Plant species origin, herbivory and disturbance: effects on seedling recruitment and consequences for grassland diversity and productivity

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„Wohl ist alles in der Natur Wechsel,
aber hinter dem Wechselnden ruht ein Ewiges.“

Johann Wolfgang von Goethe

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Summary

Biodiversity is determined by various interacting processes such as dispersal and seed limitation, herbivory, disturbance and biological invasions. Understanding these processes is challenging, but crucial for the maintenance of biodiversity and the provided ecosystem functions. In this regard, biodiversity experiments gained important insights into the mechanisms driving biodiversity and ecosystem functioning (e.g. productivity), raised fundamental ideas and theories. However, the knowledge gained from these experiments needs to be further expanded to natural ecosystems, to different plant origins and higher trophic levels. For example it is not clear how generalist herbivory by different herbivore guilds, interacts with disturbance to determine seedling recruitment of exotic and native plant species belonging to different functional groups and what the consequences are for community diversity and productivity. Moreover, current knowledge about the impact of, and the mechanisms behind biological invasions is mostly derived from studies concentrating on single species and sites and rarely tested effects across multiple species and multiple sites to derive general rather than species- or site-specific effects.

This thesis aims to gain a more complete understanding of the different processes such as seed and dispersal limitation, herbivory, disturbance and biological invasions in shaping biodiversity and ecosystem functioning of today´s ecosystems across different spatial and temporal scales. Specifically, I focused on these two research questions:

(1) How do herbivory and disturbance influence seedling recruitment of exotic compared to native plant species and how context-dependent are these effects?
(2) How does native vs. exotic plant origin impact diversity and productivity of grassland communities and how do herbivory and disturbance mediate these community responses?

I studied these processes with four comparative multi-species experiments ranging from a i) mesocosm-study, ii) complex full-factorial single-site experiment, to a iii) multi-site experiment within two regions (California, Germany) and iv) multi-site experiment within three regions (Montana, California, Germany). This approach enabled me to assess general differences between exotic and native species with respect to the different processes, but also to evaluate the context-dependency and generalizability of these effects. With respect to my research questions I obtained the following important findings:

(1) Across all experiments disturbance enhanced invasion opportunities for exotic plant species, while generalist herbivory generally decreased the recruitment success. Within a full-factorial experiment where I studied the effects of rodent herbivory, gastropod herbivory, disturbance and species origin at a single site with specific environmental conditions, generalist herbivory, disturbance and plant origin determined the rate of seedling recruitment. Specifically, gastropod herbivory reduced the positive effect of disturbance, while rodent herbivory indirectly alleviated the negative effect of resident competition on exotic compared to native species. Notwithstanding this, native and exotic seedling recruitment did not differ in response to generalist herbivory, if responses were averaged across multiple sites covering a broad range of environmental conditions. Consequently, generalist herbivores suppress recruitment of – thereby mediating resistance against – both native and exotic plant species. Together these findings imply that differential degree of herbivory may explain failures of exotic plants in certain contexts, but appears not to be the rule across various environmental conditions.

(2) Seed addition generally increased species richness and productivity, indicating that grassland communities were constrained by seed and dispersal limitation. Consistently across my studies I revealed that added exotic and native species differed in the magnitude they affected biomass production in plant communities. The introduction of exotic species resulted in higher biomass production compared to native species, which suggests the existence of differences between native and exotic species in the processes driving the relationship between diversity and productivity. I tested the latter in a mesocosm experiment in the greenhouse and found that exotic and native communities indeed differed in the processes driving the diversity-productivity relationship. However, opposing results from other studies exotic communities were governed by a larger complementarity effect, while native communities showed a larger selection effect. Trophic interactions (i.e. slug herbivory) contributed to differences in diversity effects because of differential feeding on functional groups, in monocultures vs. mixtures and in exotic vs. native communities. With respect to herbivory, the importance of functional group affiliation was also indicated in other studies of this thesis. For example, rodents preferred feeding on legumes with a high nutritional value, while gastropods fed on herb seedlings that were likely less defended. Thus, characteristics linked to nutritional value, resistance and tolerance are more important determinants of generalist herbivory than plant species origin. Seed addition generally increased species richness and productivity, indicating that grassland communities were constrained by seed and dispersal limitation.

Finally, the significance to include multiple sites with a large range of environmental conditions was demonstrated by differences in magnitude – thus context-dependency – of generalist herbivory and disturbance in determining the extent to which exotic vs. native species altered species richness, abundance and productivity in grassland ecosystems. For instance, in Germany and California disturbance allowed higher productivity of exotic vs. native species while rodents mediated resistance and reduced this positive effect on productivity. In Montana no effect of rodent herbivory on productivity was observed but disturbance allowed more exotic than native species to colonize.

In conclusion, the findings of this thesis imply that across studies exotic and native species generally differ in their way they impact ecosystems, but do not show differences in response to generalist herbivory. Furthermore the results of my thesis suggest that the search for general processes and mechanisms, e.g. in invasion biology, not only requires the consideration of multiple species but the incorporation of their responses to various processes along multiple sites with varying environmental conditions. Employing experiments that take these issues into account may unravel the discrepancy between results of different studies. Moreover it can provide the opportunity for a more complete understanding of the processes driving biodiversity and functioning in ecosystems.

Zusammenfassung

Die Biodiversität von Ökosystemen wird durch zahlreiche Prozesse wie Samen- und Ausbreitungslimitierung, Herbivorie, Strörungen und biologische Invasionen beeinflusst. Aufgrund der Komplexität ihrer Zusammenhänge ist es schwierig ein umfassendes Verständniss dieser Prozesse zu erlangen. Jedoch kommt letzterem eine große Bedeutung für den Erhalt der Biodiversität und der damit verbundenen Ökosystemfunktionen zu. Biodiversitäts-Experimente haben bereits einen großen Beitrag zum Verständniss der Zusammenhänge zwischen Biodiversität und Ökosystemfunktionen, wie der Produktivität, geleistet; dennoch kann dieses Wissen eweitert und ergänzt werden indem es auf natürliche Ökosysteme übertragen wird, Wechselwirkungen mit höheren trophischen Ebenen einbezogen und „Invasionen" exotischer Arten berücksichtigt werden. So ist beispielsweise unklar, wie sich generalistische Herbivorie unterschiedlicher Gilden, Störung und die Herkunft von Arten (exotische im Vergleich mit heimischen Arten) unterschiedlicher funktioneller Gruppen auf die Keimlingsetablierung auswirkt und welche Konsequenzen sich hieraus für die Produktivität und Biodiversität von Grünlandgemeinschaften ergeben. Zudem basiert ein großer Teil unseres Wissens über die Schlüsselfaktoren, die biologische Invasion antreiben, sowie über deren Einfluss auf die Biodiversität und das Funktionieren von Ökosystemen auf Studien, die einzelne Arten und Untersuchungsflächen betrachteten. Um verallgemeinerungsfähige Aussagen über den Einfluss biologischer Invasionen und die zugrundeliegenden Prozesse treffen zu können, werden jedoch Studien benötigt, die eine Vielzahl von Pflanzenarten und Flächen untersuchen.

Die vorliegende Doktorarbeit hatte daher zum Ziel, den Einfluss von Ausbreitungs- und Samenlimitierung, Störung und Herbivorie auf die Keimlingsetablierung exotischer und heimischer Arten, sowie deren Auswirkungen auf die Biodiversität und Produktivität in Grünlandern, auf unterschiedlichen zeitlichen und räumlichen Skalen zu untersuchen. Im speziellen wurden folgende Fragestellungen untersucht:

(1) Wie wird die Keimlingsetablierung von exotischen und heimischen Arten durch Störung und Herbivorie beeinflusst und wie abhängig sind diese Ergebnisse vom jeweils betrachteten Kontext?

(2) Wie werden Diversität und Produktivität von Grünland-Ökosystemen von der heimischen im Vergleich zur exotischen Herkunft der Arten beeinflusst, und welche Rolle spielen Herbivorie und Störung bei der Vermittlung dieser Effekte?

Um diese Fragestellungen zu beantworten, führte ich vier unterschiedliche Experimente durch, in denen jeweils eine Vielzahl heimischer mit einer Vielzahl exotischer Arten verglichen wurde. Dies erlaubte mir verallgemeinerungsfähigere Aussagen in Bezug auf Herkunftseffekte. Zudem verwendete ich unterschiedliche Ansätze: i) ein Mesokosmen-Experiment, ii) ein komplexes vierfaktorielles Experiment auf einem Standort, iii) ein Experiment auf zahlreichen Flächen in zwei Regionen (Deutschland und Kalifornien) und iv) ein Experiment auf zahlreichen Flächen in drei Regionen (Deutschland, Kalifornien und Montana). Der zugrundeliegende Gradient zwischen Präzision und Verallgemeinerungsfähigkeit ermöglichte es mir, generelle von kontext-spezifischen Effekten zu unterscheiden.

(1) Generell erhöhte Störung die Etablierungschancen exotischer im Vergleich zu heimischen Arten, während Herbivorie diese verringerte. Betrachtet man die die Keimlingsetablierung auf einem Versuchsstandort mit spezifischen Umweltbedingungen, so wurden exotische und heimische Arten unterschiedlich von der Wechselwirkung zwischen generalistischer Herbivorie und Störung beeinflusst. Die stark von Störung profitierende Keimlingsetablierung exotischer Arten wurde stärker von Schneckenherbivorie unterdrückt als die der heimischen Arten. Umgekehrt führte der negative Einfluss von Kleinsäugerherbivorie auf die Produktivität ansässiger Pflanzenarten dazu, dass sich insbesondere exotische Arten in der ungestörten Vegetation etablieren konnten. Exotische und heimische Arten wurden in gleichem Maße von generalistischer Herbivorie beinflusst, wenn ihre durchschnittliche Reaktion auf zahlreichen Flächen mit unterschiedlichen Umweltbedingungen betrachtet wurde. Dieses Ergebnis weist darauf hin, dass insbesondere die Auswirkung generalistischer Herbivorie auf die Keimlingsetablierung stark davon anhängt, in welchem Kontext sie betrachtet wird und dass Unterschiede in generalistischer Herbivorie zwischen heimischen und exotischen Pflanzenarten keine allgemeingültige Erklärung für den Erfolg oder Misserfolg exotischer Arten darstellen.

