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On species invasions in urban grasslands: Interactions with soil biota, functional diversity, and global change

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Contents:

Foreword

This dissertation is a cumulative work of manuscripts, either published in peer-reviewed journals or in preparation for submission. Therefore, this thesis is based on the following articles:

Schittko, C. and Wurst, S., 2014. Above- and belowground effects of plant-soil feedback from exotic *Solidago canadensis* on native *Tanacetum vulgare*. *Biological Invasions*, 16(7), pp.1465–1479. doi:10.1007/s10530-013-0584-y, (Submitted: 21 February 2013; Accepted: 12 November 2013; Published online: 30 November 2013; Editor: Inderjit)

Schittko, C., Hawa, M. and Wurst, S., 2014. Using a Multi-Trait Approach to Manipulate Plant Functional Diversity in a Biodiversity-Ecosystem Function Experiment. *PloS one*, 9(6), p.e99065. doi:10.1371/journal.pone.0099065, (Submitted: 29 November 2013; Accepted: 9 May 2014; Published online: 4 June 2014; Editor: Andrew Hector)

Schittko, C. and Wurst, S., 2014. Bottom-up effects of plant functional trait diversity on arthropod abundance and diversity in an urban grassland plant community. (In preparation for submission)

Schittko, C., Forstreuter, M. and Wurst, S., 2014. Linking species invasions to environmental change: Consequences of elevated temperature and soil compaction on the composition and biodiversity of an urban plant community. (In preparation for submission)

Summary

Human activities are the cause of the spread and establishment of many species around the world. The consequences are of various kinds, but species invasions are generally recognized as a major environmental problem, which can change ecosystem functioning and influence biodiversity on local and global scales. Due to their high proportion of exotic species, urban grasslands have a great potential to study the impacts of species invasions in a plant community context rather than focusing on single species. The main aims of this thesis were to elucidate (1) the ecological impacts of exotic plant species in urban grassland communities and (2) the mechanisms why these species become dominant in communities where they are not native.

In a plant-soil feedback experiment (**Chapter 2**), I investigated whether plant-soil feedback effects facilitate the invasion of an exotic plant (*Solidago canadensis*) in its new range. I hypothesized that feedback effects from the soil do not only affect plant growth but also plant interactions with organisms at higher trophic levels (i.e. shoot herbivores), which might be an important mechanism affecting plant community composition in the field. Results showed that neither growth of *S. canadensis* nor its interaction with herbivores was affected by plant-soil feedback effects. However, I found that a native competitor (*Tanacetum vulgare*) performed better with soil biota conditioned by *S. canadensis.* This is indicative for an indirect facilitative effect from an exotic plant species on a native plant species and was most likely mediated by a group of root-colonizing fungi, the dark-septate endophytes, whose abundance seems to be suppressed in *S. canadensis* soils.

In the second experiment (**Chapter 3**), I investigated in a mesocosm study the fundamental question whether the functional trait diversity of a plant community consisting of native and exotic plant species is positively related to ecosystem functions such as community productivity and resistance against invasion. As a novel aspect to the functional trait concept, I treated the species' attribute of being native or exotic as a functional trait and used it alongside morphological and resource capture related traits to predict ecosystem functions from trait diversity. Additionally, I performed a trait analysis to determine the relative importance of each trait in explaining the relationship between functional trait diversity and productivity. I found a significant positive linear correlation of functional trait diversity with aboveground productivity and a negative correlation with invasibility of the plant communities. Based on community-weighted mean calculations for each functional trait, I figured out that the traits N-fixation and the species origin, i.e. being native or exotic, played the most important role for community productivity. These results suggest that the identification of the impact of functional trait diversity and the relative contributions of relevant traits is essential for a mechanistic understanding of the role of biodiversity for ecosystem functions such as aboveground biomass production and resistance against invasion.

The fourth experiment (**Chapter 4**) was closely connected to the experiment from the previous chapter: Here I investigated whether the plant functional trait diversity affects the abundance and diversity of arthropods living on these plants. In this context the attribute of a plant species being native or exotic was considered as a functional trait as well. First, I found that the abundance of specialist aphids of the focus plant species *Cirsium arvense*, as well as the abundances of mutualistic aphid-tending ants and predatory ladybird beetles were negatively related to plant functional trait diversity. Second, and in contrast to the first result, I found that the total abundances and species richnesses of herbivores and predators present in the mesocosms were positively related to functional diversity. The diversity effect on abundances of higher trophic levels dampened from herbivores to predators. Based on community-weighted mean calculations for each functional trait, I figured out that traits related to plant quality and the plant species origin, i.e. being native or exotic, played the most important role for predicting arthropod abundance and species richness.

In my final experiment (**Chapter 5**), I focused on abiotic stresses. In a mesocosm experiment, I investigated whether individual elements of global change interact synergistically together on the shaping of plant communities. I altered the abiotic conditions temperature and soil compaction and focused on the differential responses of exotic and native plant species within that community. Furthermore, I investigated impacts of both factors on diversity, evenness, and functional trait diversity of the plant community. The results showed that elevated temperature and soil compaction had a negative and positive effect on community productivity, respectively, while no interactions between the environmental factors were found. The responses were driven by the group of exotic plant species, while the group of native plant species remained unaffected. Species diversity, evenness, and functional trait diversity were positively affected by elevated temperature but not by soil compaction. I suggest that this was likely due to a reduction of competition in the community. These results demonstrate that global change factors can have independent and contrasting impacts on the composition and biodiversity of a grassland community.

German summary (Zusammenfassung)

Menschliche Aktivitäten führen dazu, dass viele Arten sich in Gebieten ausbreiten und etablieren können, wo sie natürlicherweise nicht heimisch sind. Die Auswirkungen dieser biologischen Invasionen sind vielgestaltig; im Allgemeinen werden sie jedoch als ein globales Problem betrachtet, da sie die Funktionsweise von Ökosystemen verändern und eine Gefahr für die Biodiversität darstellen können. Pflanzengemeinschaften in urban-industriellen Lebensräumen zeichnen sich durch einen vergleichsweise sehr hohen Anteil von gebietsfremden Pflanzenarten aus. Dadurch eignen sich diese Gemeinschaften besonders gut, um die Auswirkungen von gebietsfremden Pflanzenarten auf fremde Ökosysteme, sowie die Mechanismen, die zu ihrer Etablierung geführt haben, zu erforschen.

In einem sogenannten *plant-soil feedback*-Experiment (**Kapitel 2**) wurde untersucht, ob *feedback*-Effekte zwischen Pflanze und Bodenorganismen das Wachstum einer gebietsfremden Pflanzenart (*Solidago canadensis*) in ihrem neuen Lebensraum fördert. Es wurde vermutet, dass diese *feedback*-Mechanismen nicht nur das Wachstum der Pflanze selbst, sondern auch ihre oberirdischen Interaktionen mit Herbivoren beeinflussen. Die Ergebnisse dieses Experiments haben gezeigt, dass weder das Pflanzenwachstum noch die Herbivoren-Interaktion von *S. canadensis* durch *plant-soil feedback*-Mechanismen beeinflusst wurden. Es wurde jedoch auch gezeigt, dass eine koexistierende einheimische Pflanzenart (*Tanacetum vulgare*) durch die von *S. canadensis* ausgelösten Veränderungen im Boden profitierte. Vermutlich unterdrückt *S. canadensis* eine Gruppe von wurzelbesiedelnden Endophyten, die sogenannten dunkel septierten Endophyten, was dazu führt, dass die einheimische Pflanzenart *T. vulgare* besser in Böden wächst, die von *S. canadensis* beeinflusst wurden als in ihren eigenen Böden.

Im zweiten Experiment (**Kapitel 3**) wurde in einem Mesokosmos-Versuch untersucht, ob die funktionelle Diversität einer Pflanzengemeinschaft bestehend aus einheimischen und gebietsfremden Arten, die Produktivität der Gemeinschaft, sowie deren Resistenz gegenüber weiteren Invasionen gebietsfremder Arten beeinflusst. Der floristische Status einer Pflanzenart, welcher angibt ob sie gebietsfremd oder heimisch ist, wurde neben morphologischen und physiologischen funktionellen Merkmalen benutzt, um den Zusammenhang zwischen funktioneller Merkmalsdiversität und den beiden Ökosystemfunktionen Produktivität und Resistenz gegenüber Invasionen zu erklären. Die Ergebnisse dieses Experiments haben gezeigt, dass die Produktivität dieser Pflanzengemeinschaft positiv mit der funktionellen Merkmalsdiversität und negativ mit der Invasion einer weiteren gebietsfremden Art korreliert. Des Weiteren wurde anhand einer

Merkmalsanalyse gezeigt, dass das funktionelle Merkmal Stickstofffixierung und der floristische Status einer Art die beiden ausschlaggebendsten Merkmale innerhalb der Pflanzengemeinschaft waren, um deren Produktivität zu erklären.

Die Zielstellung des dritten Experiments (**Kapitel 4**) war eng mit derjenigen des vorherigen Experiments verknüpft: Es wurde in einem Mesokosmos-Versuch untersucht, ob die funktionelle Merkmalsdiversität einer Pflanzengemeinschaft bestehend aus einheimischen und gebietsfremden Arten, die Abundanz und Diversität von Arthropoden, die in dieser Gemeinschaft leben, beeinflusst. Die Ergebnisse haben gezeigt, dass die steigende funktionelle Merkmalsdiversität der Pflanzengemeinschaft die Abundanz einer spezialistischen Blattlausart, sowie die Abundanzen ihrer Symbiosepartner (Ameisen) und Antagonisten (Marienkäfer) negativ beeinflusst. Im Gegensatz dazu wurde gezeigt, dass die funktionelle Pflanzendiversität sich positiv auf die Artenanzahlen und Abundanzen aller Herbivoren und Prädatoren in der Gesellschaft auswirkte. Das Merkmal Stickstofffixierung und der floristische Status der Pflanzenarten hatten auf diesen Zusammenhang den größten Einfluss.

Im letzten Experiment (**Kapitel 5**) wurde in einem Mesokosmos-Versuch untersucht, inwieweit sich die abiotischen Stressfaktoren Bodenverdichtung und Temperaturerhöhung auf die Produktivität und die Zusammensetzung dieser Pflanzengemeinschaft auswirken. Hinsichtlich der Produktivität hatte die Temperaturerhöhung einen negativen, und die Verdichtung des Bodens einen positiven Effekt auf die Gemeinschaft. Die Effekte wurden größtenteils durch die gebietsfremden Pflanzenarten innerhalb der Gemeinschaft hervorgerufen, da diese am stärksten auf die beiden Stressfaktoren reagierten. Der Rückgang der gebietsfremden Pflanzenarten unter erhöhten Temperaturbedingungen wirkte sich positiv auf die Diversität, Evenness und funktionelle Diversität der Gemeinschaft aus. Wahrscheinlich wurde dies durch einen Rückgang der interspezifischen Konkurrenz zwischen den Pflanzenarten hervorgerufen. Diese Ergebnisse verdeutlichen, dass verschiedene abiotische Stressfaktoren unabhängige und gegensätzliche Auswirkungen auf die Zusammensetzung und Biodiversität einer Gemeinschaft haben können.

Chapter 1

General introduction

Humans introduce plant species into new habitats both intentionally and accidentally, and many of them become established in their new ranges. The potential for these exotics to alter ecosystem structure and function has become broadly recognized in the last decades (Vitousek et al. 1997, Vilà et al. 2007). Furthermore, human introduced species impact ecosystem services that are essential for human well-being resulting in substantial economic costs (Vilà et al. 2010, Keller et al. 2011). Thus, understanding why some species establish and become dominant in communities where they are not native is of great scientific, economic and social interest as human activities such as trade, transport and travel, which cause species dispersal into new habitats, will continue to increase (Keller et al. 2011). Throughout this thesis, these newcomers in plant communities are named exotic plant species (see Bäucker [2013] for an overview on the multitude of names and terms that are also common in invasion ecology).

Although research on species invasions has a long tradition, publications on this topic have been numerous only since the 1990s (Darwin 1859, Elton 1958, Richardson and Pyšek 2008). From this point of view, invasion ecology is still a young discipline (Pyšek and Hulme 2009, Jeschke et al. 2012). Along with the impacts exotic plants bear on native communities, researchers focused intensively on the mechanisms behind the successful establishment and spread of exotic plant species (Richardson and Pyšek 2006). So far, a multitude of potential explanations for successful invasions were proposed, and many of them were supported numerous times (Mitchell et al. 2006, Catford et al. 2009, Jeschke et al. 2012), while others lack support and are discussed to be rejected (Moles et al. 2012, Jeschke et al. 2012). However, all existing explanations are still termed as ‘hypotheses’ or ‘theories’ in invasion ecology literature, which demonstrates how much the research on this field is still in progress. Catford et al. (2009) list 29 leading theories (and there are several more) and point out that many of the existing theories are redundant as they overlap with other theories.

The existing theories can be categorized depending on their characteristics/foci (Catford et al. 2009, Jeschke et al. 2012): There are theories that focus on (1) the invaded ecosystem such as the ‘biotic resistance hypothesis’ (i.e. ecosystems with high biodiversity are more resistant against invaders; Levine et al. 2004, Parker and Hay 2005, Alpert 2006). Other theories focus on (2) characteristics of the invader itself such as the ‘ideal weed hypothesis’ (i.e. life history, characteristics, and traits of the invader determine invasion success; Elton 1958, Rejmanek and Richardson 1996, Sutherland 2004).

Finally, there are theories that focus on (3) invader-ecosystem interactions such as the 'enemy release hypothesis' (i.e. exotics are released from their natural enemies in the new environment; Keane and Crawley 2002, Colautti et al. 2004). Within this thesis, I will follow approaches that belong to all three categories.

Species invasions and urbanization

Urbanization is a major global trend (UN 2010) that impacts biodiversity at different scales (Grimm et al. 2008). Within urban habitats, species assemblages are severely affected for two main reasons. First, intensified urban land use associated with habitat fragmentation (Bierwagen 2006) and changes in ecosystem functioning (Alberti 2005) lead to a decline in native plant species (Knapp et al. 2010, Duncan et al. 2011). Second, human activities, such as trade, transport, or gardening promote the arrival of exotic species (von der Lippe and Kowarik 2008, Kowarik 2010). Consequently, many urban floras show a high proportion of exotic species. In Berlin for example, exotic plant species accounted for 46 % of the present plant species richness in the year 2001 (Prasse et al. 2001). Consistently, urban-gradient studies show that, for many taxa, such as plants (Kowarik 2008), but also birds and butterflies (Blair 2001), the number of exotic species increases toward centers of urbanization, while the number of native species decreases. Within cities, the emergence of wastelands and abandoned areas (e.g. unmaintained industrial areas or railroad tracks) plays an important role for the establishment of exotic plant species (Kowarik 2011). These habitats are characterized by high levels of disturbance, altered soil, water, and air conditions, which promote the growth of stress-tolerant, early-successional vegetation (Tredici 2010). It is assumed that many exotic plant species are pre-adapted to the novel site conditions because they mimic those of their original areas (Sukopp and Wurzel 2003, Kowarik 2011). In general, the presence of wastelands in cities contributes significantly to the total biodiversity in urban areas, although the extent of their role is poorly documented (Muratet et al. 2007).

Hobbs et al. (2006) addressed the result of such changes as 'novel ecosystems', which are characterized by two features: major human-induced changes in the abiotic environment and significant changes in the species composition due to local extinctions or introduction of novel biotic elements, with the potential for changes in ecosystem functioning. Furthermore, the authors note that it is of great concern to study whether these new species combinations provoke 'new' ecosystem functioning or properties and to what extent will a new combination of species maintain similar functional properties with respect to the old species pool (Hobbs et al. 2006).

Within my thesis, I focused on this ‘novel’ vegetation of urban wastelands and abandoned areas. Due to their high proportion of exotic species, they have a great potential to study the impacts of species invasions in a plant community context rather than focusing on single taxa. I aimed to conduct my experiments with comparatively high realism. In my studies, therefore, I always maintained the ecological context of soil, plants, and organisms of higher trophic levels.

Interactions of exotic plants with soil biota

Individual exotic and native plant species are affected in their performance by direct and indirect interactions with soil biota (Wardle et al. 2004, van der Putten et al. 2007). These interactions are understood as plant-soil feedbacks (Bever 2003). In the context of plant-soil interactions, feedback mechanisms posit that a change in soil conditions causes changes in the plant component, which in turn causes further change in the soil, and vice versa (Ehrenfeld et al. 2005). Microbial activity and community composition is considered as one of the major driving factors of plant-soil feedback effects (Ehrenfeld et al. 2005). Aside from affecting plant community composition, recent work suggests that these feedbacks between exotic plants and their soil biota community increase their dominance in the new communities (Klironomos 2002, Wolfe and Klironomos 2005). A reason why exotic species can become invasive in a new habitat is that they are released from species-specific belowground enemies that control their abundance in the native range (van der Putten et al. 2013). For instance, in a study in an old field, exotic plant species had neutral to positive plant-soil feedbacks compared to dominant native plant species which had negative feedbacks (Klironomos 2002).

It is known that the effects of soil organisms on plant performance may cascade upwards to affect above-ground herbivore performance. Most of the studies investigated effects of root herbivores (e.g. Masters et al. 1993, Soler et al. 2005), arbuscular mycorrhizal fungi (Hartley and Gange 2009) and decomposers (Scheu et al. 1999, Wurst and Jones 2003) on above-ground invertebrates. However, it is largely unknown whether plant soil feedback effects affect plant interactions with herbivores (Morriën et al. 2011), which could be a potential mechanisms that contributes to the invasion success of exotic plant species.

Species invasions and ecosystem functioning

Exotic plant species can affect ecosystem processes and functions (Levine et al. 2003, Vilà et al. 2010). Two of the most observed effects are that exotic plant species reduce local plant species diversity and increase plant production of the invaded community (see Vilà et al. 2011 for a meta-analysis). This is contrary to what diversity-ecosystem functioning experiments would predict and supports the importance of sampling effects in the patterns observed in such studies (Cardinale et al. 2006). Experimental work has shown that a strong invader can essentially reverse the positive diversity–productivity relationship (Zavaleta and Hulvey 2004, Maron and Marler 2008). Recent analysis suggests that exotic plant invasions may result in a sampling effect where ecosystem production is driven by the addition of a single highly productive species, even if overall species diversity declines (Vilà et al. 2011).

Exotic plant species may also have bottom-up impacts on higher trophic levels, although these effects are of lower magnitude than those within the same trophic level (Vilà et al. 2011). The effect of exotic plants on organisms at higher trophic levels might depend on the degree of their dependence on exotic plants as a food resource (de Groot et al. 2007, Gerber et al. 2008). Studies which have simultaneously investigated the impacts of alien plants on primary productivity and on higher trophic levels are scarce (Valtonen et al. 2006, de Groot et al. 2007, Gerber et al. 2008) and more are needed to understand how frequent cascading effects occur across trophic levels.

