence in different abiotic contexts and with native and exotic provenances, would allow deducing the extent as to which evolutionary shifts might imply niche breadth adaptation during invasions (Fig. 3, RC-IA).

6.2.3 Interactions with biotic factors

The most comprehensive and elaborated work on adaptive across-hierarchy shifts during invasions has been provided to date for theories on evolutionary components of biotic relationships that relate shifts at the trophic interaction level to shifts at the within-trophic interaction level. The evolution of increased competitive ability (EICA, Table 1) hypothesis is a hypothesis (Blossey & Nötzold 1995, Maron & Vilà 2001, Bossdorf et al. 2004) that most appropriately runs the trade-off between reduced costs in enemy regulation and increased investment in vegetative growth and reproduction (Fig. 3). Several studies examining EICA have provided evidence for a loss of defence in introduced populations, and some of these have demonstrated coincidence with increased growth and reproduction (see Bossdorf et al. 2005 for an overview), thus supporting the evolutionary dimension of release leading to a change in energy allocation. Accordingly, in a common garden-experiment we found (Beckmann et al. 2011d [14]) that release from herbivory on organs of clonal growth might play an important role as a form of enemy release and a driver for post-introduction evolutionary change. In contrast, despite evidence of enemy release in the new range increased growth in the invading populations does not necessarily have to occur at the expense of loss of defences (Genton et al. 2005). Further views imply the enemy-of-my-enemy hypothesis (EEH, Colautti et al. 2004, Table 1). This concept describes mutualism – competition interactions for situations in the exotic range where natural enemies have a stronger effect on native competitors than on the exotic invader (Fig. 3, EEH). Other prominent examples relate to indirect interactions among plants being mediated by soil microbes and were summarized as the effect of biogeography on plant interactions (see examples provided in Thorpe et al. 2011). The authors suggested that biogeographical differences in the effects of allelochemicals have outstanding roles as drivers of evolution.

7 Concluding remarks and outlook

While numerous trade-offs combining release and constraints within and across hierarchic levels have been identified, further levels of factor interactions have been left open. In particular, trade-offs related to biotic levels have resulted in appropriate hypotheses, but directional trade-offs within other hierarchical levels have been neglected so far. In addition, the consistent differentiation of the direction of changes as release and constraints within hierarchical factors suggests a couple of putative trade-off relationships that are urgently worth being studied.

The previous screening suggests consistently taking evolutionary shifts for several hierarchical factors as trade-offs into account. Efforts to uncover evolutionary shifts in plant invasions should, thus, in particular consider:

1. Links between climatic range shifts and losses and gains of adaptations, i.e. to compare native and invasive populations with distinct climatically divergent niches.
2. Links between abiotic shifts and losses and gains of adaptations, i.e. to compare native populations with invasive populations being successfully introduced into different regions with different levels of resource supply.
3. Studies on how adaptation can contribute to overcome losses of facilitation in the new range, i.e. to explicitly test for the evolutionary role of mutualist compensation.
4. Studies on the evolutionary dimension of invader's response to diverse communities, which might be a suitable explanation for sudden increase in exotic abundance.

The consistent enlargement and application of this view to other hierarchical factors and their interactions suggest several trade-off relationships that need to be focused on. In parallel to the EICA hypothesis, one can easily expand the enemy release hypothesis to predict the evolution of increased invasiveness, e.g. expressed as the evolution of enhanced climate niche breadth or the evolution of broader nutrient niches at lower levels of enemy load. However, accordingly, one can also assume increased climate niche breadth at given higher resource levels, as well as broader resource niches at lower levels of biotic regulation within trophic levels.

Some recent studies have picked out such interaction effects as a central theme of scale-related effects (Diez et al. 2009, Milbau et al. 2009). Reconciling the relationships between invasion success and species richness at different spatial scales, e.g., was brought about by Shea & Chesson (2002) by consulting increasing variation of extrinsic factors at broad spatial scales. However, I would argue that "scale" as term is dispensable, since hierarchically organized filters represent "scale" by definition (Gurevitch et al. 2011). Using terms of basic ecology that properly describe the mechanistic relationships, one can easily pass on to refer more specifically to ecological processes which are hidden behind “scale”. Referring to the present framework of interacting factors should help doing so.

Part B

Publications and manuscripts

1 Multi-species approaches testing for functional differences

[1] Bachmann D., Both S., Bruelheide H., Ding B.-Y., Gao M., Härdtle W., Scherer-Lorenzen M. & **Erfmeier A.** (2011): Functional trait similarity of native and invasive herb species in subtropical China – environment-specific differences are the key (unpublished). (BEF-China)

[2] Both S., Fang T., Baruffol M., Schmid B., Bruelheide B. & **Erfmeier A**. (2011): Effects of tree sapling diversity and nutrient addition on herb-layer invasibility in young experimental communities of subtropical species (submitted). (BEF-China)

[3] **Erfmeier A.** (2011): Divergent, but climatic context dependent responses of grasses and herbs following experimental environmental change (re-submitted following Major Revision)

Aims and hypotheses

Three multi-species studies were conducted to test for generalizability of species, traits and functions according to their grouping by status (native vs. invasive species) or by functional groups (herbs vs. grasses). Given the evidence that the importance of species traits varies with the environmental abiotic and biotic conditions encountered, these studies evaluate the roles of resource availability, biodiversity and climatic context for uniformity of species' groups performance. Using the platform of the biodiversity–ecosystem functioning project (BEF-China, Bruelheide et al. 2011), we conducted two studies investigating exotic species performance and components of biotic control for their establishment. In a first study, we compared each 15 exotic invasive and 15 native herb species of resource-rich ruderal habitats in subtropical China with regard to their morphological and physiological trait performance under different experimental environmental conditions in the greenhouse, accounting for both environmental and temporal variation in these traits [1]. In a second study including a seed addition experiment with a subset of eight of the previously tested exotic species, we studied diversity x invasibility relationships in a common garden attempt in subtropical China, separating components of diversity according to strata in young experimental early-successional forest plots [2]. In a third study, I summarised results of repeated field-site common garden comparisons conducted with grasses and herbs of Central German dry grasslands by meta-analytical means to quantify the role of inter-annual climatic variability on differential performances of traits and functional groups [3].

Main conclusions

With regard to the filter levels applied (given in Fig. 2), the present studies mostly refer to effects of the climatic filter and the abiotic environment, thus, these are examples of studies on the climate match and habitat filtering hypotheses (see Table 1) at the species level. Most explicitly, the third study emphasised that interactions between environmental change and prevailing climatic conditions differentially affect the performance of species groups (CR-IA, Fig. 3). Despite the notable differences in the study systems used, a common outcome was the ambiguity encountered in experiments to summarize patterns and mechanisms when combining species in groups of interest. All studies agree in recommending careful interpretation of summarizing attempts and emphasise the risk of ignoring important sources of covariation.