(2) Die Einsaat von Pflanzenarten des regionalen Artenpools erhöhte sowohl die lokale Artenzahl als auch die Produktivität in den untersuchten Grünlandgemeinschaften, was auf eine Samen- und Ausbreitungslimitierung hindeutet. Des Weiteren zeigte sich, dass exotische und heimische Arten einen unterschiedlichen Einfluss auf die Produktivität und Biodiversität in

Grassländern hatten. Die Einsaat exotischer erhöhte die Produktivität stärker als die Einsaat heimischer Arten. Dieses verallgemeinerungsfähige Ergebnis meiner Arbeitet weist darauf hin, dass sich die Beziehung zwischen Diversität und Produktivität in heimischen und exotischen Grünlandgemeinschaften unterscheidet. In einem Mesokosmen-Experiment stellte ich fest, dass exotische und heimische Pflanzengemeinschaften in der Tat Unterschiede in den Biodiversitätseffekten aufweisen, welche die Beziehung zwischen Diversität und Produktivität steuern: entegen den Ergebnissen anderer Studien zeichneten sich exotische Gemeinschaften jedoch durch einen höheren Komplementaritätseffekt, heimische Pflanzengemeinschaften dagegen durch einen höheren Selektionseffekt aus. Allerdings wurden diese Unterschiede auch von den Fraßpräferenzen der Schnecken bezüglich der funktionellen Pflanzengruppen beeinflusst. Die Zugehörigkeit zu einer funktionellen Gruppe war auch in anderen Experimenten dieser Arbeit von Bedeutung; so präferierten Kleinsäuger Leguminosen, die dafür bekannt sind, besonders nahrhaft zu sein, während Schnecken vermehrt Keimlinge von Kräutern fraßen, die vermutlich eine geringere Resistenz gegen Herbivorie aufwiesen. Dieses Ergebnis weist darauf hin, dass Pflanzeneigenschaften wie Resistenz und Toleranz gegenüber Herbivorie sowie Nahrhaftigkeit das Ausmaß generalistischer Herbivorie steuern. In welchem Maße Herbivorie und Störung die Effekte heimischer und exotischer Einsaat auf die Diversität und Produktivität beeinflussten, hing stark von der betrachteten Region ab. Beispielsweise erhöhte Störung den Einfluss exotischer Einsaat auf die Produktivität, während Kleinsäugerherbivorie diesen veringerte. Dies war jedoch nur in Deutschland und Kalifornien der Fall, während in Montana einzig Störung einen positiven Effekt auf die Anzahl der sich etablierenden exotischen Arten hatte.

Zusammenfassend lässt sich sagen, dass sich der Einfluss exotischer und heimischer Arten auf die Produktivität von Pflanzengemeinschaften generell und unabhängig vom jeweiligen Kontext unterschied. Im Gegensatz hierzu war die jeweilige Reaktion exotischer und heimischer Arten auf generalistische Herbivorie kontextabhängig. Die Ergbnisse meiner Arbeit verdeutlichen, dass die Suche nach generellen Prozessen und Mechanismen in der Invasionsbiologie es erfordert, nicht nur eine Vielzahl von Pflanzenarten zu untersuchen, sondern auch ihre Reaktion auf einer größeren Anzahl von Flächen mit unterschiedlichen Umweltbedingungen zu berücksichtigen. Der Einsatz solcher Experimente könnte die Widersprüchlichkeit vieler Studien lösen und zu einem besseren Verständnis der Prozesse beitragen, welche die Biodiversität und das Funktionieren von Ökosystemen beinflussen.

Chapter 1

GENERAL INTRODUCTION

Biodiversity and ecosystem functioning

Understanding the complex interactions among processes affecting biodiversity and functioning of ecosystems is still a challenging goal in ecology. Comprehensive understanding of these interacting processes is, however, crucial to maintain biodiversity. Due to human alteration of the earth´s ecosystems biodiversity is declining at an alarming rate (Chapin III et al., 2000; Cardinale et al., 2012). Main drivers of this anthropogenic change in biodiversity are the increase in atmospheric carbon dioxide (CO_2), an increase in nitrogen (N) deposition, fragmentation of landscapes due to intensification of land use and habitat conversion, as well as biological invasions by exotic species (Sala et al., 2000). Based on the severity of impact on ecosystems the biodiversity decline itself is considered a main driver of global change and led to a debate about the consequences for ecosystem functioning inclusive of ecosystem services (Sala et al., 2000; Díaz et al., 2006; Hooper et al., 2012).

The question how biodiversity is linked to ecosystem functioning has been intensively studied using controlled experiments with artificially created and maintained plant communities (e.g. JENA experiment, Roscher et al., 2005; Cedar-Creek LTER experiment, Tilman et al., 1996; BIODEPTH projects, Hector et al., 1999). Most of these biodiversity experiments used grasslands as model systems and concentrated on primary productivity as it plays a major role in a wide range of ecological processes (Balvanera et al., 2006; Cardinale et al., 2011). The results of these experiments imply that the number of functional groups and/or species in grassland ecosystems is positively related to ecosystem functioning, e.g. productivity (Hector et al., 1999; Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2006). Two main, not mutually exclusive, processes are used to explain this positive connection between biodiversity and productivity (Loreau and Hector, 2001). First, the *selection effect* ascribes the higher productivity in mixture to the tendency for species interactions to "select for" or favor species with particular traits, e.g. high productivity (Hooper et al., 2005). Second, according to the *complementarity effect* higher productivity in mixture arises from niche differences among species leading to interspecific resource partitioning and facilitation (Tilman et al., 2001).

Although biodiversity experiments created tremendous insights into the mechanisms driving biodiversity and ecosystem functioning and raised fundamental ideas and theories (Balvanera et al., 2014), these experiments have their limitations:

- Artificially created and maintained biodiversity experiments may not sufficiently depict the environmental and biological complexity of real ecosystems. Thus, their relevance for natural ecosystems has been heavily debated (Huston, 1997; Loreau et al., 2001; Grace et al., 2007; Hautier et al., 2014). In natural grassland ecosystems, biodiversity and productivity are simultaneously influenced by various processes such as dispersal limitation, herbivory, disturbance or competition and biological invasions, acting separately or interactively at different spatial scales (Ritchie and Olff, 1999; Seabloom et al., 2003; Münzbergová and Herben, 2005; Zeiter et al., 2006; Duffy et al., 2007; Stein et al., 2008).

- Our understanding of biodiversity-ecosystem functioning is predominantly derived by manipulations of primary producers. So far, only rarely manipulations of trophic interactions have been integrated (but see, Duffy et al., 2007; Parker et al., 2010; Schnitzer et al., 2011; Eisenhauer et al., 2012; Cook-Patton et al., 2014). Yet, trophic interactions may shape or even drive the relationship between diversity and ecosystem functioning (Fox, 2003; Thébault and Loreau, 2003, 2005).

- Biodiversity experiments concentrated on the loss of native species but neglected the invasion by exotic species (but see e.g., Pfisterer et al., 2004) which are part of most nowadays ecosystems. Indeed, recent studies show for example that exotic dominated communities may exhibit different diversity maintenance mechanisms than native communities (Wilsey et al., 2009).

This thesis addresses these challenges and particularly focuses on the effect of biological invasions. It may thus contribute to our general understanding of the ecological processes and mechanisms that shape biodiversity and ecosystem functioning in grassland ecosystems.

Biological invasions

Biological invasions take place if species are intentionally or unintentionally introduced to areas outside their native range, establish and spread (Mack et al., 2000; Richardson et al., 2000). In the framework of this thesis I will focus on established *exotic* species – regardless of whether they are invasive or not. As exotics, I consider species introduced both, before 1492 (archaeophytes) and after 1492 (neophytes).

Biodiversity (hereafter referred to as *diversity*) and productivity of today's ecosystems is changing due to the expansion of invasive species (Chapin III et al., 2000; Sala et al., 2000; Vilà et al., 2011). Invaded communities frequently show a higher productivity than non-invaded communities (reviewed by, Liao et al., 2008; Gaertner et al., 2009; Ehrenfeld, 2010; Vilà et al., 2011; Pyšek et al., 2012). Conflicting results exist about the effect of invasions on diversity, likely due to differences in the impact of exotic species (Ortega and Pearson, 2005). Exotic plant invasions may enhance local species richness if they integrate into existing communities and co-exist with native species (Stadler et al., 2000; Sax, 2002; Sax and Gaines, 2003; Stohlgren et al., 2003; Tilman, 2011). Invaders decrease species richness, if they build dense stands and outcompete native plant species (Gaertner et al., 2009; Hejda et al., 2009; Flory and Clay, 2010; Davies, 2011; Vilà et al., 2011). This may also correspond with a decrease in the abundance of native plants (e.g., Vilà et al., 2011; Pyšek et al., 2012) and evenness of the invaded community (Hejda et al., 2009; Wilsey et al., 2009; but see, Davies, 2011). As most studies were observational, it remains largely unclear, whether changes in productivity and diversity at invaded sites arises from the addition of a new (exotic or native) species or whether it is caused by the addition of new exotic species to a system (Tilman, 1997; Davies, 2011). This problem can only be overcome by performing controlled introductions of exotic and native species into plant communities and measuring their impact on diversity and productivity.

Even though exotic plant invasions are suggested to be responsible for a change in diversity and productivity of communities or ecosystems, the underlying mechanisms are still poorly studied. Few experiments explicitly tested the contribution of exotic species to the diversity-productivity relationship (Maron and Marler, 2008; Wilsey et al., 2009; Isbell and Wilsey, 2011; Cook-Patton and Agrawal, 2014; Martin et al., 2014). Wilsey et al. (2009) provided evidence that the mechanisms driving the relationship between diversity and productivity remarkably differ between exotic and native experimental communities. Exotic communities attained a high productivity (see also, Cook-Patton and Agrawal, 2014) and were governed by a positive selection effect (Wilsey et al., 2009). In contrast, native communities were less productive and showed high complementary resource use (Wilsey et al., 2011). However, there are also partly opposing results. Cook-Patton and Agrawal (2014) revealed that even though exotic species produced more biomass in mixture, both native and exotic communities showed a positive complementarity effect. Besides from evaluating the impact of exotic plant species on diversity and ecosystem functioning, a general understanding about the environmental processes driving biological invasions is crucial, but still limited (Richardson and Pyšek, 2012; Kueffer et al., 2013). In this regard, regional and local-scale processes play an important role.