Species invasions and global change

Researchers recognize human-caused species invasions as an important element of global change (Vitousek et al. 1997, Sala et al. 2000). Other commonly recognized elements of global change include biodiversity loss, greenhouse-gas driven climate change, increasing nitrogen (N) deposition and changing patterns of land use that fragment habitats and alter disturbance regimes. These latter global change elements can affect species distributions and resource dynamics in terrestrial and aquatic ecosystems, and can consequently interact with species invasions (Dukes and Mooney 1999). Predicting the effects of the many other elements of global change on species invasions is a challenging and complex task (Huenneke 1997). However, most of the current knowledge of this field stems from predictive or theoretical work (e.g. Dukes and Mooney 1999, Pyšek and Richardson 2007, Hellmann et al. 2008) in which it is suggested that exotic plants may deal better with abiotic stresses because of certain characteristics they share. For example, it was noted that many exotic plant species have a broad environmental tolerance and show rapid growth rates (Sexton et al. 2002) which are predicted to allow them to tolerate climate change better than natives. Furthermore, as many recent established exotic plant species in Central Europe are originating from warmer climate regions (Tamis et al. 2005), they may be better able to cope with climate-induced stresses than native plant species. It was also shown that exotic plant species experience a less negative effect from their soil biota communities than related native species under current and predicted future temperatures (van Grunsven et al. 2010), indicating that plant-soil feedback processes are also relevant in future plant communities.

Besides climate change, human land use changes are regarded as one of the main drivers of biodiversity loss worldwide (Sala et al. 2000). Numerous observational studies conducted in the context of plant invasions showed that human land use changes such as urbanization (McKinney 2006), silviculture (Parker et al. 2010), agriculture (Mosher et al. 2009), or livestock grazing (Keeley et al. 2003) favor the establishment of exotic plant species. Land use change is often linked to disturbance (Hobbs 2000) and it is assumed that species may become invasive when they are confronted with similar disturbances as in their original range (Vitousek et al. 1997).

Theoretical research suggests that elements of global change such as climate change and intensified land use may have synergistic effects on species invasions which may lead to a new thread for biodiversity (Vitousek et al. 1997, Dukes and Mooney 1999, Vilà et al. 2007, Hellmann et al. 2008). However, experimental studies are still missing in this field.

Thesis outline and research objectives

The main aims of this thesis are to elucidate (1) the ecological impacts of exotic plant species in urban grassland communities, and (2) the mechanisms why these species become dominant in communities where they are not native. By utilizing current concepts of plant ecology and my own ideas to modify these concepts, I intended to make a substantial contribution to the field of invasion ecology.

I started with a plant-soil feedback experiment (**Chapter 2**) to investigate whether plant-soil feedback effects facilitate the invasion of an exotic plant (*Solidago canadensis*) in its new range. I hypothesized that feedback effects from the soil do not only affect plant growth but also plant interactions with organisms at higher trophic levels (i.e. shoot herbivores), which might be an important mechanism affecting plant community composition in the field. Additionally, I analyzed abundances of several groups of soil biota to elucidate which soil organisms contributed to the feedback effects in this study.

In the second experiment (**Chapter 3**), I investigated in a mesocosm study the fundamental question whether the functional trait diversity of a plant community consisting of natives and exotic plant species is positively related to community productivity. As a novel aspect to the functional trait concept, I treated the species' attribute of being native or exotic as a functional trait and used it alongside morphological and resource capture related traits to predict plant community productivity from trait diversity. Additionally, I performed a trait analysis to determine the relative importance of each trait in explaining the relationship between functional trait diversity and productivity. The species' attribute of being native or exotic was included in this analysis as well.

Another goal of this experiment was to elucidate whether functional trait diversity affects community resistance against invasion. This part of the experiment linked the 'biotic resistance hypothesis' to the functional trait concept. I added seeds of an exotic plant species to the pre-established communities and evaluated the seedling establishment of this species.

The fourth experiment (**Chapter 4**) was closely connected to the experiment from the previous chapter: Here I investigated whether plant functional trait diversity affects the abundance and diversity of arthropods living on these plants. In this context the attribute of a plant species being native or exotic was considered as a functional trait as well.

In my final experiment (**Chapter 5**), I focused on abiotic stresses. In a mesocosm experiment, I investigated whether individual elements of global change interact synergistically together on the shaping of plant communities. I altered the abiotic conditions temperature and soil compaction and focused on the differential responses of exotic and native plant species within that community.

Chapter 2

Above- and belowground effects of plant-soil feedback from exotic *Solidago canadensis* on native *Tanacetum vulgare*

Abstract

Plant-soil feedback responses for native and invasive plant species are well documented, but little is known about how feedback effects from the soil biota community affect plant interactions with herbivores. Here we examine whether changes of the soil biota community by the successful invader *Solidago canadensis* influence growth and herbivore susceptibility of two coexisting native plant species (*Tanacetum vulgare*, *Melilotus albus*). Root zone soil from two different habitat types ('urban' and 'suburban') was collected and used as inocula in a plant-soil feedback study. Each plant species was grown either in its own soil biota community or with the community with a history from the competitive invasive or native plant species. To identify potential drivers of responses to the different soil biota communities, we analyzed root colonization by arbuscular mycorrhizal fungi (AMF) and dark-septate endophytes (DSE), and the community composition of soil inhabiting nematodes at the end of our experiment. Results show that *S. canadensis* and *M. albus* were not affected by soil history. In contrast, *T. vulgare* showed increased plant growth in 'foreign' soil derived from *S. canadensis* root zone compared with its 'home' soil suggesting a growth promotion by the soil biota community of *S. canadensis*. From the examined drivers, the abundance of DSE explained the growth response of *T. vulgare* to the *S. canadensis* soil biota community best. However, shoot herbivory by banded snails (*Cepaea nemoralis*, *C. hortensis*) was not affected by soil history, but by the habitat type where the soil inocula originated. Our study shows that a native plant species may profit from the presence of an invasive competitor mediated by changes in the soil biota community.

Introduction

The consequences of species invasions are of various kinds, but they are generally recognized as a major environmental problem which can change ecosystem functioning and influence biodiversity on local and global scales (Vitousek et al. 1996, Vilà et al. 2007). Plenty of theories are proposed to better understand the mechanisms of the successful establishment and spread of exotic plant species in native communities (Catford et al. 2009). More recent work suggests that interactions between plants and soil biota may play an important role in the invasion process (Klironomos 2002, Wolfe and Klironomos 2005, Wurst et al. 2011).

The concept of plant-soil feedback has become widely recognized and was also incorporated in the research on plant species invasions (Klironomos 2002, Callaway et al. 2004, van Grunsven et al. 2007). The basic theoretical background of plant-soil feedback experiments is that plants first influence their soil environment by affecting the composition of the soil biota community and/or soil nutritional properties, which is called soil conditioning (Brinkman et al. 2010). Then, effects of the previous conditioning are measured by assessing the soil effects on subsequent plant growth. Most studies indicate that native plant species show a negative soil feedback (i.e. they perform better in soils that were not conditioned by themselves), whereas exotics exhibit a positive feedback (i.e. they perform better in soils that were conditioned by themselves) (Klironomos 2002) or a less negative feedback than natives (van Grunsven et al. 2007, Engelkes et al. 2008, Morriën et al. 2011). But there are also studies which found no difference in the effect strength of plant-soil feedback between native and exotic species (Dostál and Palečková 2011) and studies which documented negative soil feedbacks for successful invaders (Nijjer et al. 2007). By considering the numerous examples of impacts of exotic plant species on soil biota communities in their new ranges (Belnap and Phillips 2001, Kourtev et al. 2002, Callaway et al. 2004), the idea of linking the plant-soil feedback concept with the expansion of exotic plants becomes obvious.

The majority of studies on exotic plant invasions and interacting organisms have been conducted in a strictly bi-trophic framework involving plants and their respective antagonists or symbionts (Harvey et al. 2010). Experimental studies with a multitrophic perspective involving both, the above- and the belowground compartment, are lacking in this field, although a growing body of research highlights the importance of interactions between above- and belowground biota for plant performance (van der Putten et al. 2001, Wardle et al. 2004, Soler et al. 2005, van Dam et al. 2005, Wurst and Rillig 2011). As far as we are aware, only one study (Morriën et al. 2011) has looked at consequences of plant-soil feedback for a higher trophic level, i.e. the interaction of native and range-expanding plant species with aboveground insect herbivores. The authors did not find a correlation between the strength of aboveground herbivory and the feedback from the soil. This does not mean that plant-soil feedback effects and aboveground herbivory may not affect each other. A recent study by Bezemer et al. (2013) showed that herbivore presence during the soil conditioning phase has an influence on the soil feedback effect in the subsequent phase.

The present study links research on plant species invasions with the plant-soil feedback approach by integrating both below- and aboveground biotic interactions. We investigated whether plant-soil feedback effects facilitate the invasion of an exotic plant by using one of the most dominant exotic species in disturbed urban areas – *Solidago canadensis* – and two of its native competitors as target plant species. We used a natural experimental approach by collecting field soil samples of known plant species and using them as inocula for the feedback phase. A strength of this approach is that it uses soils conditioned by plants for long periods of time under natural field conditions (Kulmatiski and Kardol 2008). Some studies have shown that interactions between plants and soil microorganisms depend on soil conditions (Marrs et al. 1991, Marschner et al. 2004, Bezemer et al. 2006). Even within a single soil type, the biomass and activity of the soil microbial community generally depends on soil fertility conditions (Bardgett et al. 1999). In order to assess whether the plant-soil feedback effects are persistent over the range of different habitats in which *S. canadensis* is able to become abundant, we took the soil samples at sites of two different habitat types ('urban' and 'suburban'). Besides assessing the effects of soil biota history on plant biomass production (i.e. the classical plant-soil feedback approach), we investigated the effects of soil history on plant susceptibility to leaf herbivory by snails, the only herbivores we regularly found feeding on both *S. canadensis* and the two native target plant species at the study sites. As far as we are aware, only two studies have investigated plant-mediated effects of soil biota on snails (Thompson et al. 1993, Wurst and Rillig 2011), although molluscs have been reported to be the second most important herbivores after rodents in grasslands (Hulme 1996).

To elucidate which component of the soil biota community could have affected plant growth and leaf herbivore attack we focussed on arbuscular mycorrhizal fungi (AMF) and dark-septate endopyhtes (DSE) as two wide-spread root associated groups of fungi, and on soil nematodes as potential drivers of the feedback effects. AMF may affect interactions with aboveground herbivores, but investigations have shown that there is a large amount of specificity and context dependency in the outcome of these interactions, reflecting the influence of fungus and host plant, their genotypes, the insect species used, and environmental factors (Hartley and Gange 2009). Not much is known about the ecological role of DSE and to which extent they interact with plants and other plant colonizing fungi like AMF and fine endophytes (Jumpponen 2001, Postma et al. 2007). They may act as mutualists with positive effects on plant performance (Newsham 2011). But because of the high variability of their effects on plants, which may also range from neutral to negative, it is assumed by some authors that they stretch a continuum from mutualism to antagonism (Jumpponen and Trappe 1998, Jumpponen 2001, Tellenbach et al. 2011). Impacts of root-feeding nematodes on aboveground insect herbivores are varying as well, depending for example on the insect feeding guild (Wurst and van der Putten 2007, Kaplan et al. 2009).

With a full factorial greenhouse study we aimed to answer thus three major questions: (1) whether plant-soil feedback effects facilitate the invasion of an exotic plant in its new range and whether these effects are persistent in two different invaded habitat types, (2) whether feedback effects may cascade up to higher trophic levels (i.e. shoot herbivores) and (3) if any of the observed soil organisms (AMF, DSE and nematodes) may have contributed to the feedback effects.

Methods

We applied a method that differed from the known approaches of plant-soil feedback experiments conducted in other studies (Klironomos 2002, Callaway et al. 2004, van Grunsven et al. 2007, see Brinkman et al. 2010 for a comparison). One approach (e.g. Klironomos 2002) consists of a conditioning phase in the greenhouse with the experimental plant species growing twice in succession in pots and a subsequent feedback phase with every plant species growing either in ‘home’ treatment (plants growing in soil with their own respective soil history) or ‘foreign’ treatment (soil with history of other plant species). Other researchers obtained the soil directly from the rhizosphere of the target plant species in the field (Callaway et al. 2004, van Grunsven et al. 2007), sterilized half of the soil volume and used the sterile and the unsterile half as inocula for sterile background soil to compare plant growth with sterile and unsterile inoculation. The approach applied in our study is as follows: soil sampling from the root zone of the experimental plant species took place in the field, and in a subsequent feedback phase in the greenhouse we grew every plant species in sterilized background soil inoculated with field soil with a history of its own (‘home’) or of other plant species (‘foreign’). By obtaining soil samples from the root zones of the plant species in the field and using them for inoculation, we assume that the conditioning phase has already taken place in the field, thus a conventional conditioning phase in the greenhouse is unnecessary in our study.

Plant species

We tested the effects of plant-soil feedback on plant growth and leaf herbivory by snails on three plant species, specifically *Solidago canadensis* L. (Asteraceae), *Tanacetum vulgare* L. (Asteraceae), and *Melilotus albus* Medik. (Fabaceae). The Canada goldenrod *S. canadensis* is a successful worldwide invader of North American origin where it is a characteristic species of tall-grass prairies, abandoned farmland, infrequently grazed pastures, and waste land (Werner et al. 1980). Introduced in the 18th century in Europe, it began to spread in the 19th century in Central Europe where it may become a highly abundant species in a variety of habitats like abandoned fields and disturbed habitats in urban areas (Kowarik 2003). Here it typically co-exists with dense stands of *T. vulgare* (tansy) and the more dispersed occurring *M. albus* (white sweet-clover). Both plant species are suggested to be native to Eurasia (Turkington et al. 1978).

Soil sampling and site description

In July 2010, soil samples were collected for each species at six sites across Berlin, Germany. According to the site surroundings, adjacent vegetation and former land use, the sites were classified as either ‘urban’ or ‘suburban’ sites. The three ‘urban’ sites can be characterized as highly disturbed habitats with a huge impact of human activity. The sites were used mainly as storage areas for building material during the construction of nearby buildings or railroad stations and have been abandoned at least five years. The three ‘suburban’ sites were former agricultural fields located in the middle of a forest (Grunewald) on the outskirts of Berlin and thus remained free from a tree layer unlike the surrounding forest vegetation. The three ‘suburban’ sites have been abandoned at least ten years. It was relevant that sites of one habitat type did not differ considerably among each other in terms of environmental variables which may influence the composition of the soil biota community. Therefore we took plant species composition as a proxy for site environmental characteristics and, eventually, selected three sites per area type that did not differ evidently in plant species composition and used them as replicate sites for the habitat type. Only sites where all three target plant species occurred with a population size of at least ten patches of clonal colonies (in terms of *S. canadensis* and *T. vulgare*) or ten individuals (in terms of *M. albus*) were taken into account.

At each site we sampled soil from the root zone of more than six different plant individuals or six colonies of each focal plant species. Samples were taken with a shovel to a depth of 30 cm while trying to ensure that the sampling locations were only impacted by the target species. To avoid interference caused by the two other target species we only took soil samples from locations with at least 5 m distance to the two other target species. The soil was then transferred to the lab, thoroughly homogenized within sites and species, and then sieved through a 4 mm mesh to remove stones, coarse roots, and other particles. For abiotic soil characterization pH was determined on a subsample of each soil sample with a pH meter. Another subsample was ground (Mill MM 2, Retsch, Germany) and the N and C content were determined with a CN analyzer (Euro EA, HEKAtech GmbH, Germany). An ANOVA detected no differences in pH between root zone samples of the three plant species or the two habitat types ($P > 0.05$). The C:N ratio did not differ between the root zone samples of the different plant species, but it differed significantly between the two habitat types ($P < 0.05$), i.e. the soil inocula from the 'suburban' sites had a lower C:N ratio (on average 14.50 ± 0.62 SE) than the soil inocula from the 'urban' sites (on average 24.85 ± 3.17 SE).

Experimental set-up

To keep abiotic soil conditions homogenous we used steamed soil as background (steamed at 90 °C for at least three hours) and inoculated it with the collected root zone soil samples. As background soil we used a sandy loam soil (pH 7.1, C:N ratio 15.58) that was collected from an old field located in Berlin-Dahlem. Experimental 2 L plastic pots were filled with 1840 ± 0.5 g of this mixture (1405 g background soil + 435 g inoculum). The experimental plants were grown from seeds (Appels Wilde Samen GmbH, Hesse, Germany) germinated on sterilized soil.

In August 2010 seedlings of the three target plant species were transplanted into the pots with the following treatment configuration. Native plant species *T. vulgare* and *M. albus* were growing in 'home' (sterile background soil with soil inocula from *T. vulgare* or *M. albus*, respectively) and 'foreign' soil, where the sterile background soil was inoculated with root zone soil of *S. canadensis,* the invasive plant species. *S. canadensis* itself grew respectively in 'home' soil (sterile background soil inoculated with root zone soil of *S. canadensis*) or 'foreign' soil where the sterile background soil was inoculated with a 1:1 mixture from root zone soils of both native plant species. By using that mixture, we attained that *S. canadensis* had just one 'foreign' soil treatment (instead of two), because we were interested in the difference between 'home' soil vs. native conditioned 'foreign' soil and not in pair-wise species comparisons.

Soil of each of the six sites was inoculated to ten individuals per plant species that were grown individually in pots. Five out of these ten individuals were grown in 'home' treatment and five in 'foreign' treatment, respectively, resulting in 60 pots per plant species and 180 pots in total. During the whole experiment the pots were kept in a greenhouse with 16 hours a day (~ 150 $\mu E\ m^{-2}\ sec^{-1}$ PAR) and 22/18 °C day/night temperature. Their position was completely randomized twice a week.

Leaf herbivores

To examine how plant-soil feedback may cascade up to higher trophic levels we used grove snail *Cepaea nemoralis* (Linnaeus, 1758) and white-lipped snail *Cepaea hortensis* (O. F. Müller, 1774) as leaf herbivores. Individuals from both land snail species were collected in September 2010 on one of the 'urban' sites (Berlin-Südkreuz). Both species are native to Europe and among the most dominant generalist herbaceous snail species in ruderal plant communities in Berlin (personal observation). Both species were selected after herbivore surveys on our three target plant species. It turned out, that *C. nemoralis* and *C. hortensis* were the only observed herbivores on shoots of *S. canadensis* at the field sites. After collection, snail individuals were kept in plastic boxes at room temperature for four weeks and fed with lettuce and cucumber. Nine weeks after seedling transplanting the shoots of the experimental plants were covered with perforated plastic bags and two snail individuals (one from each species) were added to the plants according to the following pattern: Within each plant species and each habitat type twelve pots (out of 30) received snail addition. Six of these treated twelve plant individuals grew in 'home' soil and the other six in 'foreign' soil, respectively. Before the transfer, snails were starved for three days and weighed afterwards with a precision balance. During snail application plants were sprayed with water every second day to increase humidity inside the plastic bags. This was done to ensure that snails did not fall in an inactive state in the greenhouse due to a lack of air humidity. One day before harvesting the aboveground biomass of the plants we removed the snails and weighed them.