- We found strong overall trait similarities when comparing fundamental abiotic niches of native and exotic species comparable in growth form and habitats of occurrence; i.e. native and invasive species did basically not differ in fundamental niches. [1]
- Fundamental niche analyses displayed superiority of invasive over native species only provided under favourable conditions, namely beneficial light conditions as expressed in increased growth rates. This pattern suggests an opportunistic strategy for exotic species, and underlines strong overall abiotic context-dependency of superior performance. [1]
- Although the number of exotic species establishing in experimental young successional forest plots was reduced in situations of enhanced nutrient availability, fertilizer addition enhanced individual performance of exotics by increasing height and productivity, thus confirming opportunistic strategy of exotic species encountered. [2]
- Negative impacts of species presence in tree layers were similar for both native and invasive herb species, thus supporting the theory that co-varying factors mask mechanistic relationships in diversity x invasibility relationships during invasions. [2].
- Multispecies comparisons of realized vs. fundamental niche contrasts displayed different responsiveness between functional groups of grasses and herbs in variables of performance, with grasses showing higher correspondence between these niche types than herbs. [3]
- However, the magnitude of differences between niche types increased in study years with high precipitation and decreased in years with high mean temperatures and accordingly affected interpretations of differences between functional groups. The outcome of experimental comparisons between groups was largely affected by the climatic context of the setting and, thus, calls for careful interpretation of the validity of diverse responses encountered. [3]

Functional trait similarity of native and invasive herb species in subtropical China – environment-specific differences are the key

Dörte Bachmann[1,2], Sabine Both[1], Helge Bruelheide[1], Bing-Yang Ding[3], Mo Gao[4], Werner Härdtle[5], Michael Scherer-Lorenzen[6] and Alexandra Erfmeier[1]

[1] Martin Luther University Halle-Wittenberg, Institute of Biology / Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle, Germany; [2] current address: ETH Zurich, Institute for Agricultural Sciences, Universitaetsstrasse 2, 8092 Zurich, Switzerland; [3] Department of Biology, College of Life and Environmental Sciences, Wenzhou University, Wenzhou, Zhejiang, 325035, China; [4] Department of Biology, College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou, Zhejiang, 310036, China; [5] Institute of Ecology and Environmental Chemistry, University of Luneburg, Scharnhorststr.1, 21335 Luneburg, Germany; [6] Faculty of Biology, Geobotany, University of Freiburg, Schaenzlestr. 1, 79104 Freiburg, Germany

Author for correspondence: Dörte Bachmann, E-mail: doerte.bachmann@ipw.agrl.ethz.ch, Tel: +41 44 632 5871, Fax: +41 44 632 11 53

Abstract

The attempt to identify traits associated with plant invasions has revealed ambiguous results. Accounting for environmental and temporal variation in multispecies trait comparisons of native and exotic species might help explain such inconsistency. The relative importance of light and nutrient availability was tested in a greenhouse experiment with 15 native and 15 exotic herb species from Southeast China. In addition, N uptake and its temporal pattern were assessed by means of a 15N tracer experiment. A predominant lack of significant differences between the two status groups indicated strong overall trait similarities. However, at high light levels, the exotic species displayed significantly higher trait relative growth rates, whereas the native species had a higher tissue quality. The invasion success of the exotic species could neither be explained by a general higher N uptake nor by a distinction in temporal N uptake strategy. Despite comparable fundamental niches of the species, increased growth rates under beneficial light conditions may provide a head start advantage for exotic species compared to native ones. The present study confirms the assumption of an opportunistic strategy for exotic species and emphasizes the need to assess trait variation between native and exotic species in different environmental contexts.

Keywords

Environmental context, exotic species, fundamental niche, N uptake, resource allocation.

Effects of tree sapling diversity and nutrient addition on herb-layer invasibility in young experimental communities of subtropical species

Sabine Both[1]*, Teng Fang[2], Martin Baruffol[3], Bernhard Schmid[3], Helge Bruelheide[1] & Alexandra Erfmeier[1]

[1]Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, D-06108 Halle (Saale), Germany; [2]Gutianshan National Nature Reserve, Zhejiang, 324306 China; [3]Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

*Correspondence author: Sabine Both; E-mail: sabine.both@botanik.uni-halle; telephone: ++49-345-26199; fax: ++49-345-27228

Abstract

Exotic species are assumed to alter ecosystem functions, however, little is known about such relationships within vertically structured plant communities like forests where especially in the early phases of forest succession tree saplings of various species interact with herbaceous species. We addressed this issue experimentally by quantifying the mutual impact of tree saplings and herbaceous species under nutrient addition and the invasion of exotic herb species. We established a common garden experiment in South-East China using four broad-leaved tree species (*Elaeocarpus decipiens, Schima superba, Castanea henryi* and *Quercus serrata*) to study the relationships between tree sapling diversity and herb-layer productivity as well as invasibility.

Tree saplings were planted in monocultures, 2- and 4-species mixtures. A full-factorial design was applied in which the species compositions were crossed with fertilizer- and exotic seed-addition treatments. For the latter, mixtures of seeds from eight exotic herb species were used. Herb community attributes were assessed after a 4-month growing season. Our results indicated that certain tree species negatively affected native as well as exotic species, however, high productivity of native herbs had a stronger negative impact on exotic species than did tree saplings. Nutrient addition increased the productivity of exotic but not native herbs. Remarkably, exotics but not native herbs caused a negative feedback on the growth tree saplings.

This outcome emphasized the potential of exotic herbs to diminish tree recruitment. Although tree saplings reduced the invasion of the herb-layer by exotic species during the studied earliest phase of forest succession, nutrient addition had a more profound effect on these invaders.

Keywords

BEF-China; early-successional communities; exotic seed-addition; fertilizer application.

Divergent, but climatic context dependent responses of grasses and herbs following experimental environmental change

Alexandra Erfmeier*, Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle, Germany

Correspondence: Dr. Alexandra Erfmeier; Institute of Biology / Geobotany and Botanical Garden; Martin Luther University Halle-Wittenberg; Am Kirchtor 1; 06108 Halle, Germany; alexandra.erfmeier@botanik.uni-halle.de

Abstract

While climate change experiments have shown that altered drought and precipitation levels affect temperate grassland productivity, less attention has been paid to the role of inter-annual climatic variability on community responses and on performances of traits and functional groups to these treatments. I used meta-analytical techniques to combine results from a 5 yrs study of repeated field site–common garden comparison with grasses and herbs of Central German dry grasslands. The aim was to quantify differences in performance between these groups expressed under realized constrained situations in the field vs. optimal growing conditions in the common garden by taking the co-varying influence of climatic variables into account. Effect sizes were calculated for size variables, growth rates, allocation and fitness by study year. Negative mean effect sizes, indicating worse performance at the field site compared to the common garden, were found for root biomass and lateral expansion. For most of the variables, effect sizes were higher for grasses than for herbs, thus, displaying better relative performance of grasses at the field sites; however, there was no significant difference between groups in allocation and leafrelated traits. Effect sizes of biomass and fitness variables increased with increasing precipitation but decreased with higher mean temperatures, i.e. the difference between field site and common garden was more evident in dry and warm years. In addition, effect sizes of herbs and grasses responded differently to increasing levels of the covariates. As a conclusion, experimental environmental change differently affected the functional groups with worse performance of the herb species under field conditions and with different responses depending on the climatic context of the study year. Accounting for these differences in global vegetation models can improve predictions on shifts in plant communities and functioning under climate change.

Keywords

Dry grasslands; effect sizes; functional groups; inter-annual climatic variability; meta-analysis; porphyric outcrops; repeated transplant experiment.

2 The evolutionary dimension – the role of genetic diversity

[4] **Erfmeier A.** & Bruelheide H. (2011): Maintenance of high genetic diversity during invasion of in the British Isles. International Journal of Plant Sciences 172 (6): 795-806. DOI: 10.1086/660194.