Seed availability

Seed limitation, acting at local scales, as well as dispersal limitation and species pools, acting at regional scales, determine which exotic or native species arrive at a given site and therefore affect local species richness and composition (Tilman, 1993, 1994; Turnbull et al., 2000; Zobel et al., 2000; Foster, 2001; Foster and Dickson, 2004; Leibold et al., 2004). The importance of dispersal and seed limitation for the relationship between diversity and ecosystem functioning in natural grassland ecosystems was demonstrated by Stein et al. (2008). They showed that the positive relationship between diversity and ecosystem functioning could only be obtained after overcoming dispersal and seed limitation. As the relationship between diversity and ecosystem functioning differs for native and exotic species (see above), seed addition of exotic and native species should increase species richness and productivity of local communities to a different extent. However, this has rarely been explicitly tested.

Since the success of exotic species is determined by their ability to spread and quickly colonize new sites, dispersal and seed supply play a crucial role in biological invasions (Simberloff, 2009; Richardson and Pyšek, 2012). Colautti et al. (2006) proposed a model in which invasion success of exotic plant species was solely explained by the rate of seed supply (propagule pressure). Observational studies that investigate the impact of biological invasions on diversity and productivity and/or the involved local processes are suggested to be highly biased by differences in the propagule pressure of exotic vs. native species (Colautti et al., 2006). To appropriately address these issues, seed addition experiments are needed that “standardize” for propagule pressure of exotic and native species.

Besides dispersal ability at local and regional scales, herbivory and competition are often invoked to explain failures or success of exotic plant invasions at the community level (Shea and Chesson, 2002; Mitchell et al., 2006). Nevertheless, because the same processes that influence invasions by exotic species should also affect establishment, diversity and productivity of native species, it is essential to quantify effects on exotic species relative to native species (Van Kleunen et al., 2010a; Van Kleunen et al., 2010b; Kempel et al., 2013).

Competition and disturbance

There is long-standing evidence that interspecific competition for resources determines the composition and diversity of plant communities (Hutchinson, 1959; MacArthur and Levins, 1967; Grime, 1973; Armstrong and McGehee, 1976; Huston, 1979). The availability of key resources such as light, water and nutrients is crucial for seedlings to become established (Fenner, 2000). Seedling establishment, in turn, is known to be of vital importance for the maintenance of diversity (Grubb, 1977). Competition and disturbance can be seen as "two sides of a medal". Disturbance opposes competition as it releases seedlings or adult plants from competition and makes key resources, such as light, water and nutrients available (Eriksson and Ehrlén, 1992; Tilman, 1997; Clark et al., 2007). Disturbance does not only occur in human dominated rural areas, but is in fact part of natural ecosystem dynamics (Sousa, 1984; Fraterrigo and Rusak, 2008). For example wild boars or small mammals may create small-scale disturbances, thereby acting as ecosystem engineers (Jones et al., 1996). Physical disturbance of the soil may, however, also lead to alterations in the microbial activity and thus higher resource mobilization e.g. of nitrogen (Vitousek et al., 1979; Davies, 2011).

Consequently, competition and disturbance may have opposing effects on establishment success of exotic species: competition by resident plant species can severely limit establishment of exotic species into communities and is therefore regarded as a central source of biotic resistance to biological invasions (Elton, 2000; Levine et al., 2004; Mitchell et al., 2006). Disturbance, in contrast, was often found to promote exotic plant invasions (Hobbs and Huenneke, 1992; Seabloom et al., 2003; Jauni et al., 2014). Davis et al. (2000) proposed that "a plant community becomes more susceptible to invasions whenever there is increase in the amount of unused resources", which is typically the case following a disturbance event. Consequently, disturbances may provide invasion opportunities for exotic species (Shea and

Chesson, 2002), since they are usually excellent colonizers that germinate and grow faster in comparison to native species (Baker, 1974; Vilà and Weiner, 2004; Funk and Vitousek, 2007; Van Kleunen et al., 2010b; Van Kleunen et al., 2014b; Wilsey et al., 2014).

However, studies testing the effect of disturbance on exotic plants' success have been mostly observational, thus were not able to separate the effects of species origin from the effects of underlying site conditions. Experimentally invading disturbed and undisturbed patches with exotic and native species across various sites may solve this problem.

Herbivory

Plants are simultaneously attacked by a wide range of herbivores that differ in the way and strength they affect demographic processes, community diversity and productivity (Crawley, 1983; Huntly, 1991; Hulme, 1996; Ritchie and Olff, 1999; Bakker et al., 2006). Generally, herbivores can be categorized into *specialist herbivores*, relying on a single or a limited range of host species, and *generalist herbivores*, consuming a broad array of species (Crawley, 1983). If specialist herbivores act density dependent and suppress competitively superior host species, they allow sub-dominant species to benefit. Consequently, they may promote diversity and evenness in a community (Chesson, 2000; Allan and Crawley, 2011). How generalist herbivores affect community attributes is rather difficult to predict (Bakker et al., 2006; Ishii and Crawley, 2011), and thus poorly understood.

The effect of generalist herbivores on species richness, evenness and species composition may depend e.g. on guild-specific feeding preferences for certain functional groups or species (Scheidel and Bruelheide, 1999; Howe et al., 2006; Allan and Crawley, 2011; Barlow et al., 2013). By selectively consuming different groups of species, different guilds of herbivores may interact with each other to determine community composition and diversity (Ritchie and Olff, 1999; Allan and Crawley, 2011). During the seedling stage levels of chemical and physical defense are usually low (Boege and Marquis, 2005; Barton and Koricheva, 2010). Therefore, invertebrates such as gastropods often prefer seedlings over adult plants (Fenner et al., 1999), particularly of sub-dominant herb species (Hulme, 1994b; Hulme, 1994a; Hanley, 2004; but see, Barlow et al., 2013). Rodents are often granivorous and then prefer larger seeds with a high nutritional value, e.g. of legumes (Howe and Brown, 2000; Maron and Simms, 2001; Hulme and Benkman, 2002). Other rodents are herbivorous and are reported to feed on grasses which are easily available in grasslands due to their high dominance (Baker, 1971; Hoogenboom et al., 1984; Howe et al., 2006; Massey et al., 2008; but see, Hulme, 1994b).

There is large debate on how herbivores affect biological invasions, as exotic plant species are dislocated from enemies of their home range, but are exposed to new enemies in their invaded range (Mitchell et al., 2006). Accordingly, numerous and partly contrasting hypotheses exist within this context (Catford et al., 2009). For example, the *biotic resistance hypothesis* states that exotic plant species fail to invade because strong antagonistic interactions with resident (generalist) herbivores prevent them from becoming established (Elton, 2000; Maron and Vilà, 2001; Levine et al., 2004). Going beyond the biotic resistance hypothesis, the *new associations* or *increased susceptibility hypotheses* (Hokkanen and Pimentel, 1989; Colautti et al., 2004) state that exotic plant species are stronger attacked by resident herbivores than native plant species, because they did not develop effective defense mechanism against them. In contrast, the *enemy release hypothesis* postulates that exotic species become invasive because they are liberated from their coevolved enemies, particularly specialists (Keane and Crawley, 2002). However, the enemy release hypothesis also predicts that "generalists have a greater impact on the native competitors" (Keane and Crawley, 2002). Consequently, exotic species will gain a competitive advantage over native species. A reduced attack of exotic plants by generalists is commonly attributed to novel defenses produced by exotic species (Schaffner et al., 2011), or selection for increased levels of defenses against generalist herbivores (Joshi and Vrieling, 2005).

The role of generalist herbivores during plant invasions has received surprisingly little attention and thus remains poorly understood (Levine et al., 2004; Joshi and Vrieling, 2005; Mitchell et al., 2006; Dawson et al., 2014; Heger and Jeschke, 2014). The handful of studies that included generalist herbivory produced opposing results: greater effects of herbivory on native compared to exotics (Liu et al., 2007; Knight et al., 2009; Hahn et al., 2011; Hahn and Dornbush, 2012; Maron et al., 2012; Dawson et al., 2014), or a stronger effect on exotics compared to natives (Agrawal and Kotanen, 2003; Avanesyan and Culley, 2011; Stricker and Stiling, 2014). A frequently used but criticized measure of herbivore attack is the degree of (leaf) damage. Chun et al. (2010) showed in their meta-analysis that differences in leaf damage were not related to performance. Schutzenhofer et al. (2009) found that less herbivore damage in exotic species compared to native species had no demographic outcome.

Evidence for biotic resistance mediated by generalist herbivores primary comes from granivorous rodents (Keane and Crawley, 2002; Nunez et al., 2008; Shahid et al., 2009; Pearson et al., 2011; Pearson et al., 2012; Connolly et al., 2014; Pearson et al., 2014a). Besides rodents, few studies tested biotic resistance mediated by other guilds of herbivores, such as slugs, and these studies found contrasting results so far (but see, Parker and Hay, 2005; Joe, 2006; Joe and Daehler, 2008; Motheral and Orrock, 2010; Morrison and Hay, 2011; La Pierre et al., 2014). The complex interactions between exotic and native plants and various herbivore species, become even more challenging as numerous invertebrate herbivores have been introduced, which may also influence their effect on exotic and native plant species. In a meta-analysis Parker et al. (2006) showed that native generalist consumers provided biotic resistance against exotic species, while exotic generalist herbivores promoted the abundance of exotic species by consuming their native competitors. However, as shown in a recent meta-analysis this differential effect of exotic vs. native herbivores may not hold true for invertebrates (Oduor et al., 2010).

Equivocal results for enemy release and biotic resistance could have originated from the limited number of included plant and/or herbivore species, producing species-specific rather than generalizable results. Demographic success is a prerequisite for exotic plants to become invasive (Mitchell et al., 2006). Consequently, there is a great potential for enemy release and biotic resistance to be effective during early establishment of plant species (Levine et al., 2004). So far, studies testing biotic resistance or enemy release rarely compared demographic responses of exotic versus native plant species (but see, Maron et al., 2012). In particular, these studies did not test whether effects observed at the demographic level translate into attributes at the community level.

Experimental approaches, study species and systems

Experimental approaches. The search for general patterns in ecology requires multi-species and multi-site approaches (Fraser et al., 2012; Kueffer et al., 2013; Van Kleunen et al., 2014a). Consequently, a high degree of generalizability can be reached by combining both multi-site and multi-species experiments. However, experiments always face a trade-off between generalism and precision (Van Kleunen et al., 2014a): in multi-site experiments it is logistically infeasible to include as many experimental factors or to describe mechanisms in such precision as in single-site or in greenhouse experiments.