Harvest

Six weeks after snail addition shoots were harvested at ground level and oven-dried at 50 °C for three days. The roots were carefully washed to remove soil particles and oven-dried at 50 °C. After drying, shoots and roots were weighed with a precision balance to determine dry weight. Hereafter we performed statistical analysis on growth data (see section below for details). In the case of any detectable significant differences ($P < 0.05$) as a response to our 'home' and 'foreign' soil biota treatments within one of the three plant species, we went on with analyses of the soil nematode community composition and the percentage root colonization with AMF and DSE. This was done in order to investigate if one of these soil biota components could have played a role in achieving the observed feedback effect.

Nematode extraction

At harvest, 50 g soil were sampled from every pot and stored at 4 °C for a maximum of six days. Nematodes were extracted from soil using Cobb's decanting and sieving technique (Flegg 1967). The soil samples used for the extraction contained also root material for the inclusion of root associated nematodes into the analysis. After the extraction, nematodes were preserved in 4 % formaldehyde solution and kept at 4 °C. They were counted, and 100 individuals per sample were classified to functional groups according to feeding types (plant feeders, fungal feeders, bacterial feeders and predators) after Yeates et al. (1993) by using a microscope (400 times magnification).

Root associated fungi

Root subsamples randomly collected from the total root biomass were put in 10 ml 10 % KOH and heated for 30 minutes to 90 °C in a water bath. Afterwards, the KOH was decanted, the roots were rinsed with demineralized water and placed in 1 % HCl for five minutes. After removing the HCL the roots were covered with Trypan Blue staining solution and heated again to 90 °C for 15 minutes. For destaining the roots were placed in lactoglycerol at room temperature (Phillips and Hayman 1970). The roots were checked for percentage root colonization by fungi at 200 times magnification using the magnified intersection method, by checking 100 intersections (McGonigle et al. 1990). Hyphae associated with arbuscules or vesicules, with irregular or none cross-wall septation, and branching typically not at a right angle were noted as AMF hyphae (Rillig et al. 1998). Corresponding AMF structures (arbuscules, vesicles) were counted as well. Darkly-pigmented, septate hyphae together with clusters of inflated, rounded, thick-walled cells (the sclerotia) within the root cortical cells (Jumpponen and Trappe 1998) were associated with DSE. Fungal structures that did not follow these morphological traits were not noted.

Statistical analysis

Due to the imbalance of our experimental design and the circumstance that we incorporated fixed and random predictors that were also nested in each other, we used linear mixed-effects models for data analysis. All analyses were done in R (R Core Team 2013) with addition of the ‘nlme’ package. We performed the full model with the fixed factors being habitat type, soil history, and leaf herbivory. The sites were entered as a random factor and were nested into the factor habitat type. The model was performed on individual plant species growth data (root, shoot, and total dry weight), AMF data (% -AMF root colonization, arbuscules, vesicules), DSE data (%-DSE root colonization), the nematode data (total number and numbers of fungivorous, bacterivorous, herbivorous, and predatory nematodes), and on the weight gain of the snails. Independent from the model we also performed a single ANOVA to check for differences in total biomass production between the three focal plant species. If there was a matching pattern between the plant biomass data and the colonization data of root or soil associated organisms, we checked for a relationship between them by performing a simple linear regression with plant growth data as the dependent variable.

Results

Growth of the experimental plant species

A significant difference in total biomass production in 'home' treatment compared to 'foreign' treatment was only detected for native *T. vulgare*. Plants growing in soil inoculated with *S. canadensis* soil biota performed better than plants growing in soil inoculated with soil biota from the own root zone (Fig. 2.1, 2.2b; Table 2.1). Besides the significant effect of soil history on growth of *T. vulgare* there was a significant interaction between habitat type and snail addition on shoot and total biomass production (Fig. 2.2b; Table 2.1), i.e. the effect of snails depended on the area where the soil was collected. Snails affected the plants growing with soil inocula from 'urban' sites positively, but negatively when the plants were growing with soil biota from the 'suburban' sites.

Exotic *S. canadensis* treated with inocula from 'suburban' sites produced more aboveground biomass (Fig. 2.2a; Table 2.1) than plants inoculated with biota from 'urban' sites, while there was no difference in total biomass (Fig. 2.1). There were no effects of the soil history ('home' vs. 'foreign'), snail addition, or interaction effects between the three factors on the growth of *S. canadensis* (Fig. 2.2a; Table 2.1).

There were also no significant effects of the habitat type, the soil biota history, or snail addition on the growth of the native legume *M. albus* (Fig. 2.2c, Table 2.1). In general, total biomass production of the legume *M. albus* was 32.4 % and 28.2 % higher than total biomass production of *S. canadensis* and *T. vulgare,* respectively ($F = 27.20$, $P < 0.001$, Fig. 2.1).

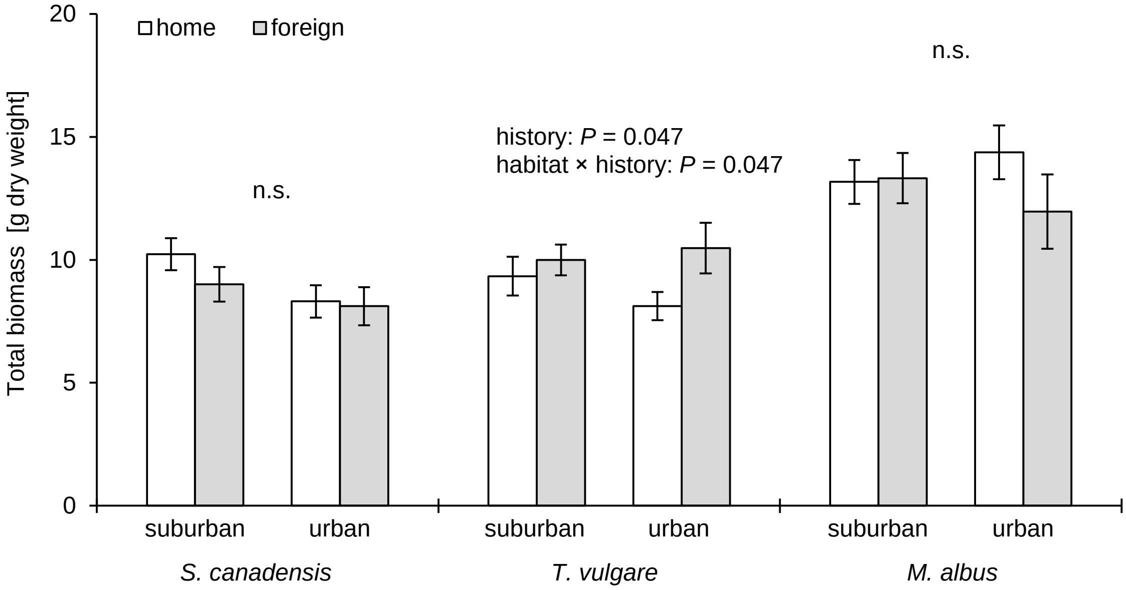

Figure 2.1 Total biomass of *Solidago canadensis*, *Tanacetum vulgare* and *Melilotus albus* plants grown either in a 'home' or in a 'foreign' soil history treatment (means ± SE, n = 15 per bar). 'Suburban' and 'urban' indicate the origin of the soil inocula that were used for the experiment. *P*-values for main and interaction effects are derived from linear mixed-effects models.

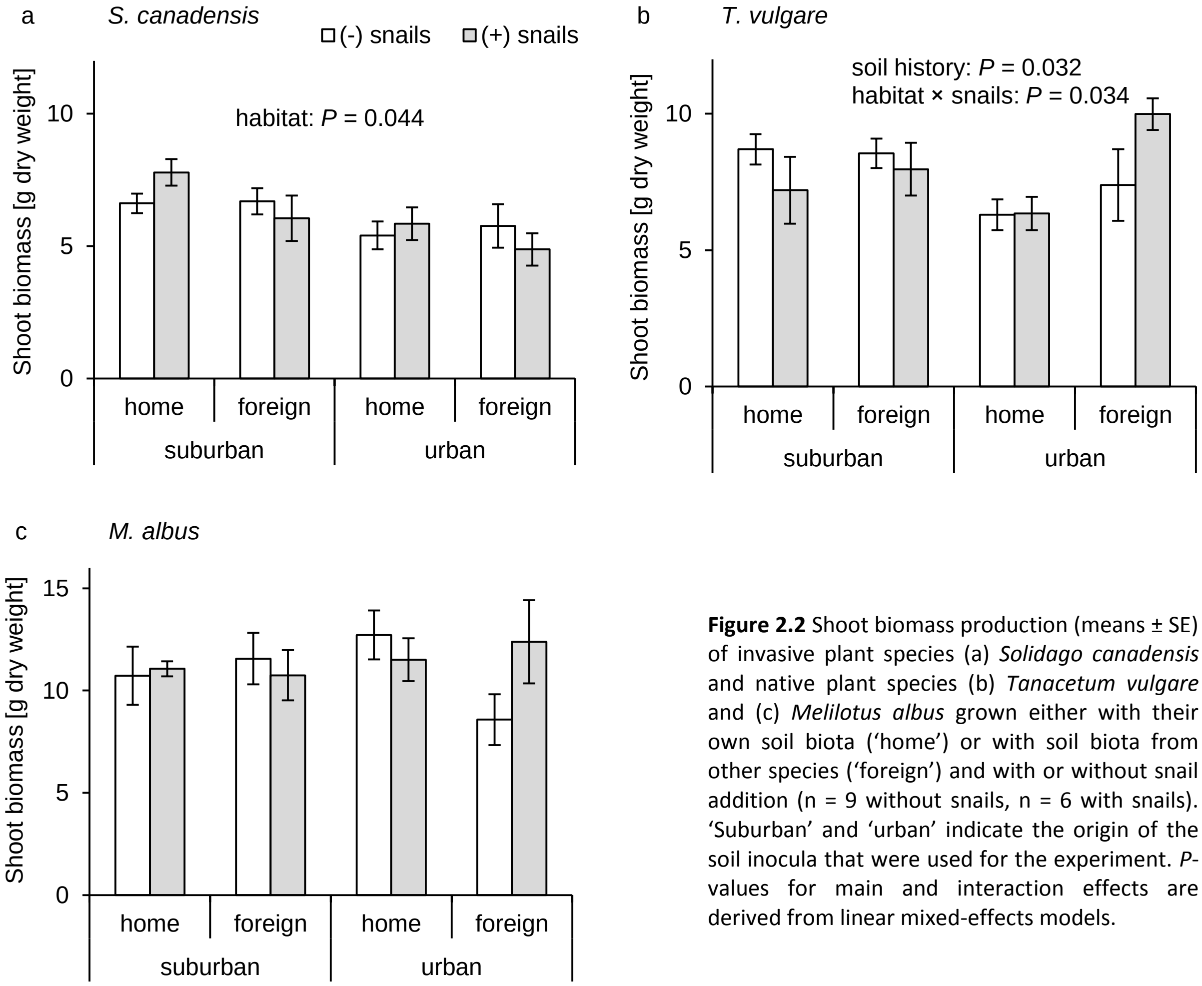

Figure 2.2 Shoot biomass production (means ± SE) of invasive plant species (a) *Solidago canadensis* and native plant species (b) *Tanacetum vulgare* and (c) *Melilotus albus* grown either with their own soil biota ('home') or with soil biota from other species ('foreign') and with or without snail addition (n = 9 without snails, n = 6 with snails). 'Suburban' and 'urban' indicate the origin of the soil inocula that were used for the experiment. *P*-values for main and interaction effects are derived from linear mixed-effects models.

Table 2.1 Results of linear mixed-effects models showing the effects of habitat type ('suburban' and 'urban'), soil history ('home' and 'foreign') and snail addition (no snails added and snails added) and their interaction on shoot and root biomass of the three plant species. Significant effects ($P < 0.05$) are in bold and marginally significant ($P < 0.10$) effects are in bold and italics.

	S. canadensis				***T. vulgare***				***M. albus***			
	Shoot		Root		Shoot		Root		Shoot		Root	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat (A)	8.45	**0.044**	0.12	0.746	0.96	0.382	2.43	0.194	0.00	0.975	0.41	0.557
History (H)	0.88	0.352	0.83	0.367	4.92	**0.032**	1.18	0.283	0.86	0.360	1.04	0.314
Snails (S)	0.00	0.961	0.54	0.464	0.07	0.788	0.06	0.806	0.32	0.572	0.03	0.856
A × H	0.29	0.590	0.72	0.400	3.45	***0.070***	0.40	0.530	1.69	0.201	0.16	0.691
A × S	0.29	0.591	0.23	0.630	4.81	**0.034**	1.26	0.268	0.93	0.339	1.89	0.176
H × S	3.11	***0.084***	3.14	***0.083***	2.53	0.119	1.30	0.261	1.24	0.272	1.01	0.320
A × H × S	0.07	0.790	1.15	0.289	0.53	0.472	0.28	0.596	2.99	***0.091***	0.00	0.956

Herbivore performance

At the end of the experiment 141 of 144 snails were recovered alive. Snail biomass on *S. canadensis*, *T. vulgare*, and *M. albus* plants increased on average by 0.53 % (SE = 1.41), 7.84 % (SE = 2.32) and 2.89 % (SE = 1.67), respectively. Neither effects of the habitat type or soil history were detected on the weight gain of the snails.

Drivers of the soil feedback effect

There were no significant effects of the habitat type, the soil biota history or snail addition on the colonization rates of the different AMF structures (hyphae, arbuscules, and vesicles) of *T. vulgare* plant roots (Table 2.2). However, the root colonization by DSE was significantly higher when plants were inoculated with their own soil biota community than when grown with the community of *S. canadensis* (Fig. 2.3; Table 2.2). Linear regression analysis indicated that there was a significant negative relationship between DSE colonization and shoot growth ($P < 0.01$, $R^2 = 0.17$) and total plant growth ($P < 0.01$, $R^2 = 0.12$), but no relationship between DSE colonization and root growth ($P > 0.1$, $R^2 = 0.01$).

Table 2.2 Results of the linear mixed-effects models showing the effects of habitat type ('suburban' and 'urban'), soil history ('home' and 'foreign') and snail addition (no snails added and snails added) and their interaction on the colonization of AMF hyphae, AMF arbuscules, AMF vesicles and DSE of *T. vulgare* roots. Significant effects (P < 0.05) are in bold and marginally significant (P < 0.10) effects are in bold and italics.

	AMF-Hyphae		**AMF-Arbuscules**		**AMF-Vesicles**		**DSE**	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat (A)	6.06	***0.070***	3.68	0.128	0.52	0.510	2.81	0.169
History (H)	0.03	0.863	0.00	0.982	0.08	0.772	4.63	**0.037**
Snails (S)	0.03	0.856	0.38	0.543	0.42	0.519	2.61	0.114
A × H	0.03	0.865	0.02	0.876	0.38	0.540	1.90	0.175
A × S	0.06	0.811	0.09	0.771	0.05	0.820	2.84	***0.099***
H × S	1.14	0.292	1.07	0.308	1.99	0.166	2.23	0.143
A × H × S	0.01	0.904	0.05	0.822	2.82	0.100	3.34	***0.075***

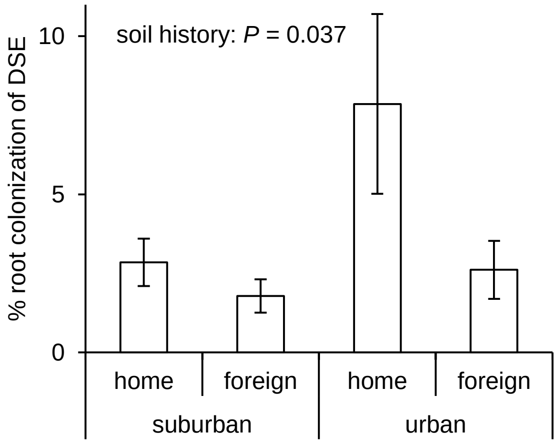

Figure 2.3 Effects of soil history ('home' and 'foreign') on the dark-septate endophyte (DSE) colonization of *Tanacetum vulgare* plants grown in soil either with 'suburban' soil biota inoculation or 'urban' soil biota inoculation (means ± SE, n = 15 per bar). The *P*-value for the soil history effect is derived from linear mixed-effects models.

There were no significant main effects on the total numbers of nematodes in soils from the *T. vulgare* pots at the end of the experiment. However, there was a significant three-way interaction between habitat type, history and snails on total nematode numbers, and a significant interaction between habitat type and history on the abundance of plant feeding nematodes (Table 2.3). When plants were inoculated with soil biota from the 'suburban' sites there were more plant feeding nematodes in 'home' soil compared to the 'foreign' soil at the end of the experiment (344 ± 98 individuals / 100 g soil in 'home' compared to 150 ± 33 in 'foreign' soil). With inoculation of 'urban' site soil biota the numbers of plant feeders did not differ significantly between 'home' and 'foreign' soil (on average 206 ± 35 individuals / 100 g soil).

Table 2.3 Abundances (means and SE) of nematodes in 100 g soil from pots with *T. vulgare* plants (upper part) and results of the linear mixed-effects models showing the effects of habitat type ('suburban' and 'urban'), soil history ('home' and 'foreign') and snail addition (no snails added and snails added) and their interaction on the nematode abundances (lower part). Displayed are abundances and effects on the total numbers of nematodes and on the four different functional groups (PF = plant feeders, BF = bacterial feeder, FF = fungal feeders, P = predatory nematodes). Significant effects ($P < 0.05$) are in bold and marginally significant effects ($P < 0.10$) are in bold and italics.