[5] **Erfmeier A.**, Tsaliki M., Roß C.A. & Bruelheide H. (2011d): Genetic and phenotypic differentiation between invasive and native *Rhododendron* (Ericaceae) taxa and the role of hybridization. Ecology and Evolution (in press).

[6] Hantsch L., Bruelheide H. & **Erfmeier A.** (2011): Phenotypic plasticity and genetic diversity jointly promote the invasiveness of an annual weed (submitted).

[7] **Erfmeier A.**, Hantsch L., Bruelheide H. (2011b): The role of propagule pressure, genetic diversity and microsite limitation for *Senecio vernalis* invasion (to be re-submitted following Major Revision)

Aims and hypotheses

Four case studies were consulted to deal exemplarily with the role and mechanisms of the maintenance of genetic diversity and phenotypic variation during invasions of two colonizing species in Europe. Two studies refer to comparisons of native and invasive provenances of *Rhododendron ponticum* and further, closely related *Rhododendron* taxa. *Rhododendron* is an example of a long-lived, insect-pollinated and woody plant invader of the Ericaceae, aggressively expanding in Atlantic Western Europe. The second study system, in contrast, refers to an annual ruderal plant species of the Asteraceae, *Senecio vernalis*, invading disturbed habitats in Central Europe.

In the first study, we studied changes in genetic diversity and differentiation of *Rhododendron ponticum* in comparing each six populations native in Georgia, in Spain, and invasive in Ireland with AFLP (amplified fragment length polymorphism) markers to trace the putative region of origin and to test the hypothesis of maintenance of high genetic diversity in the invasive range [4]. The second study, then, explicitly pursued the objective to test for evidence of introgressive hybridisation in invasive *R. ponticum* populations with North American congeneric taxa, based on molecular (AFLP), morphological and ecological data gained in a set of experiments with a total of 30 populations [5]. The third study brings within-invasive range patterns of genetic diversity and phenotypic variation in *Senecio vernalis* into focus and aims at analyzing the proportion of variance components in seed traits and germination as well as in genetic diversity ranging from the seed family level, the population level to the habitat type [6]. Finally, the last study in this section refers to seed addition experiments with seed mixtures of different levels of genotypic diversity and thus experimentally quantifies the role of genetic diversity for establishment of *S. vernalis* in relation to two major components favouring invasion success: propagule pressure and microsite limitation [7].

Main conclusions

All four studies underline that the maintenance of genetic diversity both at large geographic scale as well as at small scales of local populations and within populations seems to be an inherent feature of successful plant invasions for the species studied. While the mechanisms of maintenance might differ across species, high levels of genetic diversity, in all cases, provide the basis on which selection can operate, thus allowing for new adaptations in the invasive range. Conclusions derived from these singles studies, apart from the main awareness of high diversity, are related to presumable within-abiotic level shifts according to the framework constructed (Fig. 2): in particular, for *R. ponticum,* responses to more beneficial conditions in terms of increased availability of resources and / or climatic release can be consulted to meet the hypotheses of habitat filtering, climate match and resource enrichment hypothesis (REH; Fig. 3, Table 1).

- For *Rhododendron* ponticum, we found a within-native range differentiation in measures of genetic diversity, but no further reduction in genetic diversity in the invasive range. Overall, there was only low within-country genetic differentiation between populations, most presumably because of a multiple introductions to the invasive range and due to high levels of gene flow among populations. [4]
- We confirmed the assumption of a mainly Spanish provenance of invasive Irish populations. [4]
- Hybridisation with North American *R. catawbiense* and *R. maximum* did not contribute to explain invasiveness of *R. ponticum* in Ireland. Phenotypic similarity in size variables and germination between invasive *R. ponticum* and North American *R. catawbiense* has to be considered as independent. [5]
- Increased germination and high relative growth rates of Irish *R. ponticum* can only be attributed to a genetic shift within *R. ponticum* from native to invasive ranges. [5]
- Given the evidence of phenotypic differentiation in quantitative variables, we concluded that maintained genetic diversity in *R. ponticum* is a prerequisite to meet divergent selection regimes in the new range. [4,5]

- For *Senecio vernalis*, highest variation in seed traits and in genetic diversity was found within populations, thus, accordingly warranting a high probability of matching different and unpredictable habitats. [6]
- However, in contrast to *R. ponticum* this high variation in *S. vernalis* and the high potential for natural selection to act on has not yet been translated into differentiation in reproductive traits between habitat types. [6]
- We found experimental evidence that early life stages of *S. vernalis* were differentially affected by genetic diversity, with initial abundance being most decisively governed by propagule pressure while being independent of the genetic diversity of seed charges. In contrast, individual performance of established individuals was increased in seed mixtures with increased genetic diversity. [7]
- Mechanistic effects of genetic diversity on invasiveness of *S. vernalis* seemed to be most strongly linked to sampling effects in the mixtures and less to diversity effects per se. [7]

Maintenance of high genetic diversity during invasion of *Rhododendron ponticum*

Alexandra Erfmeier[1],* and Helge Bruelheide*

Correspondence: Institute of Botany/Geobotany and Botanical Garden, Martin Luther University Halle, Am Kirchtor 1, D-06108 Halle, Germany

Abstract

Adaptive processes in invasive plant populations may explain exotic range expansions and ecotypic shifts between native and invasive populations of the same species. Sufficient genetic variation in invasive populations occurring within the new range is a precondition for selection. While genetic diversity can be considerably reduced during invasions following founder effects and genetic drift, it can also be maintained via mechanisms of effective gene flow. *Rhododendron ponticum* L., an aggressive invader in the British Isles, is an appropriate test species for investigating changes in genetic diversity and differentiation. Six native populations in Georgia and Spain each and six invasive populations in Ireland were analyzed with amplified fragment length polymorphism markers to calculate genetic distances, genetic diversity, and differentiation within and among populations. While the highest level of genetic diversity was found within native Georgian populations, thus indicating a refugium, native Spanish and invasive Irish populations showed reduced levels of genetic diversity but displayed no further reduction in the invasive range. Genetic differentiation within countries was weak. Spanish and Irish populations showed close relationships supporting a probable Spanish provenance for the invasive *Rhododendron*. We suggest that the preservation of sufficient genetic variation in invasive *R. ponticum* populations in Ireland has been vital to the species' adaptation to new environmental conditions.

Keywords

AFLP markers, exotic species, genetic variation, native and invasive range, population structure, refugial area.

Genetic and phenotypic differentiation between invasive and native *Rhododendron* (Ericaceae) taxa and the role of hybridization

Alexandra Erfmeier[1,*], Marina Tsaliki[2], Christel A. Roß[1] and Helge Bruelheide[1]

[1]Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, D-06108 Halle; [2]Vegetation Ecology and Conservation Biology, Institute of Ecology and Evolutionary Biology, Bremen University, Leobener Str., D-28359 Bremen

Correspondence: Alexandra Erfmeier, Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany. E-mail: alexandra.erfmeier@botanik.uni-halle.de

Abstract

Hybridization has been repeatedly put forward to explain the invasiveness of *Rhododendron ponticum* L. in the British Isles. The present study investigates the pattern of ecotypic differentiation and hybridization among native North American *R. catawbiense* and *R. maximum*, native *R. ponticum* from Georgia and Spain, and invasive *R. ponticum* from Ireland and aims to assess the contribution of hybridization for *Rhododendron* invasion in the British Isles. Six populations per taxon were analyzed with AFLP markers for genetic dissimilarity, subjected to germination and growth experiments, and tested for frost hardiness.We assessed variation in morphological and ecological characteristics to identify traits displaying evidence of hybridization, thus, promoting invasiveness. Molecular marker analyses revealed a clear distinction between North American *R. catawbiense* and *R. maximum* on the one hand, and all *R. ponticum* populations on the other hand, displaying a complete intermixture of native Spanish and invasive Irish populations.Multivariate analyses of traits revealed leaf length–width ratio, relative growth rates (RGRs) in leaf length, root biomass, and shoot–root ratio to significantly discriminate between the different taxa and unequivocally assigned invasive Irish *R. ponticum* to the Spanish phenotypes.