In the present thesis all experiments follow a multi-species approach, while the number of study systems and sites varies between the different experiments. In this respect, the least general and most precise study in my PhD thesis is a mesocosm study about diversity mechanisms in exotic and native communities, followed by a highly complex four-factorial experiment with a split-split-plot design at a single experimental site. In contrast, three-factorial experiments with a split-plot design were logistically possible at multiple sites in two to three regions, reaching a high extent of generalizability (Table 1). Consequently, I evaluate whether observed effects at the demographic and community level are context-dependent or generalizable across a large range of environmental conditions. For example I compare the effect of gastropod and/or rodent herbivory on exotic vs. native species at a single-site with their effect across multiple sites. Finally, to account for functional differences between plant species in response to different processes, I controlled for, and analyzed the effect of plant functional group affiliation (i.e species that share certain phenological, morphological and physiological traits; Roscher et al., 2004).

Table 1: Overview about main characteristics of the experiments included in this thesis.

Type of experiment	**Mesocosm**	**Single-site**	**Multi-site (two regions)**	**Multi-site (three regions)**
Duration	10 weeks	2 years	2 years	4 years
Study regions (number of sites)	-	Germany (1)	Germany (10) California (8)	Germany (10) California (9) Montana (10)
Design	Randomized block	Split-split-plot	Split-plot	Split-plot
Number of experimental units	144 (mesocosms)	120 (sub-subplots)	162 (sub-plots)	696 (sub-plots)
Number of plant species	12 native 12 exotic *Σ 24 species*	20 native 20 exotic *Σ 40 species*	38 native 38 exotic *Σ 76 species*	59 native 58 exotic *Σ 117 species*
Experimental factors	Plant origin Plant diversity Slug herbivory	Plant origin Disturbance Rodent herbivory Gastropod herbivory	Plant origin Rodent herbivory Gastropod herbivory	Plant origin Disturbance Rodent herbivory

Study species. Species pools across different experiments varied slightly (Table 2). In general, exotic and native study species were selected from the regional species pools but were mostly locally uncommon at grassland sites. Some species were shared across regions, i.e. they were native in Germany and exotic in Montana and/or California or exotic across several regions (Table 2). Distribution of seed size, life-span and affiliation to plant functional groups were kept as similar as possible between exotic and native species pools within each region (see different chapters for detailed information). Selected species were predominantly grassland species, but a few species occurred also at ruderal sites or along roadsides (e.g. *Daucus carota* (California), *Falcaria vulgaris* (Germany), *Foeniculm vulgaris* (California), *Lactuca serriola* (Germany), *Cardaria drabra* (Germany)*, Senecio inaequidens* (Germany)). *Lactuca serriola* is a typical ruderal species and invades grassland systems in North America (Abella and Tendick, 2013). In Germany, some exotic species (*Cychorium intybus*, *Melilotus officinalis*, *Medicago* x *varia* and *Onobrychis viciifolia*) are included in commercially available seed mixtures for fallow land re-vegetation (Frank and John, 2007).

Table 2: List of all native and exotic study species in each region (Germany, California, Montana) which are included in this thesis. Numbers specify in which experiment species were used (1 = mesocosm, 2 = single site, 3 = multi-site (two regions), 4 = multi-site (three regions), see Table 1).

	Germany	California	Montana
NATIVE SPECIES	*Agrimonia eupatoria* ^{2,3,4}	*Agoseris grandiflora* ^{3,4}	*Anemone multifida* ^{4}
	Bromus hordeaceus ^{1,2,3,4}	*Antirrhinum vex.-caly ssp. Brew* ^{4}	*Astragalus drummondii* ^{4}
	Cynoglossum officinale ^{2,3,4}	*Clarkia purpureum* ^{3,4}	*Balsamorhiza sagittata* ^{4}
	Dactylis glomerata ^{1,2,3}	*Danthonia californica* ^{3,4}	*Collinsia parvaflora* ^{4}
	Daucus carota ^{2,3,4}	*Daucus pusillus* ^{4}	*Collomia linearis* ^{4}
	Dianthus carthusianorum ^{1,2,3,4}	*Elymus glaucus* ^{3,4}	*Delphinium bicolor* ^{4}
	Falcaria vulgaris ^{1,2,3,4}	*Croton setigerus* ^{3,4}	*Dodecatheon conjugens* ^{4}
	Galium x pomeranicum ^{4}	*Eriogonum luteolum* ^{3,4}	*Erigeron pumilus* ^{4}
	Hypericum perforatum ^{2,3,4}	*Eschscholzia californica* ^{3,4}	*Fritillaria pudica* ^{4}
	Hypochaeris radicata ^{2,3,4}	*Festuca californica* ^{3,4}	*Gaillardia aristata* ^{4}
	Inula conyzae ^{4}	*Hemizonia congesta ssp. Congesta* ^{3,4}	*Geum triflorum* ^{4}
	Inula salicina ^{1}	*Hordeum brachyantherum* ^{3,4}	*Heterotheca villosa* ^{4}
	Lactuca serriola ^{2,3,4}	*Lomatium utriculatum* ^{4}	*Lithophragma glabrum* ^{4}
	Lotus corniculatus ^{1,2,3,4}	*Acmispon americanus* ^{4}	*Lithospermum ruderale* ^{4}
	Medicago falcata ^{1,2,3}	*Lupinus nanus* ^{3,4}	*Lomatium macrocarpum* ^{4}
	Medicago lupulina ^{4}	*Lotus purshianus* ^{3}	*Lupinus sericeus* ^{4}
	Onobrychis arenaria ^{1}	*Melica californica* ^{4}	*Potentilla arguta* ^{4}
	Picris hieracioides ^{4}	*Mimulus guttatus* ^{3,4}	*Saxifraga oregano* ^{4}
	Pimpinella saxifrage ^{1,2,3}	*Stipa pulchra* ^{3,4}	*Stipa richardsonii* ^{4}
	Rumex crispus ^{2,3}	*Plantago erecta* ^{3,4}	*Zigadenus venenosus* ^{4}
	Salvia pratensis ^{2,3,4}	*Sisyrinchium bellum* ^{3,4}	
	Sanguisorba minor ^{1,2,3,4}	*Trifolium wildenowii* ^{3}	
	Securigera varia ^{2,3,4}		
	Silene vulgaris ^{2,3,4}		
	Tragopogon dubius ^{1,2,3,4}		
	Vicia cracca ^{1}		
	Vicia tetrasperma ^{2,3,4}		
EXOTIC SPECIES	*Acroptilon repens* ^{4}	*Anagalis arvensis* ^{4}	*Carduus nutans* ^{4}
	Artemisia absinthium ^{2,3,4}	*Avena fatua* ^{3,4}	*Centaurea stoebe* ^{4}
	Bromus tectorum ^{1,2,3,4}	*Brassica nigra* ^{3,4}	*Chenopodium album* ^{4}
	Bunias orientalis ^{2,3,4}	*Bromus hordeaceus* ^{3}	*Cirsium vulgare* ^{4}
	Cardaria draba ^{2,3,4}	*Cynodon dactylon* ^{4}	*Cynoglossum officinale* ^{4}
	Cichorium intybus ^{2,3,4}	*Dactylis glomerata* ^{3,4}	*Hypericum perforatum* ^{4}
	Dianthus giganteus ^{1,2,3,4}	*Daucus carota* ^{3,4}	*Lactuca serriola* ^{4}
	Diplotaxis tenuifolia ^{2,3,4}	*Festuca arundinaceae* ^{4}	*Linaria dalmatica*
	Dipsacus sylvestris ^{2,3,4}	*Foeniculum vulgare* ^{3,4}	*Linaria vulgaris* ^{4}
	Echinops sphaerocephalus ^{2,3,4}	*Hypericum perforatum* ^{3,4}	*Lithospermum arvense* ^{4}
	Foeniculum vulgare ^{1,2,3,4}	*Hypochearis radicata* ^{3}	*Melilotus officinalis* ^{4}
	Lolium multiflorum ^{1,2,3}	*Lactuca serriola* ^{4}	*Poa pratensis* ^{4}
	Lupinus polyphyllus ^{1}	*Lolium multiflorum* ^{3,4}	*Potentilla recta* ^{4}
	Medicago x varia ^{1,2,3,4}	*Lotus corniculatus* ^{3,4}	*Rumex crispus* ^{4}
	Melilotus officinalis ^{2,3,4}	*Melilotus officinalis* ^{3,4}	*Sisymbrium altissimum* ^{4}
	Onobrychis viciifolia ^{1,2,3,4}	*Petrorhagia dubia* ^{3,4}	*Taraxacum officinale* ^{4}
	Pimpinella peregrina ^{1,2,3,4}	*Plantago lanceolata* ^{3,4}	*Tragopogon dubius* ^{4}
	Sanguisorba minor subsp. Polygama ^{1,2,3,4}	*Poa pratensis* ^{4}	*Verbascum thapsus* ^{4}
	Senecio inaequidens ^{1,2,3,4}	*Raphanus sativus* ^{3,4}	*Veronica verna* ^{4}
	Sisymbrium loeselii ^{2,3,4}	*Rumex crispus* ^{3}	
	Solidago canadensis ^{1,2,3,4}	*Spergularia rubra* ^{4}	
	Vicia villosa ^{1,2,3,4}	*Trifolium hirtum* ^{3}	
		Trifolium incarnatum ^{4}	
		Trifolium repens ^{3}	
		Vicia villosa ^{3}	

Study systems. A multi-site experiment across three regions (Table 1, Fig. 1) was set up in 2009 in cooperation with the University of California Berkeley (Dr. Claudia Stein, Prof. Katharine N. Suding), the University of Montana (Prof. John L. Maron) and the Rocky Mountain Research Station of the US Forest Service (Dr. Dean E. Pearson). In 2011, a single-site experiment was established at the experimental station of the UFZ (study site 1 in Germany; Fig 1). Another multi-site experiment covering all study sites in Germany, and all sites, except study site 8, in California (Fig. 1).