Habitat	History	Snails	Total		PF		BF		FF		P	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
suburban	home	no	772.2	192.7	290.8	119.1	424.5	149.0	30.7	13.1	26.2	8.3
		yes	881.5	334.7	398.0	192.5	433.3	161.3	6.7	3.9	43.5	15.4
	foreign	no	602.7	84.1	195.8	49.9	319.5	56.6	20.4	7.3	67.1	16.5
		yes	540.0	86.5	82.4	15.0	371.9	83.8	45.4	32.9	40.3	13.6
urban	home	no	667.2	85.4	234.0	79.4	264.3	63.9	15.3	7.5	153.5	55.8
		yes	519.8	156.4	89.0	35.1	261.0	82.9	19.1	13.1	150.6	50.0
	foreign	no	872.0	131.6	291.6	69.8	426.8	55.5	26.7	7.7	126.9	38.3
		yes	628.4	133.8	186.7	55.9	332.6	85.7	6.5	2.2	102.6	24.4
			Total		PF		BF		FF		P	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat (A)			0.01	0.922	0.07	0.811	0.56	0.495	0.75	0.437	12.88	**0.023**
History (H)			0.67	0.417	1.80	0.187	0.09	0.766	0.42	0.523	0.10	0.755
Snails (S)			0.00	0.981	6.62	**0.014**	0.88	0.354	0.02	0.888	0.24	0.629
A × H			0.31	0.581	7.01	**0.011**	2.66	0.110	0.36	0.550	1.37	0.248
A × S			0.00	0.970	0.04	0.852	0.05	0.831	0.51	0.481	0.01	0.935
H × S			1.43	0.237	0.41	0.525	0.57	0.453	0.23	0.632	0.37	0.548
A × H × S			4.29	**0.044**	0.01	0.925	2.20	0.146	3.16	***0.083***	0.03	0.859

Also snail addition to *T. vulgare* plants significantly affected the abundance of plant feeding nematodes in the soil (Table 2.3). When plants encountered snails the abundance of plant feeding nematodes was lower (215 ± 45 individuals / 100 g soil) compared to the soil of plants without snails (282 ± 50 individuals / 100 g soil).

Discussion

Despite the growing number of studies that highlight the importance of a combined aboveground-belowground perspective on plant performance, little is known about how plant-soil feedback affects plant-herbivore interactions above the ground and the invasion of an exotic plant into a native plant community. We found that soil from the root zone of the dominant invader *S. canadensis* facilitates the growth of a native competitor plant species, which is a type of feedback that has been described as heterospecific positive feedback (Perkins and Nowak 2013). However, the feedback effect from the belowground compartment had no effect on the herbivore interaction in the aboveground compartment. Concerning the question which soil biota fraction may be responsible for the plant-soil feedback effect, we found that the not well studied DSE might carry over that part. In the following paragraphs the aforementioned results will be discussed in detail.

Soil feedback and plant growth

The native plant species *T. vulgare* had a negative growth response to its own soil biota community, while the exotic *S. canadensis* showed a slightly positive soil feedback, though not significant. These results agree with the general findings of other studies (Klironomos 2002, Callaway et al. 2004, van Grunsven et al. 2007, Morriën et al. 2011) which suggest that exotic plant species tend to exhibit a positive or a less negative feedback than native plant species. The better performance of *T. vulgare* with soil biota that were conditioned by *S. canadensis* compared to growth with its own soil biota community suggests that a native plant species may benefit from the presence of a dominant exotic invader. Personal observations of plant species abundance and spatial occurrence on our study sites are consistent with our experimental findings. The multi-stemmed clonal colonies of both species occur frequently in immediate vicinity to each other and collectively cover a high percentage of area on abandoned and/or disturbed urban fields.

Potential facilitative effects mediated by changes in the soil biota community among an exotic and a co-occurring native plant species are rarely reported. A meta-analysis by Suding et al. (2013) showed that the growth responses of native species were often greater in soil conditioned by native species than in soil conditioned by exotic species. Further, the majority of studies on *S. canadensis* deal with its direct and indirect negative impacts on other plants (Meiners et al. 2002, de Groot et al. 2007), soil microbial communities (Zhang et al. 2009, Zhang et al. 2010), pollinators (de Groot et al. 2007, Moroń et al. 2009), soil nematodes (Xu et al. 2011), and generalist predators like carabid beetles (de Groot et al. 2007). Positive aspects related with the integration of *S. canadensis* to the Middle European flora may be present as well, but are sparsely reported. It is discussed, for example, whether its opulent flowerage in late season increases the availability of nectar for honey bees in autumn (Kowarik 2003).

The lesser magnitude of the feedback effect strengths detected in our study compared to others could be attributed to differences in the methods used. Generally the designs of plant-soil feedback experiments can be distinguished by whether the whole soil or a soil inoculum is sterilized and plants grow thus with or without living soil biota ('sterilization approach'), or whether plants grow in 'home' or 'foreign' soils with living soil biota derived from other plant species ('conditioning approach'). Comparative studies showed that the 'sterilization approach' produces bigger effect sizes and is more likely to yield significant results (Kulmatiski and Kardol 2008, Brinkman et al. 2010), but the ecological relevance is in our opinion less clear. Also the treatment and origin of the inoculum seems to influence the experimental outcome: A meta-analytical review by Kulmatiski et al. (2008) documented that studies using soils conditioned under controlled conditions showed stronger feedback effects than studies using field-collected soils. Abiotic conditions are likely to be different in the greenhouse compared to natural field conditions, which might lead to exaggerated feedback effects of soil biota on plant growth, but may not reflect effect strengths appearing in the field (Brinkman et al. 2010).

Influence of soil feedback on aboveground herbivore interaction

We further were interested if plant-soil feedbacks may cascade up to higher trophic levels above the ground. However, soil history did not affect the impact of snails on plant growth for all three plant species. Thus, plant tolerance or resistance to aboveground herbivores was not modified by feedback effects caused by soil organisms. As far as we are aware there are only two studies that have investigated the individual and combined effects of belowground organisms on plant growth and foliage-grazing snails (Thompson et al. 1993, Wurst and Rillig 2011). Both studies focused on effects of individual soil biota fractions (earthworms and earthworms plus AMF in case of Thompson et al. 1993 and Wurst and Rillig 2011, respectively) on the productivity, structure, and diversity of experimental grassland communities, which makes the comparability to the present study that focuses on plant-soil feedback effects on individual plant species quite low.

Consistent with the results of the present study, Morriën et al. (2011), who investigated the impact of plant-soil feedbacks on aboveground insect herbivores (aphids and locusts), found no correlation between the strength of soil feedback and the effect size of insect shoot herbivory using 15 plant species in a greenhouse experiment. The authors argued that the lack of any correlation may have resulted from the independence and contrasting effects of the two main plant defense pathways involved, i.e. the jasmonic acid pathway and the salicylic acid pathway (Beckers and Spoel 2006). In our study, the non-significant interaction between soil history and snail herbivory could also have been resulted from the relative low effect size of the plant soil feedback effects compared to other feedback studies (see discussion above). Although effects of belowground organisms on aboveground herbivores are well documented, the soil history did not modify plant tolerance or resistance to aboveground herbivores in the two studies on consequences of plant soil feedbacks on higher trophic levels (our study and Morriën et al. 2011). This inconsistency may be due to the fact that the soil feedback approach investigates interactions of the soil biota community as a whole and does not focus on individual components of the soil biota community separately. The presence of soil biota fractions with different ecological roles (i.e. antagonism or mutualism) and their interactions among each other may outweigh their individual effects in the complex entity of a soil community (Ladygina et al. 2010, Wurst et al. 2012).

Drivers of the soil feedback effect

In this study we aimed to investigate which soil biota fraction may have been a causal driver of the detected feedback effect. We suspected a group supposed to be symbiotic (AMF), another one known to be pathogenic and/or parasitic (plant feeding nematodes), and a third one (DSE) with so far rather unclear consequences on plant performance. Callaway et al. (2004) and MacKay and Kotanen (2008) showed that symbionts were the dominant drivers of plant-soil feedback, Agrawal et al. (2005), van Grunsven et al. (2007) and Dostál and Palečková (2011) suggested in contrast that pathogens might play the most important role. Klironomos (2002), who studied effects of both symbionts and pathogens in a series of experiments, found that plants may benefit from positive feedback with symbiotic AMF, which may be counteracted by a negative feedback with soil pathogens. Since the root colonization of *T. vulgare* by AMF did not differ between the ‘home’ and ‘foreign’ treatment in our experiment, we have no indication that AMF played a major role for the observed feedback effect, because AMF root colonization and plant growth responsiveness are often positively related in non-leguminous plant species (Wilson and Hartnett 1998). In contrast to the study by Klironomos (2002), we used the whole soil biota community and not isolates of AMF and pathogens; therefore a potential positive effect of AMF might have been counteracted by other soil biota present in our set-up. Further, effects of AMF on plant performance depend on the specific combination of AMF and plant species (Klironomos 2003) and on the abiotic soil context in which the plant-AMF interactions take place (Hoeksema et al. 2010).

In terms of soil nematode abundance and community composition, we also have no indication that nematodes were the responsible driver for the detected feedback effect on *T. vulgare*. No significant differences in total nematode numbers and numbers within the four functional nematode groups (plant feeders, fungal feeders, bacterial feeders, predators) between the 'home' and 'foreign' treatment were detected at the end of our experiment. However, in agroecosystems, the accumulation of plant species-specific soil nematodes is a well-known phenomenon and it is a crucial factor for the implementation of crop rotation in agricultural practices (Agrios 2005). In natural systems, negative plant-soil feedback effects associated with nematode accumulation have been described for sand dune communities (van der Stoel et al. 2002). However, these effects were only detected in absence of other soil organisms, i.e. not in natural soil with a variety of interacting organisms. The above-mentioned results suggest that soil nematodes may have only minor impacts on the development of plant-soil feedback effects in natural soils, but existing data is still insufficient to draw proper conclusions.

Based on the results of our study we suggest that the worse performance of *T. vulgare* in its own soil compared to *S. canadensis* soil may be caused by DSE. The colonization by this group of ascomycetous anamorphic fungi, that colonize root tissues intracellularly and intercellularly (Jumpponen 2001), was significantly higher in 'home' soil compared to 'foreign' soil at the end of our experiment which reflected the observed soil feedback effect on shoot biomass. Consistently, data of an experimental greenhouse study by Camenzind (2010) showed that the individual root colonization of ten naturally derived DSE isolates negatively affected growth of *T. vulgare* in four cases and neutrally in the other six cases. The higher root colonization rates by DSE of *T. vulgare* grown with 'home' soil biota can either indicate that the density of these fungi is suppressed in the root zone of *S. canadensis* or enhanced in root zone soil of *T .vulgare*. The first assumption is supported by the findings of Zhang et al. (2009), which show that *S. canadensis* can suppress soil borne pathogenic fungi (*Pythium ultimum* and *Rhizoctonia solani*) through exudation of allelochemicals. The second assumption – which predicts an accumulation of pathogens in the rhizosphere of *T. vulgare* – is also possible but less likely, because two other independent plant-soil feedback studies (Petermann et al. 2008 and a yet unpublished study by ourselves) whose set of plant species also contained *T. vulgare* documented a positive soil feedback for this species. In both experiments the 'foreign' treatment soil of *T. vulgare* was influenced by other plant species than *S. canadensis*.

However, it is necessary to notice that it is still poorly understood what ecological role DSE play and to which extent they interact with plants and other plant colonizing fungi like AMF and fine endophytes (Jumpponen 2001, Postma et al. 2007). Because their impacts on plant performance are highly variable – even differing between different fungal strains and isolates – it is assumed that they stretch a continuum from mutualism to antagonism (Tellenbach et al. 2011). Future research on this relatively unknown root colonizing fungi should include questions about their role in plant-soil feedback, plant invasions, and also in plant community composition.

Herbivore effects on plant growth and soil biota

Interestingly, snail addition tended to increase shoot biomass production of *T. vulgare* (significantly) and *M. albus* (marginally significantly) when plants were growing with the *S. canadensis* soil community, but only when the soil was inoculated with biota collected from 'urban' sites. Compensatory growth following herbivory is often reported as an indicator of tolerance and plant response after tissue damage (Noy-Meir 1993, Wise and Abrahamson 2007, Ruiz-R et al. 2007). The direction and magnitude of the net effect of grazing on plant growth is assumed to depend on conditions such as amount of green leaf area, number of meristems, amount of stored nutrients and assimilates, availability of soil resources, length of growing season, and frequency and intensity of defoliation (Noy-Meir 1993). The results of our study indicate that soil biota history may be added to this list of influential factors. Soil biota history dependent compensatory shoot growth in response to snail herbivory was detectable in *T. vulgare* and *M. albus* with inoculation from the 'urban' sites and in *S. canadensis* independent of soil origin, respectively.

We found that when *T. vulgare* encountered aboveground snail attack the abundance of root feeding nematodes in the soil was lower at the end of the experiment compared to plants without snails. Responses of soil nematode abundances to aboveground herbivory have been also described by Fu et al. (2001) in agroecosystems. They found that numbers of bacterivorous and fungivorous nematodes were affected by aboveground feeding by grasshoppers, but not the numbers of root feeding nematodes as in our experiment.

Influence of habitat type

Although soil history did not affect snail herbivory, our results show that soil biota communities from different habitat types may differently influence plant interactions with aboveground herbivores. Snails positively affected *T. vulgare* plants growing with soil inocula from 'urban' sites, but had negative effects on shoot biomass when the plants were growing with soil biota from 'suburban' sites. This and the enhanced shoot growth of *S. canadensis* with soil communities from ‘suburban’ sites indicate that the soil biota communities from ‘urban’ and ‘suburban’ sites differed in their abundance and/or composition. It is also possible that the abiotic soil properties of the field-collected inocula had an effect in our experiment, although we added it to the same background soil to correct for differences in abiotic conditions. The C:N ratio did not differ between the root zone samples of the different plant species but it differed significantly between the two habitat types. The ‘suburban’ soil inocula had a lower C:N ratio as the ‘urban’ soil inocula, which might explain the higher shoot growth of *S. canadensis* with ‘suburban’ soil inoculation due to higher availability of nitrogen. However, there was no main effect of the habitat type on the other two plant species. The interaction of habitat type and snail herbivory on shoots of *T. vulgare* promotes the hypothesis that compositions and/or abundances of soil biota differed between the two habitat types. Bezemer et al. (2006) showed that effects of soil biota communities on feedback effects are not only plant species-specific but also may vary in different soils.

Conclusion

Our plant-soil feedback study found evidence for the impact of the history of the soil biota community on the biomass production of one out of three experimental plants. However, we could not show that this effect cascades up to another trophic level by affecting plant interactions with aboveground herbivores. Nevertheless, our study revealed two interesting issues that should be taken into account by future research: On the one hand we found that a native plant species (*T. vulgare*) may benefit from the presence of a dominant co-occurring exotic invader (*S. canadensis*) mediated by changes in the soil biota community. On the other hand our study puts a relatively unknown group of soil organisms – the DSE – in perspective to be a potential driver for plant-soil feedback effects, and thus also for plant competition and community composition.

Chapter 3

Using a multi-trait approach to manipulate plant functional diversity in a biodiversity-ecosystem function experiment

Abstract

A frequent pattern emerging from biodiversity-ecosystem function studies is that functional group richness enhances ecosystem functions such as primary productivity. However, the manipulation of functional group richness goes along with major disadvantages like the transformation of functional trait data into categories or the exclusion of functional differences between organisms in the same group. In a mesocosm study we manipulated plant functional diversity based on the multi-trait Functional Diversity (FD)-approach of Petchey and Gaston by using database data of seven functional traits and information on the origin of the species in terms of being native or exotic. Along a gradient ranging from low to high FD we planted 40 randomly selected eight-species mixtures under controlled conditions. We found a significant positive linear correlation of FD with aboveground productivity and a negative correlation with invasibility of the plant communities. Based on community-weighted mean calculations for each functional trait, we figured out that the traits N-fixation and species origin, i.e. being native or exotic, played the most important role for community productivity. Our results suggest that the identification of the impact of functional trait diversity and the relative contributions of relevant traits is essential for a mechanistic understanding of the role of biodiversity for ecosystem functions such as aboveground biomass production and resistance against invasion.

Introduction

Biodiversity is declining rapidly (Sala et al. 2000), which may negatively affect ecosystem functions (Hooper et al. 2005) and economically important ecosystem services at the same time (Myers 1996). The role of plant functional diversity on ecosystem properties has been a research focus in recent years (Tilman et al. 1997, Díaz and Cabido 2001, Naeem and Wright 2003). Several different experiments have shown that positive diversity effects on plant community biomass production mostly result from niche complementarity in combination with a species-specific sampling effect (Hooper and Vitousek 1997, Tilman et al. 1997, Hector et al. 1999, Marquard et al. 2009). The number of functional types or groups (e.g. C_4 grasses, C_3 grasses, N-fixing plants, and non-N-fixing plants) represented by the species in a local community is a common measure of functional diversity that is often used to manipulate functional diversity in experimental set-ups (Hooper and Vitousek 1997, Tilman et al. 1997, Díaz and Cabido 2001, Naeem and Wright 2003). However, the manipulation of functional group richness in biodiversity-ecosystem function experiments goes along with major disadvantages like the exclusion of functional differences that occur between organisms in the same group (Petchey and Gaston 2006). Further, the assumption that ecosystem processes are governed by the abundance and distribution of functional traits in a community (Díaz and Cabido 2001, McGill et al. 2006, Roscher et al. 2012) has attracted growing attention on the use of functional trait composition, rather than species or functional group richness, in the explanation of biodiversity-ecosystem functioning relationships.

The effects of functional traits on ecosystem properties are quantified by two conceptually different approaches. On the one hand, community-weighted means of trait values (CWM) are commonly computed as mean trait values weighted by the species relative abundances in a given community (Díaz et al. 2007, Lavorel et al. 2008). This single trait index is interpreted as a trait value expected from a random sample of the community and is theoretically consistent with Grime’s (Grime 1998) mass-ratio hypothesis. On the other hand, a number of new multi-trait approaches such as functional attribute diversity (FAD), functional diversity (FD) or Rao’s Q has been introduced which assess functional diversity of a community by quantifying the distances of trait values of species in a multi-dimensional trait space (Petchey and Gaston 2006, Mouchet et al. 2010). The concept of functional trait diversity is based on the assumption that greater differences between species’ trait values represent greater trait complementarity and larger functional diversity. Since the introduction of the continuous multi-trait Functional Diversity (FD) index by Petchey and Gaston (2002, 2006) it has been shown that FD explains variation in ecosystem functions, most notably plant aboveground productivity of grassland species (Mokany et al. 2008, Schumacher and Roscher 2009). However, multi-trait approaches were solely used for measuring functional diversity either on experimental communities that were compiled by another approach (e.g. species richness or functional group richness) or on natural communities.

So far, no manipulative study has used trait-based functional diversity measures to create different functional diversities during the composition of experimental communities; thus knowledge about their practicability in manipulating functional diversity in experimental set-ups is still missing. Several properties of these measures predict that they will explain greater variance in ecosystem function than either species richness or functional group richness (Petchey et al. 2004). And, already seven years ago Petchey and Gaston (2006) requested experiments that manipulate trait distributions in local assemblages while species richness is held constant, mainly due to their suggested advantage of eliminating the sampling effect.