While the Irish *R. ponticum* had similar growth traits as conspecific native *R. ponticum* provenances, germination and biomass allocation were more similar to North American *R. catawbiense* and *R. maximum*.Hybridization did not contribute to explaining invasiveness of *R. ponticum* in Ireland. The similarity in germination and biomass allocation of invasive Irish *R.*

ponticum and North American species has evolved independently and can more probably be attributed to an independent shift within the Ponticum cluster in Ireland.

Keywords

AFLP, frost hardiness, germination, introgression, RGR, *Rhododendron* section *Pontica*.

High phenotypic variation of seed traits and germination characteristics of an invasive annual weed

Lydia Hantsch*[1], Helge Bruelheide[1] and Alexandra Erfmeier[1]

[1]Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Germany

*Corresponding author: Lydia Hantsch, Am Kirchtor 1, 06108 Halle (Saale), E-mail: lydia.hantsch@botanik.uni-halle.de, Tel. +49 345 5526240, Fax + 49 345 5527228

Abstract

Both phenotypic and genetic variation can affect the establishment success of exotic species. Using the annual weed *Senecio vernalis* that was introduced to Central Europe from Southwest-Asia, we asked to which degree seed traits and germination patterns differ among different habitat disturbance types in the introduced region. We hypothesized that seed traits, maximum germination rate and germination speed differ between more and less disturbed habitats and that high phenotypic variation in these characteristics as well as high genetic variation is mainly encountered within the population level, thus enabling the offspring of any population to colonize different habitat disturbance types. We tested these hypotheses by sampling individuals from 19 populations of different habitat disturbance types in Central Germany and analysed variability and differentiation in seed traits, germination success by means of a germination experiment as well as patterns of genetic variation and genetic differentiation using AFLP markers. Contrary to our expectation habitat disturbance types did not influence patterns in seed trait variation, germination rates and genetic variation rather. Instead we found highest phenotypic and genetic variation within populations. Germination rates were positively affected by seed mass and there was a distinct association between AFLP band patterns with population size and seed width, indicating that some variation in seed traits has a genetic component. In conclusion, high variation in seed traits, overall high germination rates and a high genetic variation within populations contribute to the wide range of habitat disturbance conditions where *S. vernalis* is growing and likely ontributes to the species' invasion success.

Keywords

AFLP, exotic weed, germination ecology, population structure, seed traits, *Senecio vernalis.*

The role of propagule pressure, genetic diversity and microsite availability for *Senecio vernalis* invasion

Alexandra Erfmeier*, Lydia Hantsch and Helge Bruelheide

Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle Wittenberg, Am Kirchtor 1, 06108 Halle, Germany;

*For correspondence. E-mail alexandra.erfmeier@botanik.uni-halle.de, Tel. +49 345 5526230, Fax + 49 345 5527228

Abstract

Background and Aims Genetic diversity is supposed to support the colonization success of expanding species, in particular in the face of microsite limitation. Addressing the role of genetic diversity in plant invasion experimentally requires manipulation of genetic diversity independent of propagule pressure.

Methods To assess the relative importance of these components for the invasion of *Senecio vernalis*, we created propagule mixtures of four levels of genotype diversity by combining seeds across remote populations, across proximate populations, within single populations and within seed families. In a first container experiment with constant *Festuca rupicola* density as matrix, genotype diversity was crossed with three levels of seed density. In a second experiment, we tested for effects of establishment limitation and genotype diversity by manipulating *Festuca* densities.

Key results Increasing genetic diversity had no effects on abundance and biomass of *S. vernalis* but positively affected log size ratios. Mixtures composed from proximate populations had a significantly higher proportion of large individuals than mixtures composed from within seed families only. High propagule pressure increased emergence and establishment of *S. vernalis* but had no effect on individual performance. Establishment was favoured in containers with *Festuca*, but performance of surviving seedlings was higher in open soil treatments.

Conclusions For *S. vernalis* invasion, we found a shift in driving factors from density dependence to effects of genetic diversity across life stages. While initial abundance was mostly linked to the amount of seed input, genetic diversity, in contrast, affected later stages of colonization probably via sampling effects and seemed to contribute to filtering the genotypes that finally grew up. In consequence, when disentangling the mechanistic relationships of genetic diversity, seed density and microsite limitation in colonization of invasive plants, a clear differentiation between initial emergence and subsequent survival to juvenile and adult stages is required.

Keywords

Asteraceae, diversity levels, establishment success, genotype diversity, microsite limitation, container experiment, propagule pressure, seed mixtures, seed addition experiment, *Senecio vernalis*.

3 Native-invasive populations – field comparisons

[8] Beckmann M., **Erfmeier A.** & Bruelheide H. (2009): A comparison of native and invasive populations of three clonal plant species in Germany and New Zealand. Journal of Biogeography 36: 865-878.

[9] Beckmann M., Bruelheide H. & **Erfmeier A.** (2011a): Populations of six clonal invaders compared between native and invasive regions in Germany and New Zealand. (submitted).

[10] **Erfmeier A.** & Bruelheide H. (2010): Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive *Rhododendron ponticum* populations. – Biological Invasions 12: 657-676. DOI: 10.1007/s10530-009-9472-x.

Aims and hypotheses

These three studies were assembled to point out that field comparisons at a biogeographical scale are useful tools to identify patterns of shifts from native to invasive ranges. Two studies refer to multispecies approaches of native-invasive range comparisons for clonally growing plant species of grasslands in Germany and New Zealand in search for patterns of within-population shifts in allocation. Field surveys on native and invasive *Hieracium pilosella*, *Achillea millefolium* and *Hypericum perforatum* populations were conducted to quantify hypothesized increased performance in life-history traits for invasive occurrences. In particular, we aimed to identify shifts in trade-offs between growth and reproduction across ranges by distinguishing levels of observations, thus explicitly recording responses at the individual and at the population levels [8]. Another field campaign was designed to increase generalizability of differences in native and invasive comparisons by including a total of six clonal species with ten populations each as within-country replicates and with a higher resolution of recording levels to test for overlooked differentiation through simplified measuring procedures [9].

The third study explicitly approaches phenotypic differentiation within one study species, *Rhododendron ponticum*, in the field and attempts to relate this differentiation to a driving factor of environmental differences encountered between ranges [10].

Main conclusions

Patterns of increased performance in the invasive range seem to be a common feature of plant invasions. However, the measures of responses differ remarkably between species, even when comparing similar species of comparable life forms in common habitats. Differences identified in these biogeographical field comparisons, such as shifts in reproduction modes encountered need to be related to environmental changes along the gradient from favourable to unfavourable environments, or vice-versa (Fig. 2).