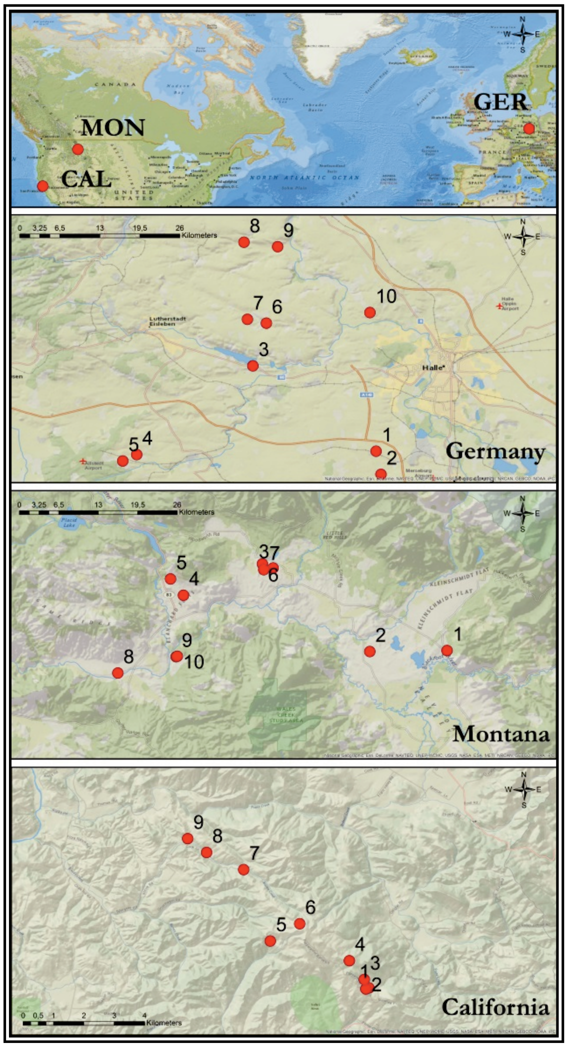

Figure 1: Overview about the three study regions (**GER** = Germany, **MON** = Montana, **CAL** = California) included in this thesis. Experimental sites within each region are indicated by red circles with the respective study site number (cartography by A. Harpke).

To distinguish context-dependent from general results, grassland sites within each region were chosen to cover a gradient in diversity and productivity, while grassland systems across regions were chosen to vary in environmental conditions such as climate, land-use, invasion history and species pools of plants and herbivores.

(1) Compared to grasslands in North America, German grasslands are less invaded by exotic plant species (Seastedt and Pyšek 2011) and need to be managed to be maintained. These temperate, semi-dry grasslands in Central Germany were dominated by perennial native grasses such as *Dactylis glomerata, Arrhenatherum elatius* and *Festuca rupicola.* Abundant rodent species in German grasslands were voles (*Microtus arvalis*, *Microtus agrestis*). In addition, rabbits (*Oryctolagus cuniculus*) occasionally occurred. The German gastropod assemblage consisted of slugs and snails. Most slugs were from the native genus *Deroceras* and the (exotic) species *Arion vulgaris.* However, recent molecular analyses question the exotic status of Arion vulgaris in Europe

(Pfenninger et al., 2014). By far the most common snail species was the native saprophagous snail *Monacha cartusiana*, primarily feeding on senescent plant material (Chatfield 1976).

(2) Continental grassland systems in the Blackfoot Valley in western Montana are one of the few remaining native grassland systems in Northern America (Maron et al., 2010; Maron and Pearson, 2011). These semi-dry, perennial grasslands were dominated by the native caespitose grasses *Festuca scabrella* and *F. idahoensis*. Dominant rodent species were granivorous deer mouse (*Peromiscus maniculatus*) and herbivorous montane voles (*Microtus montanus*). In addition, columbian ground squirrels occurred at lower densities (Maron et al., 2012).

(3) Generally, Californian grassland systems have a long history of invasions (Seastedt and Pyšek, 2011). Nevertheless, Mediterranean type grasslands in the Pepperwood Preserve are comparably little invaded and were dominated by native bunchgrasses such as *Nasella pulchra* or *Danthonia californica* and were only moderately invaded by exotic annual grasses such as *Bromus hordeaceus* and *Avena fatua*. Abundant rodent species in California included herbivorous voles (*Microtus californicus*), pocked gophers (*Thomomys bottae* spp. *bottae*) and seed feeding mice (*Reithrodontomys megalotis, Peromyscus maniculatus*). The Californian gastropod assemblage solely consisted of slugs and was dominated by the exotic *Deroceras reticulatum.*

Objectives and outline of this thesis

A central aim of this thesis was to assess how different processes – dispersal limitation, biological invasions, herbivory and disturbance – separately and interactively affect seedling recruitment, diversity and productivity across multiple grassland ecosystems that vary in environmental conditions. Accordingly, this thesis aims to expand our current knowledge about diversity and productivity to natural ecosystems, to different plant origins and to higher trophic levels. Moreover, this thesis intends to explore the context-dependency and generalization of demographic and community responses. Hence, this thesis may facilitate a deeper understanding of ecosystem functioning, community assembly and dynamics of nowadays ("novel") ecosystems with varying environmental conditions.

Specifically, I addressed the following research questions in this thesis:

1. How do herbivory and disturbance influence seedling recruitment of exotic compared to native plant species and how context-dependent are these effects?

2. How does native vs. exotic plant origin impact diversity and productivity of grassland communities and how do herbivory and disturbance mediate these community responses?

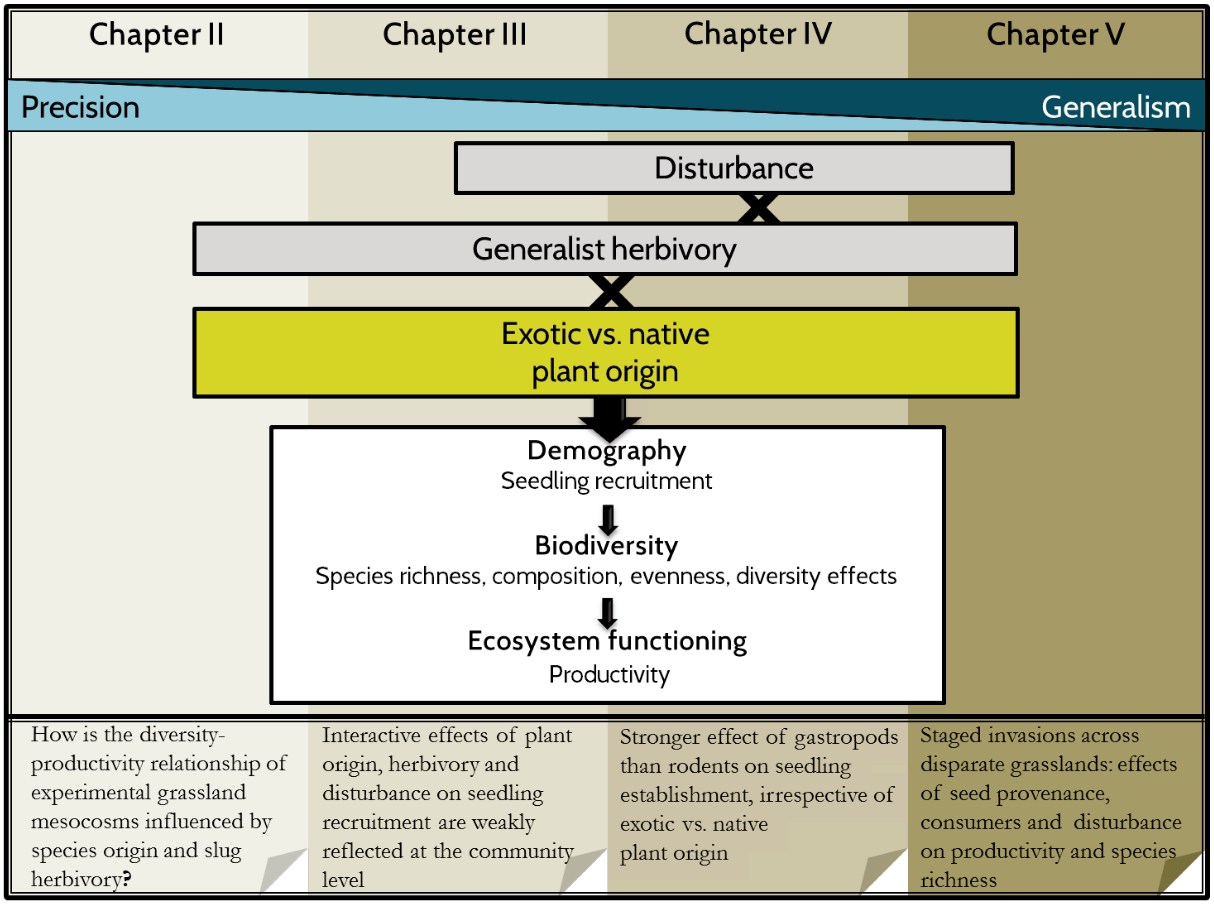

Figure 2: Outline of this PhD thesis. The chart depicts the processes that have been manipulated (disturbance, generalist herbivory and plant origin) and measured (seedling recruitment, biodiversity and ecosystem functioning) within the four chapters of this thesis. Note that disturbance is only varied in chapter 3 and 5.

The two research questions of this thesis are oriented towards the investigated processes, and thus rather crosscut the four chapters which are arranged along the precision vs. generalism trade-off (Fig. 2).

In **chapter 2**, I present results of a short-term mesocosm experiment which tested how diversity effects, evenness and productivity differed among phylogenetically adjusted assemblages of exotic and native grassland plants, and how these experimental communities were influenced by slug herbivory. I expected native species mixtures to show a stronger complementarity effect and higher evenness, and exotic mixtures to show a lower evenness and stronger selection effect. Furthermore, I expected gastropods to reduce evenness by selectively feeding on subdominant plant species, irrespective of the plant origin of species mixtures. Accordingly, this study gives important insights in the mechanisms by which diversity affects ecosystem functioning and how these mechanisms are influenced by trophic interactions in early stages of community development.