In the mesocosm study presented here we used the revised version of the FD index by Petchey and Gaston (2006) to generate a gradient of functional diversity among plant mixtures while species richness was kept constant. We used a pool of 20 plant species from the urban European flora as our model plant community. Our interest in urban floras is attributed to the fact that cities are remarkably rich in species – usually species richness is greater than in the surrounding areas – and may harbour one of the hot spots of biodiversity (Celesti-Grapow et al. 2006). As a novel aspect of this study we treated the attribute of a plant species to be alien or native (hereafter called the 'floristic status' after Klotz et al. [2002]) as an additional trait that characterizes a species such as life-history or resource capture traits do. We assume that species with different biogeographical histories differ in the number of associations they form with their biotic environment and that this will not only affect the species' own performance but also community-wide ecosystem properties like traditionally used functional traits do. We are aware that the floristic status does not fulfill the definition of a functional trait in its narrowest sense as being any morphological, physiological, or phenological plant feature (Pérez-Harguindeguy et al. 2013). However, in case of considering a functional trait as a characteristic that is relevant to ecosystem functioning (McIntyre et al. 1999, Díaz and Cabido 2001, Violle et al. 2007) or influences the own performance of an organism (McGill et al. 2006), the addition of the floristic status as additional trait to the classical functional traits appears reasonable.

In this study we explored firstly whether a positive relationship between functional diversity and aboveground productivity is detectable in plant mixtures that were compiled on the basis of the FD index. This new approach may give insight into the effectiveness and appliance of trait-based approaches for manipulative studies. Secondly, we calculated community-weighted means (CWM) of the selected plant functional traits to determine the relative importance of each trait in explaining the relationship between functional trait diversity and aboveground productivity. In a second phase of the experiment we moved the focus to the resistance to invasion, which is an ecosystem function that was linked with species diversity and functional diversity since the early days of invasion ecology (Elton 1958). Experimental studies following a functional approach showed that functional group identity rather than functional group richness limits the invasion process of alien plant species in resident communities (Pokorny et al. 2005, Byun et al. 2013), which is a finding that is consistent with the sampling effect hypothesis, but in a functional context. In our study, it was the third goal to elucidate the question whether functional trait diversity affects community resistance to invasion. Therefore we added seeds of the exotic Canada goldenrod *Solidago canadensis* to each plant mixture and monitored seed germination and seedling survival.

Methods

In this study we used a single factor regression design with functional diversity being the single continuous factor that was experimentally manipulated. Functional diversity was calculated for all possible eight-species mixtures from a pool of 20 naturally co-occurring plant species, based on the FD index introduced by Petchey and Gaston (2002, 2006). This measure of functional diversity is defined as the total branch length of a functional dendrogram, which is created from data of plant functional traits. From the total number of possible eight-species mixtures (125,970), 40 mixtures were randomly selected and planted out for the experiment. This design was chosen to cover a broad range of functional diversity (from low FD to high FD).

Species pool and functional traits

Plant species selection for the species pool of the experiment was conducted with the purpose of reflecting the composition of a ruderal plant community, which is a typical attribute of temporary abandoned fields and disturbed habitats in urban areas. Specific abiotic conditions and the proximity to human settlements and transport connections support the establishments of non-native plant species in these areas (Kowarik 2003). The species pool contained 20 angiosperm species (13 natives and 7 non-natives), of which 15 were forbs, 3 grasses, and 2 tree species (see Table S3.1). The major part of the plant seeds we used was collected on an urban abandoned site in Berlin (N52°28'30", E13°21'46"). This site was open to the public and it was no permission required to enter that site or to collect plant seeds from there. Regarding to the red list of endangered vascular plant species of Berlin (Prasse et al. 2001) none of our experimental plant species were endangered or protected. A minor part of seeds was provided by Appels Wilde Samen (Darmstadt, Germany) or by the Botanical

Garden Berlin-Dahlem. To classify each plant species functionally we used data of seven functional traits (four continuous and three categorical) plus the species' floristic status. We aimed to include traits that are related to plant productivity, resource use, coexistence, and competitive strength. The categorical traits were: life form, leaf form, and resource use strategy (i.e. root colonization with N-fixing bacteria and/or arbuscular mycorrhizal fungi, AMF). The continuous traits were: specific leaf area (SLA), canopy height, seed mass, leaf dry matter content, and floristic status. Trait values for each trait were exclusively obtained from trait-databases (BiolFlor [Klotz et al. 2002] and LEDA [Kleyer et al. 2008]) or in some cases of unavailability from approved publications. The trait floristic status defines whether a plant is native or alien to Germany. For the specification of the floristic status we followed the classification from the BiolFlor database (Klotz et al. 2002), which is based on the classification system by Schroeder (1968). This classification acts exclusively on a temporal basis excluding information about the evolutionary history, origin, or mode of introduction. Alien species are classified according to their time of human introduction: before the discovery of America (archaeophytes, trait value '2' in our data table) and after the discovery of America in 1492 (neophytes, trait value '1'). Species that colonized the focus area after the end of the last glacial period (about 12,500 years ago) without human assistance are classified as indigenous or native (trait value '3'). Our approach is backed on the aspect that native species have longer evolutionary histories with other local organisms than species that established later in the course of time (see Text S3.1 for additional information).

Calculation of Functional Diversity (FD)

The calculations of the FD index for each possible eight-species mixture (125,970 in total) were performed by the R-based software FDiversity (Casanoves et al. 2011). After calculating the FD values we ended up with a range of FD between 1.69 (lowest value) and 4.08 (highest value, see Text S3.2 for additional information on the calculation). From the 125,970 possible mixtures we randomly chose 40 mixtures with the Excel function 'randbetween' (Microsoft Excel 2007).

Experimental set-up and harvest

In November 2011 we started the experimental part of the study: We used 40 plastic pots (7.5 l volume, 21 cm height, 26 cm upper diameter, and 19 cm lower diameter) and filled them with 7 kg soil each. The soil was a loamy sand (pH 8.1, C/N ratio of 28:1, determined with an elemental analyzer Euro EA, HEKAtech GmbH, Germany) that was collected from an urban abandoned site in

Berlin (N52°28'30", E13°21'46") and sieved before the experiment (4 mm mesh size) but remained untreated otherwise. Each of our experimental plant species could be found on that site. 16 equally sized seedlings (two individuals per species) that had been grown on sterilized soil were transplanted carefully into each mesocosm according to the drawn species compositions. Each seedling was assigned by chance to one of 16 possible positions in the mesocosms. The mesocosms were distributed within the greenhouse, watered regularly, and their position was randomized twice a week. During the whole experiment the pots were kept in the greenhouse with 16 hours light a day (~ 180 µE m-2 sec-1 PAR) and 22/18 °C day/night temperature. Nine weeks after transplanting the seedlings into the mesocosms, plant shoots were harvested. Shoots were cut 3.5 cm above ground level to enable regrowth. Shoot weight was determined after drying at 50 °C for three days.

Invasion by S. canadensis

To simulate a biological invasion into an established ruderal plant community after a disturbance by cutting we added 100 achenes (hereafter called seeds) of *Solidago canadensis* L. (Asteraceae) evenly to the soil surface of each mesocosm. The Canada goldenrod *S. canadensis* is an invader of North American origin, was introduced in the 18th century in Europe and began to spread in the 19th century in Central Europe where it may become a highly dominant species on abandoned fields and disturbed habitats in urban areas (Kowarik 2003). *S. canadensis* seeds were collected on the same field described above and each seed was checked with a dissecting microscope for its color and size to prevent that they may differ in the ability to germinate. We executed the seed addition after the cutting to prevent that the seeds and seedlings of *S. canadensis* will get strong shading from the established plants. We checked the mesocosms every second day for numbers of newly emerged seeds and survived seedlings until three months after seed addition. Germination and survival rate were calculated per pot.

Data analysis

Aboveground community biomass at the time of harvest was calculated for each eight-species mixture as the sum of biomass of the 16 individuals per mixture. The influence of FD on aboveground community biomass was tested with a linear regression with FD as the predictor and biomass as response variable. Community-weighted means of trait values (CWM) were calculated for each mixture based on species biomass proportions according to the equation

$$CWM = \sum_{i=1}^{S} p_i \times t_i$$

where S is the number of species in the community, p_i is the species biomass proportion and t_i are the given trait values. To elucidate the relative contribution of CWMs of traits to the amount of explained variation in aboveground biomass production we performed multiple regressions considering statistical models with different combinations of included explanatory variables (traits). We used the Akaike information criterion (AIC) and R^2 values to select for the model with the best fit. Afterwards we performed a standardized principle components analysis (PCA) with the CWMs of the traits from the selected model to determine multiple relationships between them (Roscher et al. 2012). The influence of FD on *S. canadensis* seedling germination was tested with a regression analysis. The regression function of the curve with the best fit to our data was determined by comparing R^2 and AIC values of different regression functions (linear, exponential, logarithmic, power, polynomial). The percentage of survived seedlings was analyzed with a logistic regression model, which is an instance of a generalized linear model. The logistic function avoids predictions below and above 0 and 100 % and is widely used to analyze percentage data (Morgan 1988, Zhao et al. 2001, Kieschnick and McCullough 2003).

All models were tested for the underlying assumptions (homoscedasticity, normality). All statistical analysis were done in R (version 3.0.1, R Core Team 2013).

Results

Statistical analysis of aboveground biomass indicated a positive relationship between FD and biomass production (Fig. 3.1). Altogether, FD explained 32 % of the total variation of biomass among the 40 mesocosms.

The model selection procedure led to a model that included the traits N-fixation, floristic status, AMF, and SLA and explained 93 % of the variation in aboveground biomass (Table 3.1). N-fixation, AMF, and SLA were positive correlated with aboveground biomass whereas the floristic status showed a negative correlation. In terms of floristic status, high biomass proportions of non-native species in regard to community biomass (hence a low CWM for the trait floristic status) were accompanied with a high community biomass production.

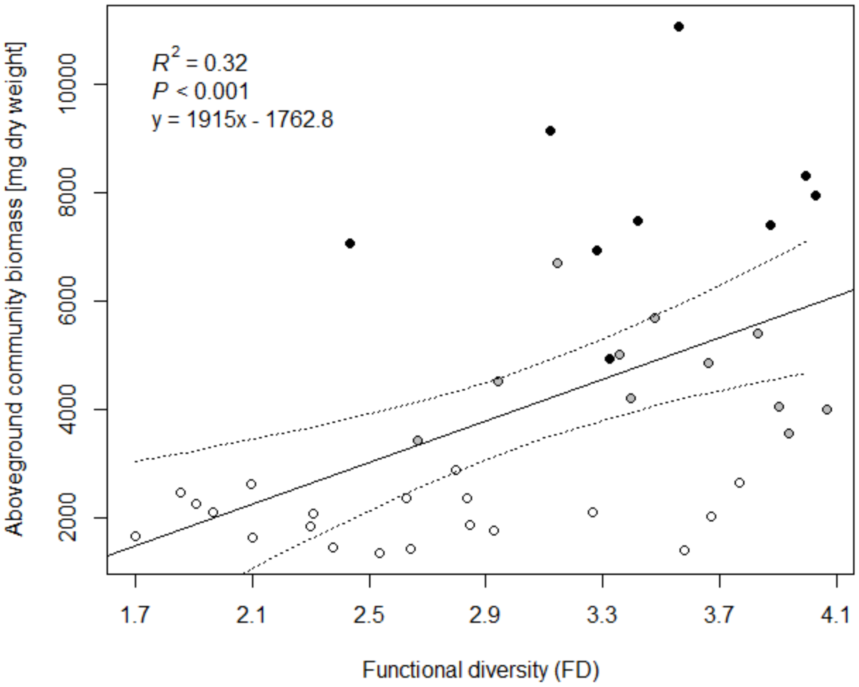

Figure 3.1 Aboveground community biomass plotted against the FD index of each eight-species mixture. Increasing FD index values represent increasing functional diversity within the mixtures. (intercept = -1762.8, SE = 1577.7, t = -1.1, slope = 1915.0, 95 % confidence intervals for slope 889.2 – 2940.9, SE = 506.8, t = 3.8, n = 40). The regression line is solid with 95 % confidence bands (dashed lines). Black points represent mixtures that contained the two most productive species of the experiment (*Melilotus albus* and *Medicago* x *varia*). Grey points represent mixtures that contained either *M. albus* or *M.* x *varia*. Empty points represent mixtures that contained neither of these two species.

Table 3.1 Summary for the best statistical model based on four predictor variables explaining the variation of aboveground community biomass.

Functional trait	***t*-value**	***P*-value**	**Partial R^2**
Nitrogen-fixation	11.718	< 0.001	positive 0.893
Floristic status	2.115	0.0416	negative 0.337
AMF	1.726	0.0933	positive 0.280
SLA	-1.966	0.0573	positive 0.315
Degrees of freedom	35		
Multiple R^2	0.9304		
***P*-value**	< 0.001		

The two leading axes of a standardized principle component analysis (PCA) on the four selected traits N-fixation, floristic status, SLA, and AMF explained about 80 % of variation (Fig. 3.2). The first principal component accounted for 50.1 % and had a high positive loading for floristic status as well as a high negative loading for N-fixation. Linear regression between total community aboveground biomass and the first PCA component showed a strong significant negative correlation ($R^2 = 0.75$, $P < 0.001$) between both variables. The second principal component accounted for 29.9 % of variation. SLA had a positive and AMF a negative loading on this axis. Linear regression between total community aboveground biomass and the second PCA component showed no significant correlation ($R^2 = 0.01$, $P > 0.05$) between both variables.

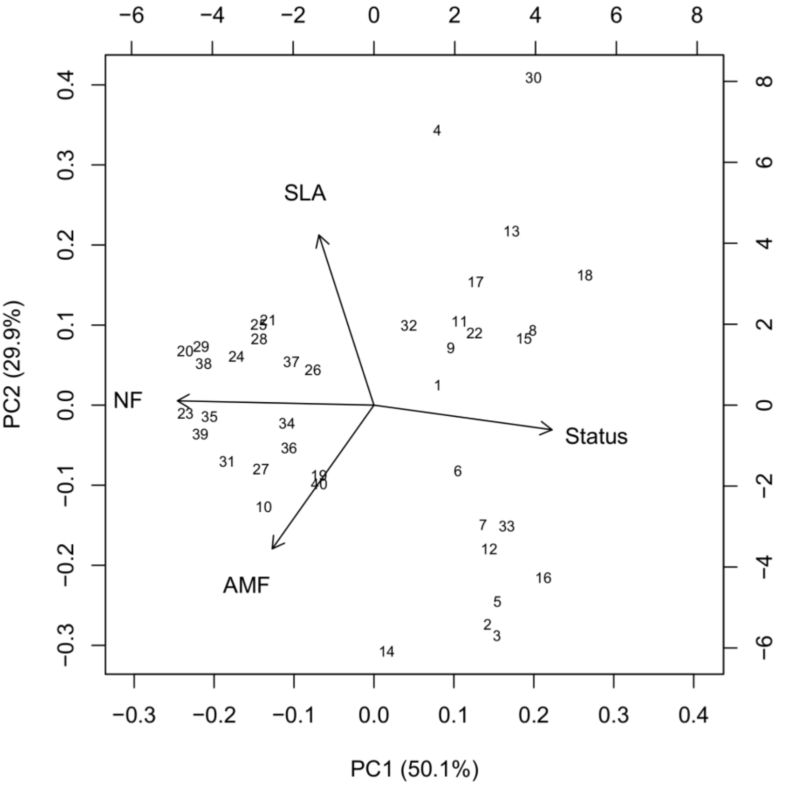

Figure 3.2 Standardized principal components analysis (PC1 vs. PC2) of the four most important traits. Plotted are the community weighted means (CWM) of the trait values of the functional traits N-fixation (NF), floristic status, specific leaf area (SLA), and arbuscular mycorrhizal fungi (AMF). CWMs of trait values were calculated for each of the 40 mixtures (plotted numbers) based on species biomass proportions.

Invasion of S. canadensis

Seedling germination rate of *S. canadensis* in the 40 mixtures is best explained by a polynomial function (Fig. 3.3A). Between FD values 1.7 (lowest FD) and 3.5 the number of germinated seeds decreased with increasing FD value. From 3.5 to 4.1 (highest FD) the number of germinated seeds increased again, but less steep and without reaching germination rates from the lowest FD values. The seedling survival rate showed a negative linear relationship with increasing FD value (Fig. 3.3B).

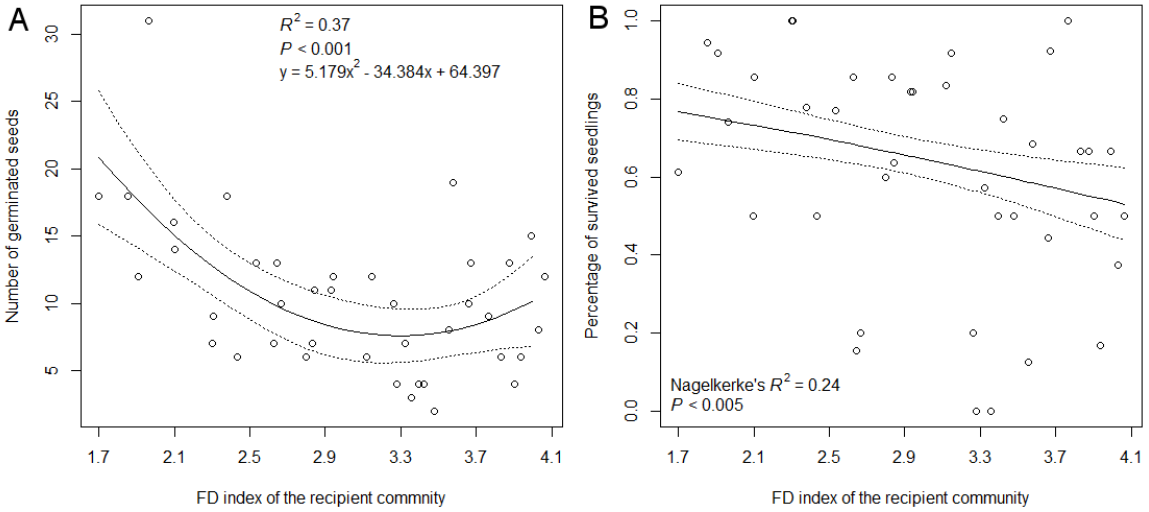

Figure 3.3 Invasion of *S.canadensis*. (A) Number of germinated seeds of *S. canadensis* from 100 sown seeds in each mesocosm (linear regression, intercept = 64.4, SE = 14.4, t = 4.5, linear coefficient = -34.4, SE = 10.1, t = -3.4, quadratic coefficient = 5.2, SE = 1.7, t = 3.1, n = 40) and (B) the percentage of survived seedlings plotted against the increasing FD index (logistic regression, intercept = 1.9, SE = 0.4, z = 4.5, slope = -0.5, SE = 0.1, z = -3.2, n = 40, note that Nagelkerke's R^2 is a pseudo R^2, comparison to standard R^2 from ordinary least square regression is not appropriate). Regression lines are solid with 95 % confidence bands (dashed lines).