- We found significant effects of increased performance at the population level with higher population densities, higher proportion of flowering plants and higher seed bank densities in the invasive range when compared to native populations. However, individual performance was less affected than expected and contradicts the general assumption that invasive individual necessarily grow taller or produce more biomass [8].
- Increased performance was apparently attributable to different growth strategies even within groups of comparable species: while two of the study species displayed increased clonal production in the invasive range, in contrast, e.g. *Hieracium pilosella* profited from increased sexual reproduction when compared to native occurrences. [8]
- Attempts with more species, more population replicates and observations at finer levels of resolution, distinguishing between population level, neighbourhood level and individual level, revealed substantial differences in population structures between species and ranges. These results call for carefully choosing measures of responses when comparing native and invasive occurrences, as one runs at the risk of ignoring important differences between species (and thus indices of shifts among ranges) by simplifying and generalizing procedures of data collection. [9]
- Attempts quantifying abiotic environmental differences between native and invasive ranges displayed high relevance of more favourable climatic conditions and increased resource supply for growth and establishment of *Rhododendron ponticum* in its invasive range when compared to sites in the native range. These findings suggest environmental release as explanation for increased vigour. [10]
- However, the results of transplantation experiments of native and invasive provenances into one common garden situation within the invasive range suggest that the environmental release has, additionally, been translated into evolutionary responses expressed as genetically based differentiations, in particular including the abandonment of adaptations to previous selection pressures and constraints. [10]

A comparison of native and invasive populations of three clonal plant species in Germany and New Zealand

Michael Beckmann*, Alexandra Erfmeier and Helge Bruelheide

Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

*Correspondence: Michael Beckmann, Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany. E-mail: michael.beckmann@botanik.uni-halle.de

Abstract:

Aim Our aim was to test for changes in growth patterns of three clonally growing plant species (*Achillea millefolium*, *Hieracium pilosella* and *Hypericum perforatum*) between native and invaded regions. We addressed the hypotheses that with differing important life-history traits, invasive populations perform better than native populations, and that this expected better performance is linked to weakened trade-offs between individual growth and sexual and clonal reproduction.

Location Germany and New Zealand.

Methods We conducted field surveys for the three above-mentioned species in both native German and invasive New Zealand populations, and collected data at both population and individual levels.

Results At the population level, the proportion of flowering plants, population size and population density were all higher in invasive populations. Similarly, at the individual level, the number of stolons per plant, stolon–biomass ratio and population crowdedness (local plant density in a specified area around a target plant) were significantly higher in New Zealand. Plant height did not differ between countries, and plant biomass was lower in New Zealand than in Germany for *Achillea millefolium* and *Hypericum perforatum*. These two species showed significant trade-offs between individual growth and sexual and clonal reproduction. *Achillea millefolium* exhibited a weakened trade-off in its invaded range, where the same proportion of flowering plants was sustained at much higher levels of population crowdedness than in its native range.

Main conclusions The apparent invasion success of the three study species is generally due to better overall performance in their respective invaded ranges. In respect of both *Achillea millefolium* and *Hypericum perforatum*, this is driven primarily by increased vegetative reproduction. In contrast, *Hieracium pilosella* seems to benefit more from increased sexual reproduction in its invaded range. Shifts in trade-offs as a general trend seem to be of minor importance.

Keywords

Achillea millefolium, biological invasion, Germany, *Hieracium pilosella*, *Hypericum perforatum*, life history, New Zealand, reproductive traits, trade-off, vegetative reproduction.

Populations of six clonal invaders compared between native and invasive regions in Germany and New Zealand

Michael Beckmann*, Helge Bruelheide & Alexandra Erfmeier

Address: Martin Luther University Halle-Wittenberg; Institute of Biology / Geobotany and Botanical Garden; Am Kirchtor 1; 06108 Halle, Germany

*corresponding author: michael.beckmann@botanik.uni-halle.de; phone: +49 345 5526198; fax: +49 345 5527228

Abstract

Most research on plant invasions is based on the assumption that invasive species occur at higher abundances in their introduced range than in their native range. However, only few studies have validated this assumption in comparative field studies. Changes in sexual and clonal reproduction have been observed in successful plant invaders and are known to affect species abundances at different scales. Here we present the results of a comparative field study on six clonal plant species in their native (Germany) and introduced (New Zealand) ranges: *Achillea millefolium*, *Hieracium pilosella*, *Hypericum perforatum*, *Prunella vulgaris*, *Leucanthemum vulgare* and *Lotus pedunculatus*. We tested if the investigation of population structures at different scales provides a useful tool to consistently identify differences between native and introduced populations. At the population scale, we assessed population density and flowering proportion; at the neighborhood scale, we determined plant densities, at the individual scale we counted the number of clonal organs and measured biomass. At the neighborhood scale we detected higher densities in NZ populations of all six species. Additionally, in NZ populations, population density was higher in four species and the production of clonal organs was higher in three species. Variables associated with sexual reproduction were higher in native, German populations of *Achillea millefolium*, *Hieracium pilosella*, *Hypericum perforatum* and *Leucanthemum vulgare*. We conclude that substantial differences in population structures between native and introduced populations can be found at different scales. Acknowledging these differences might help to identify problematic species and to prioritize management efforts.

Keywords

Achillea millefolium, biological invasion, Germany, *Hieracium pilosella*, *Hypericum perforatum*, *Leucanthemum vulgare*, *Lotus pedunculatus,* New Zealand, *Prunella vulgaris*, reproductive traits, vegetative reproduction.

Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive *Rhododendron ponticum* populations

Alexandra Erfmeier, Helge Bruelheide

Institute of Biology, Department of Geobotany and Botanical Garden, Martin Luther University Halle, Am Kirchtor 1, D-06108 Halle

Correspondence: Alexandra Erfmeier; Tel. +49 345 5526230; Fax +49 345 27228; e-mail alexandra.erfmeier@botanik.uni-halle.de

Abstract

Biological invasions are affected either by the invaders‘ genotypes, by the suitability of the new habitat or by genotype-habitat interactions expressed in adaptations to the new environment. The relevance of these factors was assessed for the invasive evergreen shrub *Rhododendron ponticum*. Habitat characteristics of soil, climate and community properties were analysed in six native populations in both Georgia (Caucasus) and Spain and in six invasive ones in Ireland. Growth variables of rhododendron individuals and seedling occurrences in the field served as response variables. We performed a reciprocal transplant experiment with rhododendron cuttings and determined survival of transplants in all countries. Due to low survival rates in Georgia and Spain, vegetative increase was only analysed for Ireland. The Irish sites showed a significantly higher nutrient supply than the Spanish and Georgian sites. We found both strong positive correlations of nutrient supply and negative correlations of seasonal temperature amplitude with growth variables of shoots and seedling density. Origin, target site and interaction effects were significant in the survival of transplanted rhododendron individuals. The Irish site was the most favourable one for all genotypes, but the invasive genotypes did not perform better than the native ones. The total increase in shoot length of transplants in Ireland was the highest in the Irish genotypes, which might suggest adaptation of the Irish populations to their new area. As a conclusion, we found evidence for invasiveness of invasive *Rhododendron ponticum* populations, but only in the invaded habitat. Nonetheless, the habitats in the new range seem to be very suitable for native Spanish populations, too, supporting the idea that invasibility of these new sites also contributes to explaning rhododendron invasion success.

Keywords

Biometry, genotype-by-environment interaction, invasive traits, reciprocal transplant experiment, regional adaptation, release hypothesis, resource availability, survival rates.

4 Experimental evidence for genetic shifts

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[12] Beckmann M., Hock M., Bruelheide H. & **Erfmeier A.** (2011c): The role of UV-B radiation in the invasion of *Hieracium pilosella* - a comparison of German and New Zealand plants. Environmental and Experimental Botany (accepted 16.09.2011). DOI: 10.1016/j.envexpbot.2011.09.010.