In **chapter 3,** I investigated how dispersal limitation, disturbance, rodent herbivory and gastropod herbivory interact with exotic and native plant origin to determine seedling recruitment and to shape community species richness, composition and productivity. Within a full-factorial design, I experimentally excluded rodents and gastropods and added 20 native and 20 exotic species to experimental plots that where either subjected to disturbance or left undisturbed. I hypothesized rodent herbivory and gastropod herbivory to show interactive effects on seedling recruitment, species richness and community composition, depending on their guild specific preferences for plants belonging to a certain functional group. I expected the effects of disturbance and gastropod or rodent herbivory on seedling recruitment to be stronger for exotic than native plant species. Furthermore, I proposed that seed addition (regardless whether native or exotic) increases species richness. Finally, I expected that exotic seed addition will increases productivity more strongly than native seed addition and this effect is enhanced by disturbance. This complex experiment is the first one assessing the joint and single effect of different herbivore guilds and disturbance on exotic versus native seedling recruitment and how these effects are reflected in diversity and productivity at the community level. The study may thus greatly contribute to our general understanding of processes determining community assembly and dynamics in the context of biological invasions.

In **chapter 4**, I compared the relative effects of gastropod and rodent herbivory on seedling recruitment and establishment of 17 to 20 exotic and 17 to 20 native species. In addition, I evaluated their effects in interaction with functional group affiliation in Californian and German grasslands. Over a period of two years, I quantified these effects across 8 and 10 grassland sites within each region, to test whether generalist herbivores are able to either mediate biotic resistance against exotic plant invasions or whether they facilitate exotic plant invasions via enemy release during early stages of establishment. The comparison of different herbivores and regions enabled me to detect whether results are generalizable or depend on the herbivore guild or region.

Together with my collaborators I elucidate in **chapter 5**, whether the effect of exotic versus native seed addition on diversity and productivity is influenced by disturbance and rodent herbivory across disparate grassland systems in Germany, California and Montana which vary considerably in their underlying environmental conditions. Across 9 to 10 grasslands in Germany, California and Montana, rodents were excluded with fences and seeds of 19-20 native and 19-20 exotic species were added to experimental plots that were either subjected to disturbance or left undisturbed. This broad approach enabled us to quantify the strength and consistency of how seed addition of exotic versus native plants influences productivity and diversity and to investigate how generalist herbivory and disturbance mediate this effect across different grassland ecosystems.

In **chapter 6**, I summarize the key results and highlight the links between the different chapters. Particularly, I will discuss the obtained results with respect to their context-dependency or generalizability. Finally, I will draw conclusions for future research and further studies.

Chapter 2

HOW IS THE DIVERSITY-PRODUCTIVITY RELATIONSHIP OF EXPERIMENTAL GRASSLAND MESOCOSMS INFLUENCED BY NATIVE VERSUS EXOTIC SPECIES ORIGIN AND SLUG HERBIVORY?

Lotte Korell, Robin Schmidt, Helge Bruelheide, Isabell Hensen, Harald Auge

Oecologia (in revision)

ABSTRACT

Biodiversity experiments have shown that productivity usually increases with plant species richness. Most of these studies however disregarded the importance of trophic interactions for the diversity-productivity relationship, and focused on the loss of native species but ignored the invasion by exotic species. Yet, as niche complementarity and impact of plant antagonists are likely to differ between native and exotic communities, the diversity-productivity relationship may change when native communities are invaded by exotic species. We conducted a mesocosm experiment to test how diversity effects, evenness and productivity differed among exotic and native assemblages of grassland plants, and how these communities were influenced by slug herbivory. In line with other experiments we found a higher productivity in exotic than in native communities. However, diversity effects contributed differently to this positive diversity-productivity relationship of exotic and native communities. Against expectations native communities showed much lower evenness and a higher selection effect, suggesting that competitive dominance among native species may be even stronger than among exotic species. Slug herbivory decreased productivity, independently of species origin and species diversity. However, exotic communities showed a three-fold higher complementarity effect than native communities in the absence of slugs, which was mainly driven by differences in the response of native and exotic legumes and non-legume herbs. Our results imply that underlying mechanisms for the positive diversity-productivity relationship differ among native and exotic communities also in early stages of community development, and that differential responses of plant functional groups to generalist herbivory can contribute to this pattern.

Key words: complementarity effect, selection effect, evenness, *Arion vulgaris*, functional groups

Chapter 3

INTERACTIVE EFFECTS OF PLANT ORIGIN, HERBIVORY AND DISTURBANCE ON SEEDLING RECRUITMENT ARE WEAKLY REFLECTED AT THE COMMUNITY LEVEL

Lotte Korell, Birgit Lang, Isabell Hensen, Harald Auge, Helge Bruelheide

(to be submitted)

ABSTRACT

Disturbance, generalist herbivory and dispersal limitation can interactively affect seedling recruitment of exotic and native plant species and may in turn affect community diversity and productivity. However different guilds of generalist herbivores, i.e. gastropods and rodents, may have non-additive effects on exotic and native seedling recruitment, species richness and community composition because of guild specific feeding preferences. Therefore, we set up a combined exclosure (rodents vs. gastropods), disturbance (disturbance vs. no disturbance) and seed-addition (20 exotic vs. 20 native species) split-split-plot experiment in a resident grassland community in Central Germany. Gastropod and rodent herbivory interacted with disturbance and plant origin to determine seedling recruitment but not species richness, composition and productivity. Likely via selective feeding on subordinate species during seedling recruitment, gastropods reduced species richness while rodents had strong negative effects on aboveground productivity, leading to non-additive effects of both herbivore guilds on community composition and species richness. Productivity was enhanced to a greater extent by exotic than native seed addition, while the opposite was true for species richness, suggesting that different mechanisms are responsible for the relationship between diversity and productivity in native- vs. exotic-dominated communities. The results indicate that complex interactions may be evident during seedling recruitment but may be weakly reflected at the community level which may have important implications for the understanding of biological invasions as well as community dynamics.

Key words: biological invasions, biotic resistance, disturbance, gastropod herbivory, non-additive effects, productivity, rodent herbivory, seedling recruitment, species richness

Chapter 4

STRONGER EFFECT OF GASTROPODS THAN RODENTS ON SEEDLING ESTABLISHMENT, IRRESPECTIVE OF EXOTIC OR NATIVE PLANT ORIGIN

Lotte Korell, Claudia Stein, Isabell Hensen, Helge Bruelheide, Katherine N. Suding, Harald Auge

Ecology (under review)

ABSTRACT

Experimental evidence about how generalist consumers affect exotic plant invasions is equivocal, but most tests have been limited to few plant species, single herbivore guilds, and single locations. We experimentally studied effects of gastropods and rodents on seedling recruitment of 37 exotic and 37 native plant species affiliated to three different functional groups (i.e. grasses, legumes and no-legume herbs) across multiple grassland sites in California and Germany. Gastropods reduced seedling recruitment to a greater extent than rodents and particularly of non-legume herbs and legumes, but not of grasses. The general effect of gastropod exclusion was remarkably stronger in California than Germany. Contrastingly, the effect of rodents on seedling recruitment was negative in Germany and positive in California, likely driven by region-specific differences in the rodent assemblages. Exotics had twice as high first-year seedling establishment than natives, indicating that higher recruitment constitutes an inherent feature of exotic species. Native and exotic species did, however, not differ in their response to herbivory, suggesting that generalist consumers inhibit seedling recruitment irrespective of plant species origin. Our results demonstrate the importance of a multi-species, multi-site approach to separate general responses of exotic and native plants to generalist herbivory from local, regional or species-specific peculiarities.

Key words: biological invasions, biotic resistance, California, enemy release, gastropod exclusion, Germany, grasslands, multi-site, multi-species, rodent exclusion, plant functional groups

Chapter 5

STAGED INVASIONS ACROSS DISPARATE GRASSLANDS: EFFECTS OF SEED PROVENANCE, CONSUMERS AND DISTURBANCE ON PRODUCTIVITY AND SPECIES RICHNESS

John Maron, Harald Auge, Dean Pearson, Lotte Korell, Katharine Suding,
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LETTER

Staged invasions across disparate grasslands: effects of seed provenance, consumers and disturbance on productivity and species richness

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Suding[6] and Claudia Stein[6†]

Abstract

Exotic plant invasions are thought to alter productivity and species richness, yet these patterns are typically correlative. Few studies have experimentally invaded sites and asked how addition of novel species influences ecosystem function and community structure and examined the role of competitors and/or consumers in mediating these patterns. We invaded disturbed and undisturbed subplots in and out of rodent exclosures with seeds of native or exotic species in grasslands in Montana, California and Germany. Seed addition enhanced aboveground biomass and species richness compared with no-seeds-added controls, with exotics having disproportionate effects on productivity compared with natives. Disturbance enhanced the effects of seed addition on productivity and species richness, whereas rodents reduced productivity, but only in Germany and California. Our results demonstrate that experimental introduction of novel species can alter ecosystem function and community structure, but that local filters such as competition and herbivory influence the magnitude of these impacts.

Keywords

Community assembly, exotic species, grasslands, invasion, local filters, plant competition, plant productivity, small mammals, species richness.

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Chapter 6

SYNTHESIS

General discussion

This thesis focused on the separate and interactive effects of dispersal and seed limitation, disturbance, herbivory and biological invasions on seedling recruitment, diversity and productivity in grassland ecosystems. Including a comprehensive number of study species and several experiments, this thesis gained important insights into the generalizability and context-dependency of the processes that influence biological invasions, community assembly and community dynamics and drive diversity and ecosystem functioning in grassland communities. The key results were as follows:

i. Exotic species displayed increased seedling recruitment compared to native species. While gastropod herbivory reduced the positive effect of disturbance, rodent herbivory indirectly alleviated the negative effect of resident competition on exotic compared to native species. However, these complex interactions between disturbance, herbivory and species origin were context-dependent because when averaged across a large range of environmental conditions, generalist herbivory had strong, but equal effects, on both exotic and native seedling recruitment.

ii. Plots to which exotic species were added attained higher productivity than those to which native species were added, while species richness increased to similar or lower extents in exotic compared to native species assemblages. The mechanisms behind the positive diversity-productivity relationship did indeed vary between native and exotic experimental communities, but opposing my *a priori* expectations. Disturbance increased the impact of exotic plant invasions on species richness and productivity. Generalist herbivory varied among plant functional groups but equally reduced the productivity of both exotic and native plant species. The effect of disturbance and herbivory varied in magnitude among distinct geographical regions.

How do disturbance and herbivory influence seedling recruitment of exotic compared to native plant species and how context-dependent are these effects?