Discussion

A few approaches and tools have been developed for measuring and assessing community's functional diversity based on functional traits, which led to our first research question, whether the proposed positive relationship between functional diversity and aboveground productivity is also prevalent when communities were assembled on the basis of the FD index by Petchey and Gaston (2002, 2006). A strength of our experimental approach is that species richness is held constant which may lead to the result that a positive functional diversity-productivity relationship would be explained by species' complementarity only, whereas the sampling effect would have been eliminated, as suggested by Petchey and Gaston (2006).

Biomass production is related to functional trait diversity

Our finding that aboveground biomass production is positively related to functional diversity is consistent with the well-known experimental grassland studies like the one carried out at the Cedar creek ecosystem science reserve (Tilman et al. 1997), in California (Hooper and Vitousek 1997), the BIODEPTH sites in Europe (Hector et al. 1999), or the Jena experiment (Marquard et al. 2009). By comparing the amount of variation in aboveground biomass production between our small-scale and short-term greenhouse study and these large-scale and long-term field experiments it is notable that functional diversity explained a higher amount of variation in our experiment (32 %) than in the other studies (14 % at Cedar Creek, 13 % at the California experiment, and 15 % at the Jena experiment; there is no comparable R^2 value reported from the BIODEPTH experiment), even though Tilman et al. (2001) showed that diversity effects strengthen through time. Spaekova and Lepš (2001), who manipulated plant species richness in a greenhouse pot experiment, also found more pronounced effects of diversity in the greenhouse compared to similar field experiments.

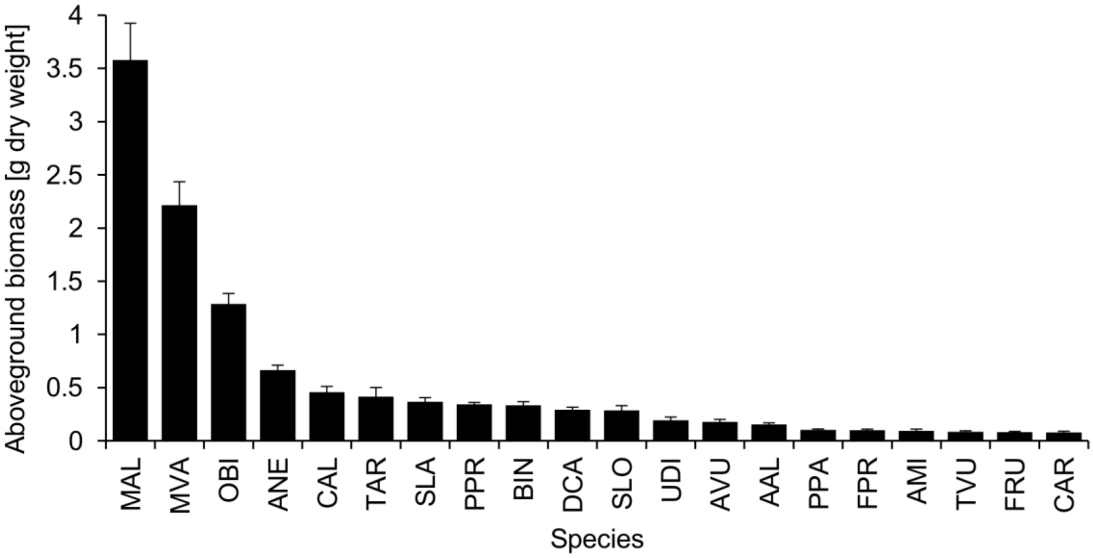

Figure 3.4 Species-specific plant productivities. Bars represent the mean dry weight of each species from the experiment. Error bars represent SE. Species abbreviations: ANE = *Acer negundo*, AMI = *Achillea millefolium*, AAL = *Ailanthus altissima*, AVU = *Artemisia vulgaris*, BIN = *Berteroa incana*, CAL = *Chenopodium album*, CAR = *Cirsium arvense*, DCA = *Daucus carota*, FPR = *Festuca pratensis*, FRU = *Festuca rubra*, MVA = *Medicago* x *varia*, MAL = *Melilotus albus*, OBI = *Oenothera biennis*, PPR = *Petrorhagia prolifera*, PPA = *Poa pratensis*, SLA = *Silene latifolia*, SLO = *Sisymbrium loeselii*, TVU = *Tanacetum vulgare*, TAR = *Trifolium arvense*, UDI = *Urtica dioica*.

However, the biomass production of the 20 plant species was very uneven in our experiment (Fig. 3.4). Our most productive species (*Melilotus albus*) was on average over 45 times more productive than our least productive species (*Cirsium arvense*). That the two most productive species (*M. albus* and *Medicago* x *varia*) were both legumes is most likely caused by the N-poor soil we used (which had a C/N ratio of 28:1). Although we did not manipulate the composition of the randomly chosen mixtures that were planted out for the experiment, the two most productive species were not distributed evenly over the range of the FD index values. Both species entered the experiment at a FD index value at 2.4, which is the point where the community biomass of mixtures that contained one or both of the two species is markedly increased (Fig. 3.1, black and grey points). Combining this random compositional effect with our finding that the trait N-fixation played the most important role in explaining aboveground productivity leads to the indication that a sampling effect contributed to the positive relationship between functional diversity and productivity in our experiment. The sampling effect is generally defined as an increased probability of including a species of greatest inherent productivity in a plot that is more diverse. That the sampling effect may not only be important at the species level, but also at the trait level, confirms the suggestion of Lepš et al. (1982) that life history strategies of constituent species are more important for ecosystem function than species richness. It is also consistent with a recently conducted trait analysis of the Jena experiment by Roscher et al. (2012), where the authors showed that increasing community biomass production was best explained by CWMs and suggested that traits of the dominant species were most important for high productivity. In our case, the differences between high productive and less productive species had such a huge dimension that it becomes obvious that the inherent traits of the dominant species are most influential on community productivity when the traits are separately analyzed via the CWM method. Further, we conducted two separated linear regressions, one that included the mixtures without legumes and a second one with all legume-mixtures (data not shown), and found no relationship between FD and productivity ($P > 0.05$) within these subsamples, which is another hint that there may have been a sampling effect present in our experiment. However, having a sampling effect in our set-up does not necessarily mean that there was no complementarity among species present. One common form of complementarity in plant communities (which involves both resource partitioning and facilitation) develops between legumes, which have the ability to fix atmospheric N, and other plants, which have access only to soil nitrogen (Loreau and Hector 2001). The sum of both complementarity and sampling effect is the net biodiversity effect (Loreau and Hector 2001), and furthermore it is assumed that both may interact with each other (Flombaum et al. 2014). However, within our set-up, it is not possible to identify their individual contributions to the net biodiversity effect since we had no monocultures in our set-up and cannot apply an additive partitioning method.

Data analysis via CWMs also revealed that the species’ floristic status was the second most important trait after N-fixation. In our study the loadings of the traits N-fixation and floristic status are opposite in direction on the first PCA axis which tells that the two CWMs have opposite effects, i.e. N-fixation is positively and the floristic status negatively related to productivity. In the case of floristic status it is unlikely that this effect is driven exclusively by a few high productive species, since the three most productive species of our experiment represent all three trait characteristics (native, archaeophyte, and neophyte). Moreover, this result is consistent with the finding of a meta-analysis by Vilà et al. (2011) that investigated the ecological impacts of exotic plant species and found that exotics have a general negative impact on native species’ productivity, abundance and diversity, but they increased total community production by 56.8 %.

Our results also showed that not only weighted means of N-fixing plants and exotic species, but also CWMs of a larger set of traits (including the traits SLA and AMF), explained variation in community biomass. But given the facts that *P*-values for both traits are not significant and the second PCA component (on which both traits have high loadings) is not significantly correlated with community biomass indicates that their influence in explaining variation in community biomass is rather negligible (Crawley 2009). Concerning SLA, this result is consistent with findings from the Jena experiment (Roscher et al. 2012) where the CWM of SLA also did not contribute to the explanation of aboveground productivity.

Invasion of S. canadensis

In terms of seedling survival rate of the invading species *S. canadensis* our results are consistent with previous invasion experiments at small scales, which have shown that increased functional group diversity decreased invasion (Tilman et al. 1996). The invasion resistance effect has been attributed to the ability of diverse communities to occupy more space, generate more biomass, and use more resources which are than not available to the invading species (Tilman 1999, Tilman et al. 2001). But also the trait characteristics of resident species seem to play an important role in the establishment of invading species, i.e. negative and positive effects on the invaders have been associated with specific functional traits of single species within the resident community (Díaz and Cabido 2001). For example, strong negative effects on invaders are reported from C_4 grasses (Fargione and Tilman 2005), whereas legumes are generally known to have positive effects on invaders (Prieur-Richard et al. 2002). Especially the latter finding is inconsistent with the results from our experiment. We found in the first phase of our study that the dominance of the two productive legumes was highest at intermediate levels of FD, which indicates, that their strong effect on overall community productivity has been responsible for the minimum of the *S. canadensis* seed germination rate at an intermediate FD level. The beneficial role mediated by N-supply, which legumes may have for the invaders in long-term studies and under natural conditions, seems to be not relevant in our short-term study. Maybe this negative short term effect of legumes on invaders also explains why our focal plant community has a low proportion of exotic plant species and a high proportion of legumes at a very early successional stage (i.e. in the first year after abandonment) in the field (Schittko, personal observation). It is also known that alfalfa (*Medicago sativa*, which is one of the parent species of *M.* x *varia*) produces root exudates with strong allelopathic agents that may reduce seed germination of other species by 50 % (Abdul-Rahman and Habib 1989). Allelopathic effects and the strong dominance of legumes at intermediate FD levels may have led to the minimum of the *S. canadensis* seed germination. That the germination rate increased again slightly at high FD levels may be explained by the fact that legume dominance and thereby community biomass was decreased at these levels.

Conclusion

The approach of using a multi-trait measure for the manipulation of functional diversity can be the superior method because it may explain greater variance in ecosystem functioning than species richness or functional group richness. Our results emphasize the need to incorporate different aspects of functional composition (functional traits, functional diversity) in studies of biodiversity-ecosystem functioning relationships. Besides N-fixation, it was the species' floristic status that explained variation in community productivity second most in our experiment. This finding underlines the fact that exotic plants pose significant impacts at the community and ecosystem level.

In addition, we hope that this article serves as a methodological reference for future ecological multi-species studies in two ways. First, manipulative studies on functional diversity may assume the use of a continuous trait-based approach, and second, the species' attribute of being exotic or native may be seen in a functional context and included in the set of functional traits that are commonly used. In this paper we avoided to label the floristic status as 'functional trait' because it breaks with the strict definition of a functional trait as being any morphological, physiological, or phenological feature. It should be considered rather as an 'effect trait' that can determine effects of plants on ecosystem functions (Lavorel and Garnier 2002). However, the difficulty in classifying this trait should not prevent community ecologists from its inclusion in studies using trait based approaches, since it can significantly explain variation in functions such as productivity and invasibility.

Acknowledgements

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Supporting information

Table S3.1 List of the plant species pool and the functional traits.

Plant species	Family	FS	LiF	RUS	SM	CH	SLA	LDMC	LeF
Acer negundo L.	Sapindaceae	1	M	AMF	41.2	11.5	15.27	390	pinnate
Achillea millefolium L.	Asteraceae	3	H	AMF	0.1	0.5	17.32	172.2	pinnatified
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	1	M	AMF	33.6	25.5	17.8	n.a.	pinnate
Artemisia vulgaris L.	Asteraceae	3	H	AMF	0.1	1.4	24.122	258	pinnatified
Berteroa incana (L.) DC.	Brassicaceae	1	H	no	0.7	0.3	20.62	245.24	long-leaf
Chenopodium album L.	Amaranthaceae	2	T	no	1.1	0.8	34.84	164.33	simple
Cirsium arvense (L.) Scop.	Asteraceae	3	G	AMF	1.2	0.9	10.07	162.1	pinnatified
Daucus carota L.	Apiaceae	3	H	AMF	1.1	1	21.7	209.51	bipinnate
Festuca pratensis s. l. HUDS	Poaceae	3	H	AMF	2.1	0.6	33.71	279.05	grass-like
Festuca rubra L.	Poaceae	3	H	AMF	0.8	0.5	16.23	277.66	grass-like
Medicago x *varia* MARTYN	Fabaceae	1	C	AMF/NF	1.75	0.4	18.1	218.66	palmate
Melilotus albus MEDIK.	Fabaceae	2	H	AMF/NF	1.9	0.9	25.37	159.25	palmate
Oenothera biennis L.	Onagraceae	3	H	AMF	0.4	1.1	13.5	180	long-leaf
Petrorhagia prolifera (L.) P.W. Ball et Heywood	Caryophyllaceae	3	T	no	0.3	0.3	17.63	231.22	long-leaf
Poa pratensis L.	Poaceae	3	H	AMF	0.3	0.3	24.57	282.15	grass-like
Silene latifolia MILL.	Caryophyllaceae	3	H	no	0.8	0.6	21.625	142.5	simple
Sisymbrium loeselii L.	Brassicaceae	1	H	no	0.1	0.6	14.26	201.24	pinnatified
Tanacetum vulgare L.	Asteraceae	3	H	AMF	0.1	0.8	16.02	221	pinnatified
Trifolium arvense L.	Fabaceae	3	T	AMF/NF	0.4	0.2	20.33	317.34	palmate
Urtica dioica L.	Urticaceae	3	H	AMF	0.15	1.1	31.58	212.5	full

Abbreviations: FS = Floristic status (1 = Neophyte, 2 = Archeophyte, 3 = Native), LiF = Life form (M = Macrophanerophyte, H = Hemicryptophyte, T = Therophyte, G = Geophyte, C = Chamaephyte), RUS = Resource use strategy (NF = Nitrogen-fixation, AMF = Arbuscular mycorrhizal fungi), SM = Seed mass, CH = Canopy height, SLA = Specific leaf area, LDMC = Leaf dry matter content, LeF = Leaf form.

Text S3.1

Additional information on trait data

Values for floristic status, seed mass, life form, and leaf form were obtained from the BiolFlor database (Klotz et al. 2002), and values for specific leaf area and leaf dry matter content were taken from the LEDA database (Kleyer et al. 2008). Regarding the LEDA database, we chose the aggregated values from the species fact sheets, and if not available, we used the implemented web query tool to aggregate suitable data manually.

For information about plant association with mycorrhizal fungi we checked appropriate publications (Harley and Harley 1987, Peat and Fitter 2006, Wang and Qiu 2006, Huebner et al. 2007, Bainard et al. 2011). Because none of our selected plant species is associated with other mycorrhizal types than arbuscular mycorrhizal fungi (e.g. ectomycorrhizal fungi), there was no other trait values than ‘no’, ‘AMF’ or ‘AMF/NF’ (the latter means that the plant species is associated with AMF and nitrogen-fixing bacteria simultaneously).

The trait floristic status defines whether a plant is native or alien to Germany. For the specification of the floristic status we followed the classification from the BiolFlor database (Klotz et al. 2002), which is based on the classification system by Schroeder (1968) and is also used by other authors (Kowarik 2010). This classification acts exclusively on a temporal basis excluding information about the evolutionary history, origin, or mode of introduction. Alien species are classified according to their time of human introduction: before the discovery of America (archaeophytes) and after the discovery of America in 1492 (neophytes). Species that colonized the focus area after the end of the last glacial period (about 12,500 years ago) without human assistance are classified as indigenous or native. Contrary to other studies engaged with biological invasions that classify species into the two categories ‘native’ or ‘alien’, we treated the floristic status as a continuous variable based on time of introduction or appearance. This approach is backed on the aspect that native species have longer evolutionary histories with other local organisms than species that established later in the course of time. In our trait matrix, native species were characterized by the trait value ‘3’ (longest history), archeophytes by a value of ‘2’ and neophytes by the value ‘1’ (shortest history). We are aware that the distances between the three trait values are equal but the time ranges that define the categories are unequal. However, having a true continuous variable for the time of species’ appearances would have required accurate data for the evolution and historical distribution of each species; this data were only available for a few species of our pool. Due to this lack, we decided to use this three group classification approach (natives, archeophytes, neophytes) which is most commonly used in Central Europe (Wittig 2004) and has data available for all our species.

Text S3.2

Additional information on the calculation of FD

In R (R Core Team 2013) we used the function combn() in the ‘utils’ package to create a matrix with every possible eight-species mixture from the 20-species pool. With the function melt() in the ‘reshape’ package we transformed that matrix into a table. Further actions were performed by the R-based software FDiversity (Casanoves et al. 2011), which is a free tool developed to estimate and analyze indices of functional diversity. Here we merged the species mixtures table with our trait matrix. Each categorical variable was transformed beforehand into several binary variables (also called dummy variables). Afterwards, we calculated the community based FD value of every eight-species mixture (125,970 in total). The community based FD index (Petchey and Gaston 2006) is a revised version of the plot based version introduced in 2002 (Petchey and Gaston 2002). In order to construct the functional dendrogram from which FD is measured one needs to calculate pair wise distances between species, and then use a clustering algorithm. As distance measure we used Gower distance because of its ability to cope with mixed trait data (categorical and continuous) and missing values (Podani and Schmera 2006, Petchey and Gaston 2007). We used UPGMA (average linkage) as clustering algorithm since Podani and Schmera (2006) showed the UPGMA algorithm outperformed other procedures (e.g. UPGMC, WPGMC, single linkage, complete linkage, etc.) in measuring FD indices.

From the 125,970 mixtures we randomly chose 40 mixtures with the Excel function randbetween(). We interfered to the procedure when it happened by chance that FD values of the chosen mixtures resembled each other within two positions behind the decimal point. In these cases we discarded one of the two values and drew a new mixture to achieve an even distribution of FD values along their full range within the 40 plant mixtures.

Chapter 4

Bottom-up effects of plant functional trait diversity on arthropod abundance and diversity in an urban grassland plant community

Abstract

Plant species diversity has been recognized as an important factor influencing the abundance and species richness of organisms at higher trophic levels. However, although plant functional diversity has been regarded in recent years to be a better predictor of ecosystem processes and functions than species diversity, the impact of functional diversity on higher trophic levels is less understood. In a mesocosm study we manipulated plant functional diversity based on the multi-trait Functional Diversity (FD)-approach of Petchey and Gaston by using data of seven functional traits and information on the origin of the species in terms of being native or exotic. Along a gradient ranging from low to high FD we planted 40 randomly selected eight-species mixtures. First, we found that the abundance of specialist aphids of the focus plant species *Cirsium arvense*, as well as the abundances of mutualistic aphid-tending ants and predatory ladybird beetles were negatively related to plant functional trait diversity. Second, and in contrast to the first result, we found that the total abundances and species richnesses of herbivores and predators present in the mesocosms were positively related to functional diversity. The diversity effect on abundances of higher trophic levels dampened from herbivores to predators. Based on community-weighted mean calculations for each functional trait, we figured out that traits related to plant quality and the plant species origin, i.e. being native or exotic, played the most important role for predicting arthropod abundance and species richness. Our results demonstrate that the identification of the impact of functional trait diversity and the relative contributions of relevant traits are essential for a mechanistic understanding of ecosystem processes.