[13] **Erfmeier A.**, Böhnke M. & Bruelheide H. (2011a): Secondary invasion of *Acer negundo* – A shift in strategies from reproduction towards persistence? Biological Invasions 13(7): 1599-1614. DOI: 10.1007/s10530-010-9917-2

[14] Beckmann M., Bruelheide H. & **Erfmeier, A.** (2011d): Reduced tolerance to herbivory on clonal organs in alien genotypes – a multi-species experiment with native and introduced origins. (submitted)

[15] **Erfmeier A.**, Klein S., Welk E. & Bruelheide H. (2011c): Native and invasive populations in common environment experiments – A meta-analysis with chorological predictors (unpublished).

Aims and hypotheses

The studies joined and arranged in this chapter all provide experimental approaches testing for evidence of genetic shifts during invasions. These examples either comprise experimental comparisons of native and invasive provenances under controlled conditions in common gardens, greenhouses and growth cabinets or more explicitly address the question of additional post-introduction differentiation favouring secondary invasion. Two investigations revisit the multispecies approaches conducted at the observational field level (see [8] and [9]) and test for evidence of genetic differentiation in germination patterns of clonal growing plant species from Germany and New Zealand. The first study explicitly addresses presumable shifts in traits of early life history stages and tests for genetic shifts in germination responses between ranges [11]. The second study uses experimental environmental manipulation in light quality and attempts to assess the probability of different UV-B levels between ranges of the northern and the southern hemisphere for being a driver of adaptive differentiation [12]. Genetic evidence of habitat type-dependent different performance of invasive *Acer negundo* populations within the species' invasive range was picked out as a central theme in the third study, thus, elucidating the relative importance of different stages in invasions [13]. A fourth study represents an experimental multi-species approach with native and invasive provenances of clonal plant species simulating herbivory on clonal organs and different patterns of spatial nutrient supply. This study explicitly accounts for interaction effects between herbivory on clonal organs and foraging strategies [14]. The final study, in conclusion, provides a meta-analysis on experimental comparisons of native and invasive populations published so far to provide evidence for the generalisability of genetic shift during plant invasions and to address its context-dependency by testing for co-varying effects of climatic niche differences and study type [15].

Main conclusions

There is profound evidence for an evolutionary dimension during invasions both, in comparing native and invasive ranges as well as for ongoing post-introduction evolution evoking additional differentiation within invasive ranges. In particular, the evidence of interacting forces being involved in drivingdifferentiation across ranges allows for a better understanding of evolution during invasions. This finding can be integrated in the frame outlined as one example that supports the resource-enemy release hypotheis (RERH, Fig. 3), thus accounting for trade-offs between levels of biotic and abiotic factors. This awareness calls for integrating more than just simple one-directional drivers of differentiation into frameworks on evolution during plant invasions.

- We found increased responses in maximum germination in two out of the three study species, and increased germination velocity in invasive provenances of all three species investigated, thus confirming the hypothesis of a shift in germination for *Hypericum perforatum*, *Hieracium pilosella* and *Achillea millefolium* in parts of its invasive range if compared to populations native in origin. [11]
- These findings suggest a genetic shift in germination strategies, in particular in characteristics of germination timing, in the new range in response to altered climatic and/or abiotic conditions. [11]
- We found evidence that different levels of UV-B radiation between ranges can affect the role of adaptation and phenotypic plasticity durng plant invasions. UV-B radiation may, therefore, act as an environmental filter upon introduction on the species- as well as on the genotype-level. [12]
- While both native and invasive provenances displayed typical stress responses towards increased UV-B treatments, invasive provenances of *Hieracium pilosella* differed from native provenances in altered leaf traits performances which suggest a suitable predisposition for coping with increased stress in response to altered radiation intensity. However, the evidence of adaptation still needs experimental confirmation. [12]

- Reduced germination velocity was found to be realized in invasive populations of *Acer negundo* originating from dry habitat types which have only started being colonized during the last decades. In comparison to populations from moist habitats, dry origins also displayed increased leaf life span as evidenced in a reciprocal transplant experiment across habitat types, hinting at a shift in life history strategy. [13]
- In conclusion, we found support for the idea of change in the relative importance of species traits during invasions, thus allowing for post-introduction and secondary invasion into more constrained habitats following ongoing adaptations. [13]
- Experimental multi-species comparisons with provenances of six clonal plant species displayed broad evidence for a shift towards reduced tolerance to herbivory on clonal organs in the invaded range consistently applying to all species tested. [14]
- In particular, invasive provenances have proven to be more effective in capturing resources in the absence of herbivory by increasing the production of clonal organs. This study explicitly supports the hypothesis of interacting effects between enemy release and nutrient availability to drive adaptive evolution and invasion in the new range in the face of heterogeneous conditions of resource availability. [14]
- Meta-analytical approaches summarizing growth responses of native and invasive populations across multiple common environment studies confirmed increased growth for invasive origins, thus, underlining the evolutionary basis of invasiveness. [15]
- We found evidence for climatic niche shifts to occur across native and invasive ranges for some of the invasive species tested. Thus, for some examples of successful plant invasions, the ability to cope with altered climatic conditions is, indeed, reflected in different climatic niches occupied between the ranges, suggesting genetic adaptation. [15]
- However, although being important in some invasions, the magnitude of climatic niche shifts did not per se account for additional variation encountered in the effect sizes calculated for common environment comparisons of native and invasive populations. In contrast, discovering evidence of genetic shifts strongly depended on the study type conducted, either being a greenhouse or a common garden study. [15]

Germination responses of three grassland species differ between native and invasive origins

Michael Beckmann, Helge Bruelheide and Alexandra Erfmeier

Corresponding author: Michael Beckmann; michael.beckmann@botanik.uni-halle.de; Institute of Biology / Geobotany and Botanical Garden; Martin Luther University of Halle Wittenberg; Am Kirchtor 1; 06108 Halle, Germany; phone: ++49 345 5526240; fax: +49 345 5527228

Abstract

The germination stage is critical in plant life history and is also a key process during the expansion of species' ranges into new environments. In this study we investigated the germination patterns of three plant species (*Achillea millefolium*, *Hieracium pilosella* and *Hypericum perforatum*) that are invasive to New Zealand (NZ) and native to Central Europe. We asked whether the species show differences in germination temperature requirements, germination speed and maximum germination rates, and thus, whether they display evidence of adaptation to different conditions in the invasive range. Seeds from three populations per species and region were subjected to three different temperature regimes to compare germination rates among origins and across temperature conditions. For *Achillea millefolium* and *Hypericum perforatum*, germination rates were significantly higher for invasive NZ provenances than for native German ones. Seeds from invasive populations of all three species displayed increased maximum germination at medium temperature conditions when compared to native populations, which indicates altered germination strategies in the invaded range. Changes in temporal development patterns were most conspicuous for invasive *Hieracium pilosella* and *Hypericum perforatum* populations. These findings imply that adaptation in germination patterns towards different climatic conditions in invasive populations has occurred. Our study emphasises the importance of the germination stage during plant invasion and its role in explaining range expansion of these species.

Keywords

Biological invasion, germination rates, germination velocity, *Achillea millefolium*, *Hieracium pilosella*, *Hypericum perforatum*.