After overcoming dispersal and seed limitation by seed addition, exotic species consistently experienced higher rates of seedling recruitment compared to native species (**chapter 3 and 4**). Higher rates of seedling recruitment of exotic than native species were also obtained e.g. by Wainwright and Cleland (2013), Pearson et al.(2014b), Wilsey et al. (2015) (but see Kempel et al., 2013). Furthermore, the increased seedling recruitment across varying environmental conditions found in **chapter 4** indicates that exotics might be more able to cope with varying environmental conditions (see, Dostál et al., 2013b), probably because of a higher germination plasticity.

Disturbance had stronger positive effects on seedling recruitment and colonization of exotic compared to native species at one experimental site in Germany (**chapter 3**). Stronger responses of exotic compared to native species to disturbance were reported by Maron et al. (2012) as well, and indicate that exotic species may possess "weedy" characteristics that make them better colonizers (Baker, 1974; Davis et al., 2000; Ehrenfeld, 2003; Jauni et al., 2014). For example faster and more profuse germination could allow exotic species to occupy competition free space earlier (e.g., Van Kleunen and Johnson, 2007; Schlaepfer et al., 2010), which may ultimately result in competitive advantages over native species (Verdú and Traveset, 2005; Grman and Suding, 2010).

In contrast to disturbance, gastropod herbivory suppressed exotic over native seedling recruitment at one experimental site (**chapter 3**). This finding clearly supports the biotic resistance hypothesis (Maron and Vilà, 2001) as well as the hypotheses of new associations and of increased susceptibility (Hokkanen and Pimentel, 1989; Colautti et al., 2004). Strikingly, this interactive effect was more pronounced in disturbed than undisturbed plots (see, Maron et al., 2012), suggesting that generalist herbivores may, to a certain extent, decrease invasion opportunities provided by disturbance (McEvoy and Coombs, 1999; Shea and Chesson, 2002). However, rodent herbivory had positive effects on seedling recruitment, particularly of exotics (but see, Pearson et al., 2011; Pearson et al., 2012; Pearson et al., 2014a) and more in undisturbed compared to disturbed plots (**chapter 3**). This pattern was most likely driven indirectly by the strong negative effects of rodents on productivity (Howe and Brown, 1999; Peters, 2007). Consequently, rodents may locally assist exotic plant establishment into intact communities by relaxing competitive interactions with resident species (Hobbs and Mooney, 1991; D'Antonio, 1993).

In contrast to the complex interactions between herbivory, disturbance and species origin at one experimental site, generalist herbivores had strong, but equal effects on exotic and native seedling recruitment when average responses of plant species across multiple sites were considered (**chapter 4**). The finding that generalist herbivory was context-dependent during early life stages, i.e. why I observed herbivore preferences for exotics only at a single site and not at multiple sites, is difficult to elucidate (Maron et al., 2014). Differences in the availability of resources, community productivity and species richness may have caused variation in the extent of herbivory on exotic and native plant species among sites (Blumenthal, 2006; Dostál et al., 2013a; Maron et al., 2014; Preukschas et al., 2014).

How does native vs. exotic plant origin impact diversity and productivity of grassland communities and how do herbivory and disturbance mediate these community responses?

The general finding of increased species richness and productivity after seed addition indicates that communities were not saturated with species due to dispersal and seed limitation (Foster, 2001; Riibak et al., 2014). Dispersal and seed limitation are common in many ecosystems (Turnbull et al., 2000) and have been even found to superimpose the relationship between diversity and productivity (Stein et al., 2008).

Moreover, a key result of this thesis was that exotic seed addition increased productivity to a greater extent than native seed addition (**chapter 3 and 5**). Importantly, this effect was consistent across different grassland sites in Germany, California and Montana, which demonstrates the generalizability of this effect. Evidence for increased productivity in exotic vs. native dominated communities has been demonstrated in experiments (Maron and Marler, 2008; Wilsey et al., 2009; Martin et al., 2014) but particularly in observational studies (reviewed by, Vilà et al., 2011). There are several plausible explanations for this effect, all related to the non-random naturalization of exotic plants. Fist, many exotic species have been intentionally introduced by humans which selected for certain favorable characteristics, such as high productivity or faster germination (Chrobock et al., 2011; Pyšek et al., 2014; but see, Wilsey et al., 2014). Second, even if exotic species have been introduced unintentionally, other local (abiotic and biotic) filters might have selected for characteristics related to high productivity, such as rapid growth, large plant size as well as high resource use efficiency (Baker, 1974; Ehrenfeld, 2010; Van Kleunen et al., 2010b).

Compared to the pronounced effect of species origin on productivity, no such clear difference was found for species richness. If all biotic filters were in place, exotic and native seed addition increased species richness to nearly similar extents (**chapter 5**). Indeed, native seed addition increased species richness in Germany (at single site and across multiple sites) to a greater magnitude than exotic seed addition, suggesting that grassland communities are not inherently more open to invasions by exotic species and that native colonizers may exhibit stronger niche complementarity with resident species (Thorpe et al., 2011). The finding of increased productivity but equal or even lower species richness in exotic vs. native communities, suggests the existence of differences in the mechanisms contributing to the relationship between diversity and productivity. In a mesocosm experiment I tested for the effect of plant origin and slug herbivory on the relationship between diversity and on productivity. Indeed, I found that exotic communities showed a higher productivity than native communities (**chapter 2**). However, against expectations, increased productivity was promoted by a higher complementarity effect in exotic, and a higher selection effect in native communities. There is only a handful of studies that explicitly compared diversity effects and underlying mechanisms between native and exotic communities (but see, Maron and Marler, 2008; Wilsey et al., 2009; Cook-Patton and Agrawal, 2014; Martin et al., 2014) and only one study included interactions with higher trophic levels (Cook-Patton and Agrawal, 2014). My results are in contrast those by Wilsey et al. (2009) but partly in line with those by Cook-Patton and Agrawal (2014). A higher complementarity effect in exotic and a higher selection effect in native assemblages indicates, that i) competitive dominance may be equal or even stronger among native compared with exotic species and that ii) exotic species may also benefit from interspecific resource partitioning or facilitation, probably because originating from the same regions.

However, how do herbivory and disturbance mediate community responses to "invasions" by exotic and native species? By decreasing competition intensity, disturbance rather enhanced the effect of seed addition on productivity and species richness (Foster and Gross, 1998; Zobel et al., 2000; Clark et al., 2007), whereas generalist herbivory reduced the effect of seed addition (Shea and Chesson, 2002; Levine et al., 2004). The magnitude in the degree to which disturbance interacted with seed addition of exotic and native species varied among regions (**chapter 5**): disturbance opened colonization opportunities for exotic species in Montana, likely because resident bunchgrasses mediated strong competitive biotic resistance (Maron et al., 2012). In Germany and California, once established and released from competition, particularly exotic legume species attained high productivity quickly in disturbed compared to undisturbed plots.

In contrast to disturbance, generalist herbivores reduced productivity independent of plant origin, i.e. they mediated resistance against both native and exotic species (Preukschas et al., 2014). However, both herbivore guilds differed in their impact on community attributes (**chapter 3**): gastropods had negative effects on species richness and productivity which confirms the results of Buschmann et al. (2005) and Peters (2007), while rodents solely reduced productivity, which was in line with the study of Howe and Brown (2001). Moreover, region-specific differences in the impact of generalist herbivory were most likely driven by differences in the herbivore assemblages (**chapter 5**). To my knowledge there are only very few other studies that combined a multi-site with a multi-species approach, which is a requirement for detecting general patterns in invasion biology (Kempel et al., 2013; Kueffer et al., 2013; Van Kleunen et al., 2014a). One of these studies, i.e. the one of Maron et al. (2012), showed that granivorous rodents more strongly suppressed native than exotic species, due to their on average smaller seed size (but see, Blaney and Kotanen, 2001b, a; Agrawal et al., 2005; Preukschas et al., 2014). In my studies rodents were primarily herbivores rather than granivores and thus seed size played a minor role. However, confirming my results Strauss et al. (2009) found equal effects of invertebrate herbivory (particularly slugs) on exotic and native seedling recruitment in comparative multi-species study. Thus, although differential herbivory by generalists may determine failure or success of some exotic plant species (e.g., La Pierre et al., 2010; Motheral and Orrock, 2010; Hahn and Dornbush, 2012; Pearson et al., 2012) it is context-dependent (**chapter 3**) and appears to be no general mechanisms to explain biological invasions.

Notwithstanding this, I found indication that both herbivore guilds display a certain degree of specialization in their food sources (e.g., Hulme, 1994a; Bruelheide and Scheidel, 1999; Scheidel and Bruelheide, 1999; Maron and Simms, 2001; Pearson et al., 2012; Barlow et al., 2013; La Pierre et al., 2014). For example rodents preferred species with a high nutritional value, e.g.

nitrogen-fixing legume species (e.g. *Medicago* x *varia*, *Onobrychis viciifolia*, *Vicia villosa*)(**chapter 5**). Gastropods consumed (seedlings) of herbs or legumes that likely showed a lower structural and chemical defense against herbivory (**chapter 3 and 4**) (Boege and Marquis, 2005; Barton and Koricheva, 2010). Grasses were least preferred by both herbivore guilds. In contrast grasses are known to be hardly digestible because of high silica contents (Vicari and Bazely, 1993), but may also better tolerate herbivore damage (Tscharntke and Greiler, 1995). This selective feeding of gastropods became particularly evident in my mesocosm study (**chapter 3**). Although slugs equally reduced biomass of both exotic and native experimental communities, differential slug grazing between different functional groups and between monocultures vs. mixtures contributed to differences in diversity effects among native and exotic assemblages. Specifically, via selective grazing on subordinate exotic non-legume (and legume) species relative to exotic grasses in mixtures, slug herbivory likely increased dominance of the latter in exotic experimental communities. This was not the case in native experimental communities (but see, Scherber et al., 2010 for insect herbivory). These findings suggest that characteristics linked to nutritional value, resistance and tolerance – some of them being reflected in functional group affiliation – are important determinants of generalist herbivory (Kempel et al., 2013).