Introduction

As biodiversity loss increases rapidly (Sala et al. 2000), ecologists intensified the effort to understand how these declines will affect ecosystem functioning (Tilman 1999, Loreau et al. 2001, Marquard et al. 2009). Most research has focused on plant biodiversity (Cardinale et al. 2012), and how loss of plant species or functional groups affects processes such as ecosystem productivity (Hector et al. 1999, Tilman 1999, Cardinale et al. 2007), nutrient cycling (Hooper and Vitousek 1998), and ecosystem stability (Tilman et al. 2006). Furthermore, plant community diversity has been recognized as an important factor influencing the abundance and species richness of organisms at higher trophic levels (Elton 1958, Hutchinson 1959, Hunter and Price 1992). Recent field experiments at different study sites (Koricheva et al. 2000, Haddad et al. 2009, Scherber et al. 2010) have shown plant species diversity effects on a wide range of different groups of organisms, including primary producers, herbivores, predators, detritivores, fungal pathogens, and mycorrhizal fungi. But in contrast to the well documented effects of plant species diversity, the impact of plant functional diversity on organisms at higher trophic levels is less understood.

One common measure of functional diversity that is often used to manipulate functional diversity in experimental set-ups is the number of functional types or groups (e.g. C_4 grasses, C_3 grasses, N-fixing plants, and non-N-fixing plants) represented by the species in a local community (e.g. Tilman et al. 1997, Hooper and Vitousek 1997, Díaz and Cabido 2001, Naeem and Wright 2003). Previous experiments that employed the functional group concept to investigate the impact of plant functional diversity on the diversity and structure of higher trophic levels reported conflicting results: While the field studies of Siemann et al. (1998) and Symstad et al. (2000) found no relationship between arthropod species richness and plant functional group richness or composition, Haddad et al. (2001) documented a negative impact of plant functional group richness on arthropod abundances but a positive impact on arthropod species richness. However, these inconsistency in results (compared among each other and also compared to studies on plant species richness) may be due to weaknesses of the functional group concept: The manipulation of functional group diversity in biodiversity-ecosystem function experiments goes along with major disadvantages like the exclusion of functional differences that occur between organisms in the same group (Petchey and Gaston 2006). This led to some concerns whether this concept is the right method to predict effects of plant functional diversity on arthropods living on that plant communities (Siemann et al. 1998, Symstad et al. 2000). On the other hand, the assumption that ecosystem processes are governed by the abundance and distribution of functional traits in a community (Díaz and Cabido 2001, McGill et al. 2006, Roscher et al. 2012) has attracted growing attention on the use of functional trait composition, rather than species or functional group richness, in the explanation of biodiversity-ecosystem functioning relationships. A number of new multi-trait approaches such as functional attribute diversity (FAD), functional diversity (FD) or Rao’s Q has been introduced which assess functional diversity of a community by quantifying the distances of trait values of species in a multi-dimensional trait space (Petchey and Gaston 2006, Mouchet et al. 2010). The concept of functional trait diversity is based on the assumption that greater differences between species’ trait values represent greater trait complementarity and larger functional diversity. Since the introduction of the continuous multi-trait Functional Diversity (FD) index by Petchey and Gaston (2002, 2006), it has been shown that FD explains variation in ecosystem functions, most notably plant aboveground productivity of grassland species (Mokany et al. 2008, Schumacher and Roscher 2009, Schittko et al. 2014).

In addition, most studies that examined the effects of species or functional diversity on higher trophic levels have dealt with herbivory or predator-prey systems, while only a few studies have documented diversity effects in mutualistic systems (for example, Scherber et al. [2010] reported plant species diversity effects on pollinators and mycorrhizal fungi). In temperate regions, aphids are the most important honeydew producers, many of which have developed a mutualistic relationship with ants (Buckley 1987, Völkl et al. 1999). Aphids benefit from this mutualism with ants by reduced predation and parasitism and by a reduced risk of fungal infection. In return, honeydew excreted by aphids provides a food source for tending ants (e.g. Banks 1962, Way 1963, Völkl et al. 1999). The functioning of this mutualistic relationship depends on various factors, among which are species-specific differences between the involved aphid and ant species (Addicott 1978, Bristow 1984), density-dependent effects (Itioka and Inoue 1996), host plant quality (Auclair 1963, Breton and Addicott 1992), and seasonal differences in the honeydew demand of the ants (Sudd and Sudd 1985).

In this study, we conducted a mesocosm field experiment to understand how bottom-up effects of plant functional trait diversity affect species interactions across multiple trophic levels. Our objectives were twofold. First, we sought to understand the importance of plant functional diversity in affecting the distinctive interactions of a focus plant species (*Cirsium arvense*) with a specialist aphid herbivore (*Brachycaudus cardui*) and its mutualists (ants) and predators (ladybird beetles). Within that study system, we predict that bottom-up effect of plant functional trait diversity influence the abundance of aphids, mutualistic ants, and predatory ladybird beetles.

In our second objective we focused on the relationship between plant functional trait diversity and the abundance and diversity of organisms on higher trophic levels. Within this objective, we focused first on the question whether trait diversity effects are passed from one trophic level to the next. Based on comparable studies on plant species richness (e.g. Scherber et al. 2010), we hypothesized that diversity effects are dampened with increasing trophic level (i.e. the effect of functional trait diversity is stronger on herbivores than on predators). Second, we investigated the relative importance of each selected plant trait in explaining the relationship between functional trait diversity and the abundance and species richness at higher trophic levels. Here we hypothesized that plant traits related to tissue quality may be the most relevant for plant interactions with higher trophic level organisms.

Methods

In this study we used a single factor regression design with functional diversity being the single continuous factor that was experimentally manipulated. Functional diversity was calculated for all possible eight-species mixtures from a pool of 20 naturally co-occurring plant species, based on the FD index introduced by Petchey and Gaston (2002, 2006). This measure of functional diversity is defined as the total branch length of a functional dendrogram, which is created from data of plant functional traits. From the total number of possible eight-species mixtures (125,970), 40 mixtures were randomly selected and planted out for the experiment. This design was chosen to cover a broad range of functional diversity (from low FD to high FD).

Plant species pool and functional traits

Plant species selection for the species pool of the experiment was conducted with the purpose of reflecting the composition of a ruderal plant community, which is a typical attribute of temporary abandoned fields and disturbed habitats in urban areas. Specific abiotic conditions and the vicinity to human settlements and transport connections support the establishments of non-native plant species in these areas (Kowarik 2003). The species pool was compiled after several vegetation surveys in 2011 on appropriate sites across Berlin (Germany). The species pool contained 20 angiosperm species (13 natives and 7 non-natives), of which 15 were forbs, 3 grasses, and 2 tree species (see Schittko et al. [2014] for detailed information). The major part of the plant seeds we used was collected on an urban abandoned site in Berlin (N52°28'30", E13°21'46"). A minor part of seeds was provided by Appels Wilde Samen (Darmstadt, Germany) or by the Botanical Garden Berlin-Dahlem. To classify each plant species functionally we used data of seven functional traits (four continuous and three categorical) plus the species' floristic status (which defines whether a plant is native or exotic). Trait values for each trait were exclusively obtained from trait-databases (BiolFlor [Klotz et al. 2002] and LEDA [Kleyer et al. 2008]) or in some cases of unavailability from approved publications (Harley and Harley 1987, Peat and Fitter 2006, Wang and Qiu 2006, Huebner et al. 2007, Bainard et al. 2011). The three categorical traits were: 'life form' (i.e. macrophanerophyte, hemicryptophyte, therophyte, geophyte, chamaephyte), ‘leaf form’ (i.e. simple, full, long, grass-like, palmate, pinnate, pinnatified), and ‘resource use strategy’ (i.e. root colonization with nitrogen-fixing bacteria and/or arbuscular mycorrhizal fungi, AMF). The four continuous traits were: ‘specific leaf area’ (SLA), ‘canopy height’, ‘seed mass’, and ‘leaf dry matter content’ (LDMC). The trait ‘floristic status’ defines whether a plant is native or exotic to Germany and was treated as a continuous trait as well. For the specification of the floristic status we followed the classification from the BiolFlor database, which is based on the classification system by Schroeder (1968). This classification acts exclusively on a temporal basis excluding information about the evolutionary history, origin, or mode of introduction. Exotic plant species are classified according to their time of human introduction: after the discovery of America in 1492 (neophytes, trait value ‘1’ in our data table), before the discovery of America (archaeophytes, trait value ‘2’) and species that colonized the focus area after the end of the last glacial period (about 12,500 years ago) without human assistance are classified as indigenous or native (trait value ‘3’). Our approach is backed on the aspect that native species have longer evolutionary histories with other local organisms than species that established later in the course of time.

Calculation of Functional Diversity (FD)

The calculations of the FD index for each possible eight-species mixture (125,970 in total) were performed by the R-based software FDiversity (Casanoves et al. 2011). After calculating the FD values we ended up with a range of FD between 1.69 (lowest value) and 4.08 (highest value, see Schittko et al. [2014] for additional information on the calculation). From the 125,970 possible mixtures we randomly chose 40 mixtures with the Excel function ‘randbetween’ (Microsoft Excel 2007).

Experimental set-up

The experimental part started in November 2011 and was composed of three stages. The first two stages dealt with plant community productivity and invasibility and are described elsewhere (Schittko et al. 2014), whereas this manuscript focuses on the third stage. For each stage we used the same 40 mesocosms, which consisted of plastic pots (7.5 l volume, 21 cm height, 26 cm upper diameter, and 19 cm lower diameter) filled with 7 kg soil each. The soil was a loamy sand (pH 8.1, C/N ratio of 28:1, determined with an elemental analyzer Euro EA, HEKAtech GmbH, Germany) that was collected from an urban abandoned site in Berlin (N52°28'30", E13°21'46") and sieved before the experiment (4 mm mesh size) but remained untreated otherwise. Each of our experimental plant species could be found on that site. 16 equally sized seedlings (two individuals per species) that had been grown on sterilized soil were transplanted carefully into each mesocosm according to the drawn species compositions. Each seedling was assigned by chance to one of 16 possible positions in the mesocosms. During the first two experimental stages the mesocosms remained within a greenhouse. Two times, at the end of stage one (January 2012) and stage two (March 2012), aboveground plant biomass was cut. The shoots were cut 3.5 cm above ground level to enable regrowth for the subsequent stage. With beginning of the third stage in late March 2012, the mesocosms were placed outside on a former agricultural site (N52°27'26", E13°18'05") within the campus of the Freie Universität Berlin where they remained during this final stage of the experiment. There, the mesocosms were placed at least 1.70 m apart from each other, their position was randomized once a week, and they were watered regularly.

Measurements and harvest

In June and July 2012 we surveyed abundances of aphids, ants and ladybird beetles on the focus plant species *Cirsium arvense* (L.) Scop. (the Creeping Thistle). Though each of our experimental mesocosms had a unique composition of plant species, *C. arvense* was present in 14 out of the 40 mesocosms. These 14 mesocosms that contained *C. arvense* covered a range of FD index values from 2.1 to 4.1. On five sampling dates at weekly intervals we counted the instantaneous numbers of organisms that were present on *C. arvense*, mainly aphids, ants, and ladybird beetles. Other organisms occurred only in small numbers and were excluded from the survey. Over the whole survey period there was only one aphid species (the Thistle aphid *Brachycaudus cardui*), one ant species (the black garden ant *Lasius niger*), and one ladybird beetle species (the seven-spot ladybird *Coccinella septempunctata*) present on *C. arvense*. Between weeks four and five of the survey the number of aphids declined dramatically (only two individuals were found at the fifth sampling date) most probably due to harsh climate conditions (heavy rainfall), which caused our decision to exclude the abundance data of the fifth sampling date from the subsequent analysis. Aphid population size did not recover later during this year. After harvesting the experiment (see below) we determined the shoot nitrogen content of *C. arvense* plants. Therefore we used stem material because we found aphids feeding on plant stems exclusively. Dry stem samples were ground in Eppendorf tubes by using a mixer mill (MM400, Retsch GmbH, Germany) and were dried again for at least 24 hours. Afterwards, nitrogen content was determined by using an elemental analyser (Euro EA, HEKAtech GmbH, Germany).

In late August 2012, we harvested the aboveground plant parts of the experiment and took the samples for total arthropod abundance and species richness. Therefore, each mesocosm was inspected by one person for ten minutes and arthropods were collected by using tweezers and a pooter. Afterwards, the plant shoots were cut individually and were beaten five times onto a plastic collecting tray from which the arthropods were collected as well. This procedure was repeated once for each plant shoot. The plant shoots were separated according to species, dried in an oven for three days at 50 °C, and dry weights were determined with a fine balance.

The arthropod samples from each mesocosm were identified, sorted to species or morphospecies, and individuals were counted. In addition, arthropod species were assigned to one of four trophic categories, herbivores, parasitoids, predators, or omnivores, based on mouth part and consultation with the literature. For the purposes of this manuscript, we focus on herbivore and predator response, since the number of parasitoids and omnivores was very low in our samples. Therefore, the collected parasitoids were grouped into predators (Haddad et al. 2009) and the collected omnivores into one of both categories (e.g. if organisms having different feeding modes in different stages of their life cycles, they were classified based on their stage present in our samples, Haddad et al. [2001]).

Data analysis

To analyze the repeated-measurement data of the mid-season sampling (aphids, ants, and ladybird beetles abundances) we used a linear mixed effects model (LMEM) to measure the effects of functional trait diversity and time (both fixed effects) on the abundance of the respective organism group (response variable) of the mesocosms (random effect). Additionally, we used simple linear regression to test for the relationship between functional diversity and shoot nitrogen content of *C. arvense* plants.

For the late-season sampling dataset we used simple linear regressions to test for the effects of functional diversity on total arthropod abundance, arthropod species richness and abundance, and species richness of the two trophic categories herbivores and predators. To test whether the effect of functional diversity dampens along trophic cascades we performed an ANCOVA with the respective abundance or species richness as response variable, the trophic category as explanatory variable and the FD index as continuous co-variable. This procedure allows us to tell whether there is a significant difference between slopes from the previous performed linear regressions.

To elucidate the relative contribution of plant functional traits to the amount of explained variation of arthropod abundance and species richness we performed multiple regressions with a stepwise model selection procedure comparing statistical models with different combinations of included explanatory variables (traits). Beforehand, community-weighted means of plant trait values (CWM) were calculated for each mixture based on plant species biomass proportions according to the equation

$$CWM = \sum_{i=1}^{S} p_i \times t_i$$

where S is the number of species in the community, p_i is the species biomass proportion and t_i are the given trait values. These CWMs are weighted average trait values and were calculated for each trait. We used the Akaike information criterion (AIC) and R^2 values to select for the model with the best fit in the model selection procedure.

All models were tested for the underlying assumptions (homoscedasticity, normality). All statistical analyses were performed in R (version 3.0.2, R Core Team 2013) with addition of the nlme package (Pinheiro et al. 2013) for the linear mixed effects model and the leaps package (Lumley and Miller 2009) for the model selection procedure.

Results

Effects of plant functional diversity on aphids, ants, and ladybird beetles on C. arvense

Plant functional trait diversity had a negative effect on the mid-season aphid infestation of *Cirsium arvense* (LMEM: $F = 5.92$, $P = 0.019$, Fig. 4.1a). On average, the aphid population size infesting *C. arvense* was 24 times smaller when *C. arvense* was surrounded by a community with a high functional trait diversity compared to communities with lower functional diversity. Accordingly, with increasing plant functional diversity the abundance of aphids-tending ants was decreasing as well (LMEM: $F = 19.65$, $P < 0.001$, Fig. 4.1b). Likewise, increasing plant functional diversity had also a negative effect on abundances of predatory ladybird beetles on *C. arvense* (LMEM: $F = 9.08$, $P = 0.004$, Fig. 4.1c). The shoot nitrogen content of *C. arvense* was negatively related to the functional trait diversity of the surrounding plant community (Linear regression: $t = -3.38$, $P = 0.005$, Fig. 4.1d). However, aboveground biomass of *C. arvense* was not related to functional diversity at the time the plants were harvested (Linear regression: $P > 0.05$).

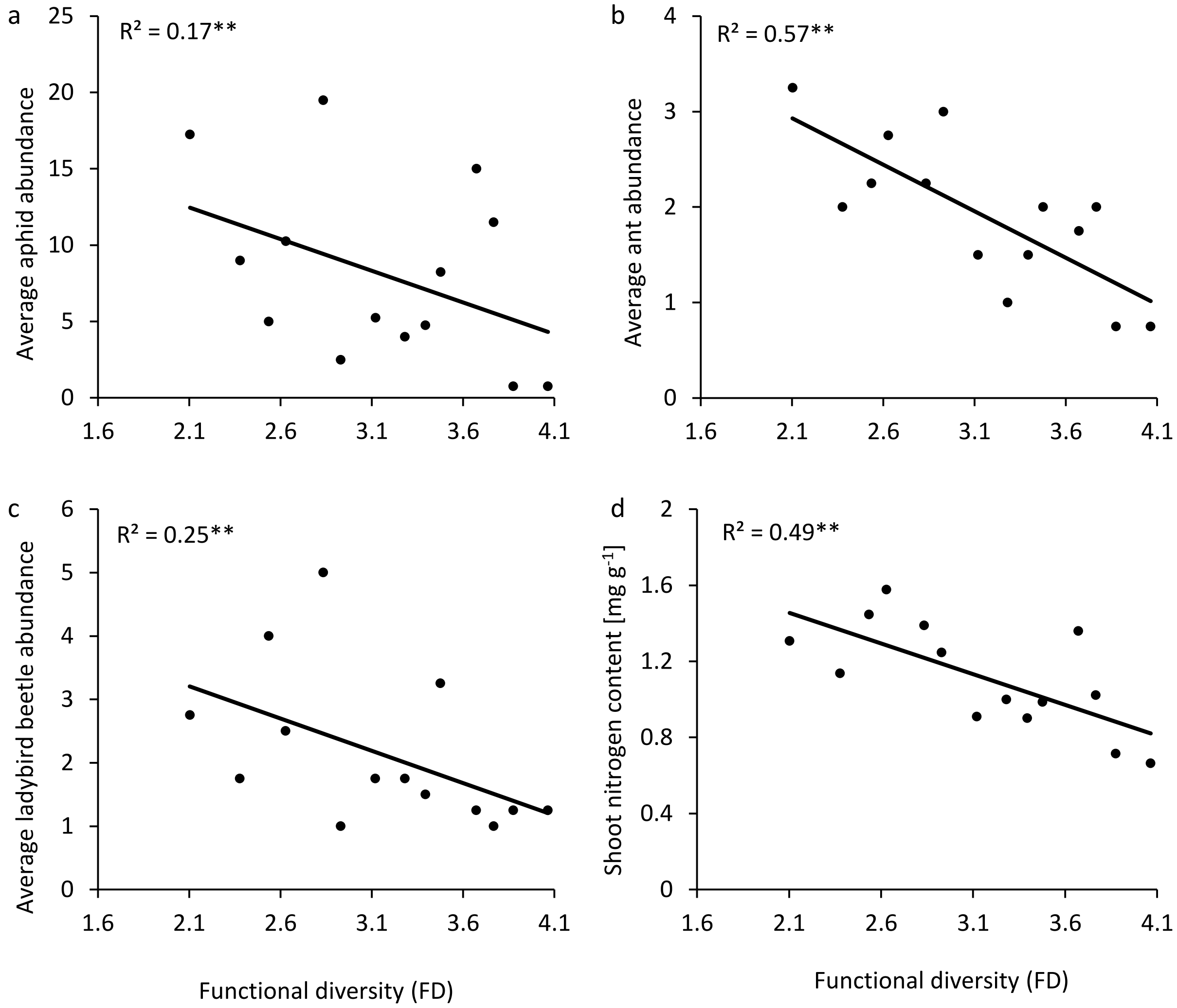

Figure 4.1 Average abundances of (a) aphids, (b) mutualistic ants, (c) predatory ladybird beetles, and the (d) shoot nitrogen content of *C. arvense* plotted against the FD index of each eight-species mixture (n = 14, df = 12). Increasing FD index values represent increasing functional diversity within the mixtures. Please note: Abundance data were analyzed with a repeated measure analysis (see main text). For the purpose of visualization we show in this figure averaged values over the four measurements. Regression lines and R^2-values originate from simple linear regressions on the averaged abundance data.