The role of UV-B radiation in the invasion of *Hieracium pilosella* - a comparison of German and New Zealand plants

Authors: Michael Beckmann*, Maria Hock, Helge Bruelheide & Alexandra Erfmeier

*corresponding author: michael.beckmann@botanik.uni-halle.de, phone: +49 345 5526198, fax: +49 345 5527228; Address: Martin Luther University of Halle-Wittenberg, Institute of Biology / Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle, Germany

Abstract

Intensity of ultraviolet-B radiation (UV-B) differs between northern and southern hemispheres. Therefore, exotic plants species that originate from the northern hemisphere provide an opportunity to study the effects of UV-B on plant physiology and growth, and their implications for the role of adaptation and phenotypic plasticity during plant invasion on the southern hemisphere.

We conducted a growth-chamber experiment with and without UV-B on *Hieracium pilosella* plants from Germany, where the species occurs natively and New Zealand (NZ), where it is invasive. We tested the hypothesis that: (i) *H. pilosella* plants respond to UV-B with high phenotypic plasticity, demonstrating the ability to react to changes in UV-B, and (ii) NZ plants are better adapted to UV-B than German plants as a result of directional selection of well adapted phenotypes.

Consistent with our first hypothesis *H. pilosella* plants reacted plastically to UV-B by producing longer foliar hairs and a higher leaf dry matter content (LDMC) when they were treated with UV-B regardless of their origin. Additionally, irrespective of the treatment, plants from NZ displayed a higher LDMC and grew less but longer leaves than German plants.

Plants showed typical stress responses and a reduction in growth caused by the UV-B treatment: below-ground biomass and production of ramets were reduced when plants were treated with UV-B. *H. pilosella* proved to be particularly well predisposed to grow in areas of high UV-B radiation.

Our findings hint at the necessity to consider UV-B radiation in future research on mechanisms of invasions in regions with high UV-B irradiation. Species that provide the ability to respond directly to UV-B might have an advantage to invade these areas. As UV-B intensity is likely to change in the future due to ongoing ozone depletion, research addressing the effects of UV-B during plant invasions is of increasing importance.

Keywords

Adaptation, biological invasions, global change, *Hieracium pilosella*, phenotypic plasticity, ultraviolet radiation.

Secondary invasion of *Acer negundo* – The role of phenotypic responses versus local adaptation

Alexandra Erfmeier, Martin Böhnke and Helge Bruelheide

Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, D-06108 Halle

Correspondence: Alexandra Erfmeier; Tel. +49 345 5526230; Fax +49 345 27228; e-mail alexandra.erfmeier@botanik.uni-halle.de

Abstract

During plant species invasions, the role of adaptive processes is particularly of interest in later stages of range expansion when populations start invading habitats that initially have not been disposed to invasions. The dioecious tree *Acer negundo*, primarily invasive in Europe in wet habitats along riversides and in floodplains, has increased its abundance in dry habitats of industrial wasteland and ruderal sites during the last decades in Eastern Germany. We chose 21 invasive populations from wet and from dry habitats in the region of Halle, Saxony-Anhalt, Germany, to test whether *Acer negundo* exhibits a shift in life-history strategy during expansion into more stressful habitats. We analyzed variables of habitat quality (pH, soil moisture, exchangeable cations, total C and N content) and determined density, sex ratio and regeneration of the populations. In addition, we conducted germination experiments and greenhouse studies with seedlings in four different soil moisture environments. Local adaptation was studied in a reciprocal transplant experiment. We found habitat type differentiation with lower nutrient and water supply at the dry sites than at the moist sites and significant differences in the number of seedlings in the field. In accordance, seeds from moist habitats responded significantly faster to germination treatments. In the transplant experiment, leaf life span was significantly larger for populations originating from dry habitat types than from moist habitats. This observed shift in life history strategy during secondary invasion of *A. negundo* from traits of establishment and rapid growth towards traits connected with persistence might be counteracted by high gene flow among populations of the different habitat types. However, prolonged leaf life span at dry sites contributed remarkably to the invasion of less favourable habitats, and, thus, is a first indication of ongoing adaptation.

Keywords

Germination velocity, leaf life span, ecotypes, reciprocal transplant experiment, RGR, secondary phase of invasion.

Reduced tolerance to herbivory on clonal organs in alien genotypes – a multi-species experiment with native and introduced origins

Michael Beckmann*†, Helge Bruelheide† & Alexandra Erfmeier†

*corresponding author: michael.beckmann@ufz.de, UFZ – Helmholtz Centre for Environment Research, Department of Computational Landscape Ecology, Permoserstraße 15, 04318 Leipzig, Germany, phone: 0049-341-235-1946, fax: 0049-341-235-1939

†Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle Wittenberg, Am Kirchtor 1, 06108 Halle, German

Abstract

1. Clonal growth has been suggested to increase the likelihood of plant species to become invasive in a new environment. Being an efficient foraging strategy, clonal growth may be advantageous in habitats of heterogeneous nutrient availability often encountered during plant species invasions. Enemy release and EICA hypotheses predict post-introduction evolutionary change in favour of genotypes that invest less resources into defence and more into vigour and reproduction.

Here we investigated the effect of herbivory on organs of clonal growth and its potential to drive post-introduction evolutionary change.

2. In a common-garden experiment we compared plants from native German and naturalized New Zealand (NZ) populations of six plant species with different clonal growth forms and invasive status in NZ. We tested the hypothesis that loss of herbivory on organs of clonal growth has led to reduced tolerance to herbivory on organs of clonal growth in alien genotypes. In a directional nutrient treatment in combination with simulated herbivory on clonal organs we also tested for origin-dependent differences in sexual reproduction, plant growth and the production of clonal organs.

3. Across all species, NZ plants were less tolerant to simulated herbivory on clonal organs than German plants. Without simulated herbivory, NZ plants grew more clonal organs in the direction of the provided nutrients than German plants. With additional herbivory treatment this response inverted in favour of German plants that then produced more clonal organs.

4. *Synthesis:* We interpret the results of this study as evidence for post-introduction evolutionary change as an outcome of a release from herbivory on clonal organs. The consistency of the results

over six independent species that differ in forms of clonal growth and invasive status underlines the importance of evolutionary changes in clonal growth as an important driver in plant invasions. Additionally, our results might help explain the globally observed pattern that clonal species contribute a large proportion among successful invaders.

Keywords: *Achillea millefolium* L., clonal growth, enemy release, Germany, *Hieracium pilosella* L., *Hypericum perforatum* L., *Leucanthemum vulgare* Lam., *Lotus pedunculatus* Cav., New Zealand, nutrient foraging, plant invasions, *Prunella vulgaris* L.

The role of climatic niche shifts and study type for phenotypic differentiation – A meta-analysis on native and invasive population comparisons in common environment studies

Alexandra Erfmeier[1*,] Simone Klein[1], Erik Welk[1] & Helge Bruelheide[1]

Institute of Biology/ Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany; E-mail: alexandra.erfmeier@botanik.uni-halle.de, simone.klein@student.uni-halle.de, erik.welk@botanik.uni-halle.de, helge.bruelheide@botanik.uni-halle.de

*Corresponding author: Alexandra Erfmeier, Martin Luther University Halle-Wittenberg, Institute of Biology / Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle, Tel. +49 345 5526230; Fax +49 345 27228; e-mail alexandra.erfmeier@botanik.uni-halle.de

Abstract

The multitude of common environment experiments to test for differences in native and invasive populations have often provided inconsistent results, which can be explained by ignoring important sources of covariation. We conducted a metaanalysis on 37 common environment experiments with 27 invasive species and calculated standardized effect sizes for the response traits growth and size separately for greenhouse and common garden studies as well as for studies located in the native or invasive area. Putative climatic niche shifts between native and invaded ranges were quantified and related to effect sizes in order to analyze their impact on plant performances.