Conclusions and future challenges

Since a long time, but particular since Davis et al. (2011) published their paper “Don´t judge species on their origin”, a lively debate has been going on about the question whether exotic species substantially differ from natives e.g. in response to different ecological factors (e.g. herbivory, disturbance) or in their impact on ecosystems. Nevertheless, studies were often limited in their ability to derive general conclusions due to the low number of study species, sites and regions. By a combination of multi-site and multi-species experiments, I overcame these limitations in my thesis. My results imply that:

(1) Averaged across a notable number of species and across multiple sites covering broad range of environmental conditions, **native and exotic seedling recruitment does not differ in response to generalist herbivory.** Consequently, generalist herbivores suppress recruitment of – thereby mediating resistance against – both native and exotic plant species. This does not exclude that in some environments and during certain ontogenetic stages, generalist herbivores may affect exotic and native species differently. Hence, **differential attack by generalists may**

explain failures of exotic plants in certain contexts, but appears not to be the rule across various environmental conditions.

(2) **Exotics and natives differ in their rate of seedling recruitment and the magnitude they affect biomass production** in plant communities. Across all experiments, the introduction of exotic species resulted in higher biomass production, compared to native species. This suggests the existence of differences between native and exotic species, on the one hand, in characteristics related to plant growth, and on other hand, in the mechanisms driving the relationship between diversity and productivity. I tested the latter and found that **exotic and native communities differed in the mechanisms driving the diversity-productivity relationship**, but in the opposite direction as hypothesized. Finally, the importance to include a large range of environmental conditions (i.e. multiple sites and regions) was demonstrated by the differences in magnitude – thus context-dependency – of generalist herbivory and disturbance in determining exotic vs. native colonization success (i.e. increase in species richness), abundance and productivity.

Our general understanding of biological invasions is still limited (Gurevitch et al., 2000; Kueffer et al., 2013). Results of my thesis clearly emphasize the need for more multi-site and multi-species experiments, to disentangle context-dependency from general mechanisms. The finding that the magnitude of local processes as disturbance and herbivory is context-dependent, suggests also to re-consider the generality of other hypotheses (such as the one of enemy release by specialists) and processes (e.g. positive vs. negative soil feedbacks) in the context of biological invasions by the usage of multi-species and multi-site studies. A further challenge for future studies is to elucidate the strategies (i.e tolerance vs resistance) of exotic and native plants to cope with (generalist) herbivory across i) ontogenetic stages and ii) multiple plant species. One approach could be to measure differences in trait combinations relevant to herbivory (see, Loranger et al. 2013) between those native and exotic species which were able to become established at a given site and to them with traits of resident species. This could likely help to remove the context-dependency of response to herbivory. Furthermore, it would be pivotal for our understanding of biological invasions to find the characteristics and processes that lead to higher recruitment success and productivity in exotic species. In this regard research on i) germination characteristics (e.g. higher germination plasticity vs. constantly high germination rates, Wainwright and Cleland, 2013) and ii) plant-soil feedbacks (Levine et al., 2006; Kulmatiski et al., 2008) across multiple species and along natural environmental gradients is needed. Finally, despite the fact that nowadays ecosystems are composed both out of native and exotic species, research on the mechanisms driving the relationship between diversity and ecosystem functioning is derived primarily from native systems and rarely interactions with higher trophic levels are included. In this regard my results indicate that in-depth research is urgently needed to gain a better and more complete understanding about the mechanisms shaping diversity and ecosystem functioning in these "novel" ecosystems. To conclude, approaching these challenges in the future may help to derive a more complete understanding of the processes and mechanisms driving biological invasions and the consequences for diversity and functioning in ecosystems.

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APPENDIX

CURRICULUM VITAE

LOTTE KORELL

Date and place of birth: 15.05.1986, Hamburg
Nationality: German
Address: Nauestraße 14
06110 Halle (Saale)
Email: lo.korell@gmail.com

Education

02/2011- present	PhD study at Martin-Luther-University of Halle-Wittenberg (MLU), Institute of Biology/ Geobotany and Botanical Garden. Research topic: “*The role of seed limitation, herbivory and biological invasions for biodiversity and productivity of herbaceous communities*“ Funding: Graduate school of UFZ (HIGRADE) Thesis advisors: Prof. I. Hensen (MLU), Prof. H. Bruelheide (MLU), Dr. H. Auge (UFZ),
10/2008-01/2011	Master in Biology at the University of Hamburg with special focus on Biodiversity and Ecology. MSc Thesis: „*Vegetation of floodplain meadows along the climatic gradient at the Middle Elbe River*“(1.0, excellent) Thesis advisors: Prof. K. Jensen Final mark: 1.18 (excellent)
10/2005-10/2008	Bachelor in Biology at the University of Hamburg BSc Thesis: „*Studies on the reproductive biology of Fritillaria meleagris L. in the Haseldorfer Marsch*“(1.0, excellent) Thesis advisors: Prof. K. Jensen Final mark: 1.65 (good) – among the 5% best
08/1992-07/2005	Abitur (secondary school leaving examination) at the Rudolf-Steiner-Schule Hamburg-Altona Final mark: 1.9 (good)

Occupational and practical competences

02/2011 - present	Attendance of the graduate school HIGRADE (UFZ)
11/2007 - 01/2011	Research assistance at University of Hamburg, Prof. K. Jensen: - *Apium repens*-monitoring - field and laboratory work in diverse PhD projects - digitalizing of vegetation maps, research project BASSIA - teaching assistance in University courses
07/2009 - 08/2009	International summer school „Wetland Science and Management“ at Hamburg University (Prof. K. Jensen and Prof. A. Baldwin)
08/2007 - 09/2007	Practical training in the development association of the Biosphere Reserve Oberlausitzer Heide- und Teichlandschaft (conservation ecology, management of heathland habitats, environmental education)

Teaching and supervision

05/2013 - 04/2014	Birgit Lang. Master Thesis: „*Effekte generalistischer Herbivorie, Störung, und funktioneller Merkmale auf die Keimlingsetablierung und Produktivität nativer und exotischer Graslandarten*“(now PhD student at University of Jena)
05/2012 - 06/2013	Robin Schmidt. Diploma Thesis: „*The impact of exotic vs. native plant species origin and gastropod herbivory on productivity of experimental grassland communities*” (now PhD student at iDiv)
03/2012 - 12/2012	Lisa Petter. Bachelor Thesis: „*Räumliche Variation der Schneckenfauna in Grünländern der Region Halle-Herbivorie an ausgewählten Grünlandarten*“
10/2011 - 12/2011	Robin Schmidt. Research group internship: „*Die Rolle von Ausbreitungslimitierung, Herbivorie und invasiven Pflanzenarten auf die Diversität und Produktivität von Grünland-Ökosystemen*“
08/2011 - 03/2012	Sonja Nakasian (Internship, USA)
05/2011	Student excursion „Vegetation of forests”, University of Halle-Wittenberg (MLU), Institute of Biology/ Geobotany and Botanical Garden

Research experience abroad

05/2013 05/2012 02/2012 09-10/2011	Fieldwork in California (USA), Pepperwood Preserve, for PhD thesis in cooperation with Dr. C. Stein, UC Berkeley (DAAD travel grant)
08/2008	International summer school „Wetland Science and Management“ at University of Maryland College Park, hosted by Prof. K. Jensen and Prof. A. Baldwin (DAAD travel grant)

List of publications

Publications of this thesis

Korell, L., Schmidt, R., Bruelheide, H., Hensen, I., Auge, H. (in revision) How is the diversity-productivity relationship of experimental grassland mesocosms influenced by native versus exotic species origin and slug herbivory? *Oecologia.*

Korell, L., Lang, B., Hensen, I., Auge, H., Bruelheide, H. (to be submitted) Interactive effects of plant origin, herbivory and disturbance on seedling recruitment are weakly reflected at the community level.

Korell, L., Stein, C., Hensen, I., Bruelheide, Suding, K.N., H., Auge, H. (under review) Stronger effect of gastropods than rodents on seedling establishment, irrespective of native or exotic plant origin. *Ecology*.

Maron, J. L., Auge, H., Pearson, D. E., **Korell, L**., Hensen, I., Suding, K. N., Stein, C. (2014) Staged invasions across disparate grasslands: effects of seed provenance, consumers and disturbance on productivity and species richness. *Ecology Letters*, 17: 499-507.

Other publications by the author

Ludewig, K., **Korell, L.,** Löffler, F., Scholtz, M., Mosner, E., Jensen, K. (2014) Vegetation patterns of floodplain meadows along the climatic gradient at the Middle Elbe River. *Flora*, 8, 446-455.

Conference contributions and invited talks

Korell, L., Stein, C. , Hensen, I., Bruelheide, H., Auge, H. (2014) *Generalist herbivores determine seedling establishment independent of native or exotic plant species origin*. Talk (Award, 2nd best presentation), 27th Annual conference of the Population Biology Section of the Ecological Society of Germany, Switzerland and Austria (GFÖ), Konstanz

Korell, L. Stein, C. , Hensen, I., Bruelheide, H., Auge, H. (2014) *Aliens versus predators: experimental invasions in grassland ecosystem*. Talk, HIGRADE Spring-Conference (UFZ), Leipzig

Korell, L. Stein, C., Suding, K.N., Hensen, I., Bruelheide, H., Auge, H. (2013) *How is seedling recruitment of exotic vs. native species influenced by rodents and terrestrial gastropods*? Invited talk together with C. Stein, working group Prof. J. Bartolome, UC Berkeley

Korell, L. Stein, C., Hensen, I., Bruelheide, H., Auge, H. (2012) *Effects of rodent herbivory on diversity and productivity of native versus invaded grassland communities.* Talk, 42th Annual conference of Ecological Society of Germany, Switzerland and Austria (GFÖ), Lüneburg

Korell, L. Stein, C., Hensen, I., Bruelheide, H., Auge, H. (2012) *The role of seed limitation, herbivory and biological invasions for species diversity and productivity in herbaceous communities.* Invited talk, working group Prof. K.N. Suding, UC Berkeley

Korell, L., Ludewig, K., Löffler, F., Jensen, K. (2011) *How does a regional climatic gradient affect vegetation of floodplain meadows*. Poster, 41th Annual conference of Ecological Society of Germany, Switzerland and Austria (GFÖ), Oldenburg

Korell, L., Ludewig, K., Löffler, F., Jensen, K. (2010) *Vegetation patterns of floodplain meadows along the regional climatic gradient along the Middle Elbe river.* Poster, 40th Annual conference of Ecological Society of Germany, Switzerland and Austria (GFÖ), Giessen

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „ Plant species origin, herbivory and disturbance: effects on seedling recruitment and consequences for grassland diversity and productivity“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), 10.02.2015

Lotte Korell