The results confirmed previous findings of increased growth of invasive populations, while the location of the experiment in either the native or the invasive range displayed no significant effect. Study type turned out to be of particular importance, as superiority of invasive populations in aboveground biomass and individual plant height was only detectable in common garden but not in greenhouse situations. Climatic niche shifts were confirmed for some species, while the magnitude of niche shift had no effect on differences in plant performance. Pre-adaptation to climatic factors seems to be of low importance for explaining differences between native and invasive populations.

Keywords

Meta-analysis, common garden, invasive plant species, native and invasive range, principal component analysis, between-class analysis, climatic niche shift.

Closing remarks

In 50 years of research in invasion biology (Richardson & Pyšek 2008) much has been achieved, yet, much is still unexplored. This statement is certainly also appropriate for this thesis. The importance of genetic diversity, the multitude of traits in which genetic differentiation can be expressed has already been explored in great detail. For future research, the most pressing part is to consistently quantify the trade-offs between hierarchical factors. Without any doubt, it can be assumed that relationships between these factors are even more complex than pictured in the presented framework that integrates two-fold interactions at the most. In consequence, one can still quest for more sophisticated explanations including three-fold (or more) interactions. However, at the moment, it is a particular challenge to study trade-offs integrating biotic interactions, given the difficulties to manipulate these interactions in simple common garden experiments. A promising approach for future research would be to apply the presented framework to large scale cooperative research projects in which biotic interactions have been manipulated (tree diversity experiments, climate change experiments, trophic interaction experiments etc.), and to study trade-offs across these different settings. Personally, I believe that investment in exploring the evolution of macroclimate niche breadth in response to altered resource levels and testing the resource-enemy release hypothesis for further resource-biotic trophic level interactions is the most rewarding line of invasion research. Linking questions of plant invasions with experimental research on climate change scenarios can make a valuable contribution to the understanding of biotic-abiotic interactions.

Another aspect is to consider how trade-offs at the community level might scale up to the properties at the ecosystem or biome level. Traits involved in the fundamental acquisition/conservation trade-off in an invaded community, for example, might scale up to components of carbon and nutrient cycles at the ecosystem level (Chapin 1993, Lavorel & Garnier 2002, Wright et al. 2004). Following this line of research would provide a link between evolutionary invasion biology and practical conservation biology.

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Summary

The present thesis describes a set of studies performed to identify and to comprehend the evolutionary background of plant invasions using several study organisms and approaches. Methodologically, these studies a) refer to comparisons at the species level being classified in native and invasive species or functional groups, b) examine the preconditions of maintaining genetic and phenotypic variation for successful invasions, c) integrate within-species comparisons at the observational level across native and invasive ranges and within the invasive range, and finally d) include experimental and meta-analytical approaches to discover evidence of evolutionary shifts.

Multi-species comparisons of native and invasive species and of functional groups have agreed on the idiosyncrasy of successful invasions and suggest that a more explicit accounting for the context-dependency of the studies is advised. This applies similarly to attempts that try to generalize pattern and mechanisms of evolutionary within-species differentiation. Many examples have proven that mechanisms to maintain high genetic and phenotypic diversity are effective during invasions, thus, preconditions for contemporary evolution are often met. In addition, there is evidence for biogeographical differences in native and invasive plant performance at the observational level. Experimental and summarizing approaches to identify the evolutionary dimension have demonstrated that adaptive adjustments do occur during plant invasions. However, as a conclusion a consistent frame that integrates the context-dependency against an evolutionary background and that accounts for the covariation of factors is still lacking.

One such frame is presented in a review-like summary and suggests to account for the direction of environmental changes. Applying the filter theory of species sorting, the present thesis considers different filters at different scales explaining evolutionary changes during invasions. This hierarchical approach focuses on the filters climate, abiotic environment and biotic environment, thereby distinguishing trophic interactions and within-trophic level interactions. The thesis summarizes the evidence of adaptive shifts from native to exotic ranges and differentiates the direction of shifts from either constrained or released situations. A second step focuses on interacting effects of hierarchical factors on adaptive evolution during invasions by highlighting examples of trade-off situations across hierarchical levels. More beneficial situations with regard to one factor acting as filter may afford adaptation to less favourable situations with regard to other factorial levels. While some of these trade-offs have already been coined and confirmed in repeatedly tested hypotheses, others have not been explicitly addressed to date.

Following this systematic approach, the present thesis identifies further trade-offs within- and across-hierarchical levels that complement already existing hypotheses for biotic interactions. In doing so, the present thesis points at current gaps and suggests research attempts that try to enhance the understanding of context-dependency in invasions. In particular, the role of climatic changes should more explicitly be linked with evolutionary responses during invasions. Studying successfully invading exotic species in several regions with different environmental conditions will be a promising starting point to enlarge the understanding of context-dependency of invasions.

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Curriculum vitae

Personal data

Name: Alexandra Erfmeier

Address (office): Institute of Botany / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany, Tel.: +49-(0)345-5526230
alexandra.erfmeier@botanik.uni-halle.de

Date / place of birth: 10.05.1971, in Lünen, Germany
Nationality: German

Education

04/2004	Ph.D. University of Göttingen, Germany "Invasion of *Rhododendron ponticum* L. on the British Isles: The role of habitat and genotype"
05/1998	Diploma Biology, University of Göttingen, Germany "Vegetation and soil conditions along a climatic gradient in the Harz Mountains: Beech forests with diabase bedrock"
10/1991 – 5/1998	Studies of Biology (Botany, Ecology, Zoology, Soil sciences), University Göttingen
05/1990	Abitur (A-level)

Stay abroad

1990 - 1991	au-pair, Louveciennes, France

Academic positions and working experience:

Since 03/2004	*Research Scientist* at the Institute of Biology / Geobotany and Botanical Garden, MLU Halle-Wittenberg
2000 to 2003	*Research assistant* Department of Plant Ecology, University of Göttingen
1999 to 2000	*Research fellow* at the Department of Plant Ecology, University of Göttingen
1998 to 1999	*Assistant lecturer* and *Research associate* at the Dep. of Plant Ecology and Dep. of Systematic Botany, University of Göttingen

Further activities

Since 2004	Workshops on training of gender equality in academia (gleichstellung *concret* GBR)

Grants and Awards:

1999 Postgraduate grant of the University of Göttingen

Activities as reviewer

Applied Vegetation Science, *Australian Journal of Botany*, *Basic and Applied Ecology*, *Biological Invasions*, *Biology and Environment*, *Botany*, *Ecological Informatics*, *Ecological Modelling*, *International Journal of Plant Sciences*, *Journal of Biogeography*, *Journal of Vegetation Science*, *Plant Biology*, *Plant Ecology and Diversity*

Membership in scientific societies:

- Ecological Society of Germany, Austria, Switzerland, Liechtenstein (GfÖ)
- Floristisch-Soziologische AG e.V. (Flor.-Soz.)

Principal research interests

- Invasion biology
- Population ecology
- Community ecology
- Biodiversity & ecosystem functioning.

(Alexandra Erfmeier)

Erklärung zur vorgelegten schriftlichen Leistung

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