Arthropod abundance and species richness

In total, arthropod sampling at the end of the experiment caught 1196 individuals of 39 different species. From the total number of individuals, 847 and 349 were counted as herbivores and predators, respectively, whereas from the total number of species, 23 and 16 were identified as herbivores and predators, respectively. Simple linear regression of total arthropod abundance and species richness on plant functional trait diversity showed that both were positively related with the FD index (Fig. 4.2a, b). Likewise, abundances and species richnesses of organisms of the two higher trophic levels herbivores and predators were positively related with plant functional diversity as well (Fig. 4.2c–f).

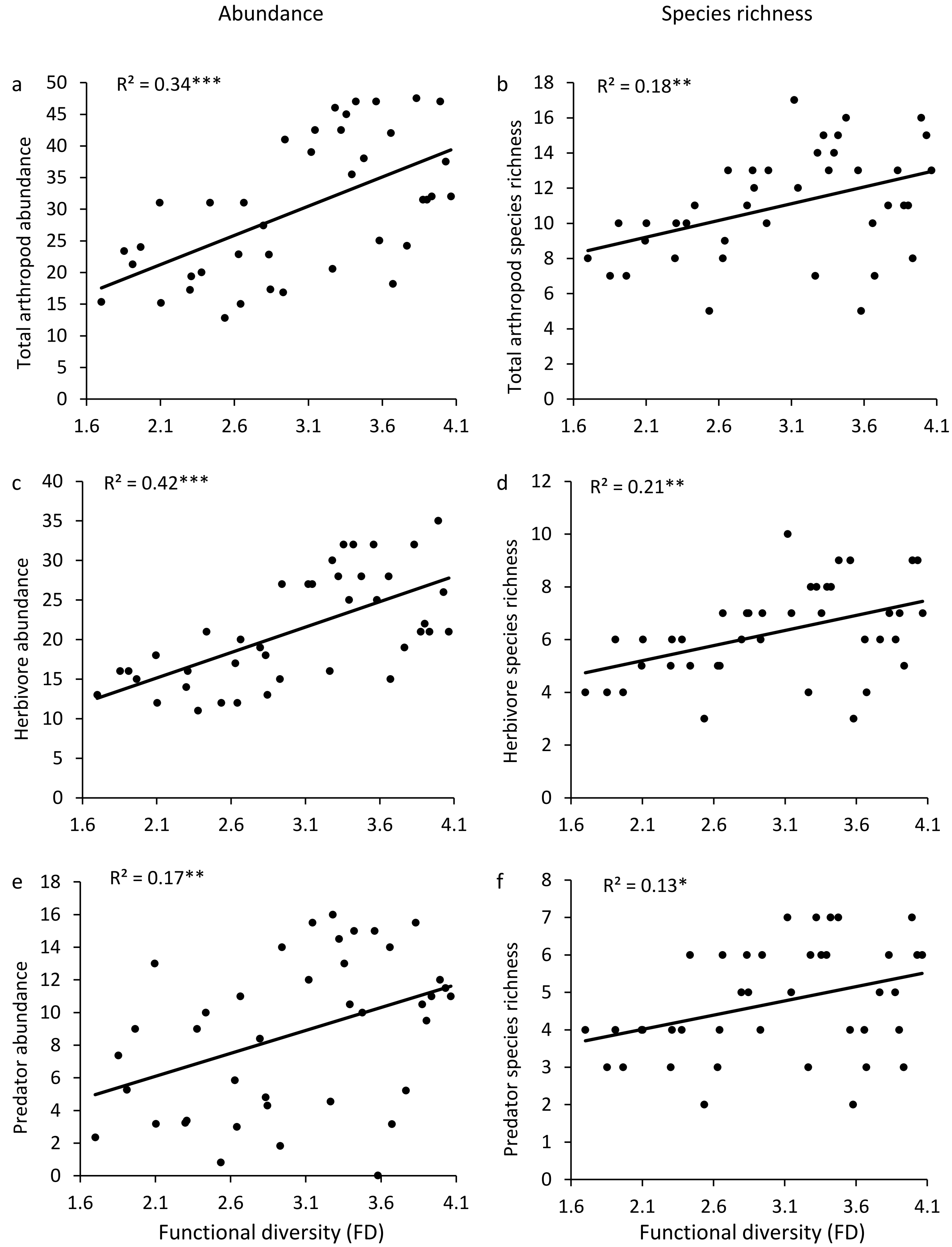

Figure 4.2 Abundances and species richnesses of arthropods and of the two trophic categories plotted against the FD index of each eight-species mixture. (a) Total arthropod abundance (intercept = 1.31, SE = 6.55, *t* = 0.20, slope = 9.43, 95 % confidence intervals for slope 5.88 – 12.98, SE = 2.11, *t* = 4.48). (c) Herbivore abundance (intercept = 1.69, SE = 3.84, *t* = 0.44, slope = 6.42, 95 % confidence intervals for slope 4.33 – 8.10, SE = 1.23, *t* = 5.20. (e) Predator abundance (intercept = -0.37, SE = 3.19, *t* = -0.12, slope = 3.01, 95 % confidence intervals for slope 1.29 – 4.74, SE = 1.02, *t* = 2.94. (b) Arthropod species richness (intercept = 5.21, SE = 2.03, *t* = 2.57, slope = 1.91, 95 % confidence intervals for slope 0.87 – 2.94, SE = 0.65, *t* = 2.93. (d) Herbivore species richness (intercept = 2.79, SE = 1.13, *t* = 2.47, slope = 1.15, 95 % confidence intervals for slope 0.53 – 1.76, SE = 0.36, *t* = 3.16. (f) Predator species richness (intercept = 2.42, SE = 1.00, *t* = 2.42, slope = 0.76, 95 % confidence intervals for slope 0.22 – 1.30, SE = 0.32, *t* = 2.36. For each panel: n = 40, df = 38.

To determine whether the effects of plant functional diversity are dampened with increasing trophic distance we compared the regression slopes of the trophic levels. We found that the response of predator abundance was smaller compared to the herbivore abundance (i.e. the regression slope was significant less steep, ANCOVA: $F = 4.50$, $P = 0.037$). However, there was no significant difference between the responses of species richnesses of herbivores and predators (ANCOVA: $P > 0.05$).

Relative importance of plant traits

By investigating the relative importance for each individual plant trait for the response variables total arthropod abundance, arthropod species richness, herbivore abundance, herbivore species richness, predator abundance, and predator species richness we found that the total arthropod abundance was best explained by a certain composition of plant functional traits. The model selection procedure led to a model that included the traits nitrogen-fixation, floristic status, LDMC, and grassy leafs and explained 37 % of the variation in total arthropod abundance (Table 4.1). Nitrogen-fixation and the floristic status were positive correlated with arthropod abundance, whereas LDMC and grassy leafs showed a negative correlation. In terms of floristic status, high biomass proportions of exotic species in regard to community biomass (hence a low CWM for the trait floristic status) were accompanied with a lower arthropod abundance. The model for arthropod species richness included the same set of functional traits but explained less variation (24 %). Similarly, the models for abundances and species richnesses of the two trophic levels herbivores and predators have also nitrogen-fixation and the floristic status included, although the proportion of explained variation is lower compared to the total arthropod data (Table 4.1).

Table 4.1 Summaries for the best statistical models based on different sets of predictor variables (traits) explaining the variation of total arthropod abundance and species richness, and abundance and species richness of the trophic categories herbivores and predators. A (+) or (-) indicates whether this trait is positively or negatively related to the response variable.

Model parameter				**Parameter of included traits**			
Response variable	**df**	**Multiple R^2**	***P***	**Functional traits**	***t***	***P***	**Partial R^2**
Total arthropod abundance	35	0.37	< 0.01	Nitrogen-fixation (+)	11.72	< 0.001	0.69
				Floristic status (+)	2.01	0.032	0.23
				LDMC (-)	1.72	0.043	0.21
				Leaf form : grass (-)	-1.97	0.057	0.17
Total arthropod species richness	35	0.24	0.024	Nitrogen-fixation (+)	9.89	0.002	0.58
				LDMC (-)	2.87	0.041	0.23
				Floristic status (+)	2.96	0.043	0.24
				Leaf form : grass (-)	-0.67	0.056	0.15
Herbivore abundance	35	0.32	0.013	Nitrogen-fixation (+)	9.62	< 0.001	0.61
				Floristic status (+)	2.11	0.038	0.18
				LDMC (-)	1.82	0.039	0.17
				Leaf form : grass (-)	-1.97	0.044	0.11
Herbivore species richness	36	0.21	0.026	Nitrogen-fixation (+)	9.02	0.003	0.52
				Floristic status (+)	2.81	0.042	0.19
				LDMC (-)	1.72	0.058	0.17
Predator abundance	36	0.23	0.031	Nitrogen-fixation (+)	7.63	0.009	0.41
				Floristic status (+)	2.12	0.049	0.13
				Leaf form : grass (-)	-0.57	0.055	0.10
Predator species richness	37	0.15	0.045	Nitrogen-fixation (+)	8.01	0.008	0.45
				Floristic status (+)	2.01	0.057	0.13

Discussion

This study demonstrates the importance of plant functional trait diversity for predicting the effects of plant communities on the abundance and diversity of higher trophic levels. Although our study lasted only a single vegetation period, the effects were evident along trophic cascades. However, concerning functional diversity effects on arthropod abundances our results from the two sampling approaches were apparently opposing each other: In the mid-season sampling, functional plant diversity had significant negative effects on the abundances of the three studied organisms (aphids, ants, and ladybird beetles) on *C. arvense*, while the total numbers of arthropods (and also numbers herbivores and predators) were positively related to plant functional diversity in the late-season sampling. Although seasonality is known to have an influence on arthropod abundance and diversity (e.g. Lowman 1982, Pinheiro et al. 2002), we assume that the different responses were a matter of the different scales of our two sampling approaches (one focus plant vs. mesocosm community). From this perspective, we suppose that our contrasting results were generated by different mechanisms that are related to certain characteristics of plant functional trait diversity, and which will be discussed in the following paragraphs.

Effects of plant functional diversity on aphids, ants, and ladybird beetles on C. arvense plants

Increasing functional diversity negatively affected numbers of specialist aphids, the abundance of aphid-tending ants, and the number of predatory ladybird beetles on the focus plant *C. arvense*. We furthermore found that shoot nitrogen content of *C. arvense* decreased with increasing functional diversity, which is indicative for a relationship between levels of shoot nitrogen content and aphid abundance. This is supported by previous studies. For example, Zehnder and Hunter (2008) found that soil nitrogen fertilization increased foliar nitrogen content and led eventually to an increased aphid population growth on *Asclepias tuberosa* plants. Consistently, Aqueel and Leather (2011) reported that nitrogen fertilization had positive effects on adult weight, fecundity, and longevity of two aphid species feeding on *Triticum aestivum*. Apart from studies focusing explicit on plant-aphid interactions, it is a well-known phenomenon that host plant quality may influence the performance of herbivorous insects (e.g. Awmack and Leather 2002, De Bruyn et al. 2002, Soler et al. 2005). However, if aphid abundance was affected by plant shoot nitrogen content in our experiment, one crucial question remains: what could have caused these different nitrogen levels of *C. arvense* shoots? We propose two mechanisms that are both related to the functional diversity gradient in our experiment. First, complementarity effects, where resource partitioning and facilitation among species result in a more complete use of available resources in plant communities of increasing diversity (Tilman et al. 1997, Hooper et al. 2005), might have played a role. As shown in the Jena experiment, total nitrogen uptake from the soil may increase with increasing diversity (either of species or functional groups) of grassland communities leading to a decrease of soil nitrate (Oelmann et al. 2007, Gubsch et al. 2011). This process affect the species' individual nitrogen uptake and produces species-specific responses of foliar nitrogen content in mixtures of increasing diversity, i.e. some species showed increases in foliar nitrogen content and some decreases (Gubsch et al. 2011, Roscher et al. 2011). Second, increasing functional diversity resulted in an increase of plant community productivity in our experiment (data not shown). Since nitrogen uptake and community productivity are often positively related (Finzi et al. 2007), it is reasonable to suppose that the soil from communities with higher functional diversity experienced a higher nitrogen depletion rate, what might have caused the lower nitrogen levels in shoots of *C. arvense* in communities with increasing functional diversity.

In summary, we assume that the increasing level of functional diversity in our experiment negatively affected shoot nitrogen content of *C. arvense* and thus affecting indirectly the specialist aphid population on that plant species. Furthermore, we also detected negative relationships between functional diversity and aphid-tending ants, and functional diversity and predatory ladybird beetles. This indicates that the effect on the third trophic level (ants and ladybird beetles) was a density-mediated indirect effect owing to changes in aphid abundance. Similarly, Moreira and Mooney (2013) reported bottom-up effects from plant genetic diversity on aphid abundances, which resulted in a parallel variation in ants and parasitoid abundances. Further, Petermann et al. (2010) showed that both the proportion of winged aphid morphs and the number of aphid parasitoids decreased with increasing plant species richness in a grassland biodiversity experiment. However, our experimental set-up does not allow explicit testing whether plant functional diversity affected the third trophic level also independent from changes in aphid abundances which is an effect that was reported from some similar work (Johnson et al. 2006, Moreira et al. 2012).

Arthropod abundance and species richness

We found that plant functional trait diversity positively affected total arthropod abundance and diversity in the mesocosms in the late-season sampling. In a broader context, this finding is consistent with field studies on plant biodiversity and arthropod assemblages, such as studies on plant species richness (Siemann et al. 1998, Haddad et al. 2001, 2009, Scherber et al. 2010), on plant phylogentic diversity (Dinnage et al. 2012) and genotypic diversity (Johnson et al. 2006). However, studies that focused explicit on functional diversity reported inconsistent results so far: While Siemann et al. (1998) and Symstad et al. (2000) found in field experiments no relationship between plant functional group richness or composition and arthropod species richness, Haddad et al. (2001) documented that plant functional group richness had a negative impact on arthropod abundances but a positive influence on arthropod species richness. These previous studies had in common that they employed the functional group concept to manipulate functional diversity in their experiments. It was argued by the authors whether the categorizations of plant species into the typical functional groups (e.g. C_4 grasses and C_3 grasses, N-fixing plants and non-N-fixing plants, forbs and woody species) are less relevant to arthropods living on the plants than they are for ecosystem functions such as plant productivity (Siemann et al. 1998, Symstad et al. 2000). Many herbivorous arthropods feed on only one or a few species of plants, rejecting even those in the same genus or family. We assume that these specialist host-herbivore relationships are poorly predicted by the presence or absence of certain functional groups because the members of the same plant family are also often categorized into the same functional group. In contrast, approaches based on individual functional traits may even capture subtle functional differences between species from the same genus which makes them likely the superior method in predicting changes on higher trophic levels. The finding from our experiment that both arthropod abundance and species richness were predicted by plant functional trait diversity is more similar to studies that manipulated plant species richness (Siemann et al. 1998, Koricheva et al. 2000, Scherber et al. 2010) than functional group richness and underlines the assumption that species richness can be seen as a predictor of functional diversity (Flynn et al. 2009, Mason et al. 2013).

Furthermore, we found that the response of predator abundance was smaller compared to the herbivore abundance (i.e. the predator regression line was less steep), which is an indication that the effect of functional diversity declines with increasing trophic level. This finding is consistent with a study on the Jena experiment (Scherber et al. 2010) in which the authors show that the effect of plant species richness steadily decreases along a trophic cascade of herbivores, carnivores, parasitoids, and omnivores. However, in contrast to the aforementioned study, we found no attenuation of the functional diversity effect from herbivore to predator species richnesses.

Relative importance of plant traits

The step-wise modelling procedure including CWMs of the functional traits as predictor variables applied to explore their relative contribution in explaining variation in arthropod abundance and species richness resulted in models that showed similar explanatory power like the FD regression models Nitrogen-fixing plants had the strongest effects across trophic levels: their dominance was positively related to the abundances and species richnesses of total arthropods, herbivores, and predators. This finding is consistent with experiments that manipulated functional group richness (Siemann et al. 1998, Symstad et al. 2000, Haddad et al. 2009). Additionally, herbivore abundance and species richness were negative correlated with plant’s LDMC. Both traits (N-fixation and LDMC) are indirectly related to plant leaf quality and thus with palatability to herbivores. While legumes are known for their high nutritional value (e.g. Iqbal et al. 2006), a high LDMC, on the other hand, is often considered to be related to higher leaf robustness and toughness (Poorter et al. 2009, Kitajima and Poorter 2010) and with less palatability (Kitajima and Poorter 2010) .

Furthermore, data analysis via CWMs revealed that the species' floristic status was an important trait for the prediction of plant community effects on higher trophic levels. In this case, higher abundances of exotic plant species had a negative impact on both the herbivore and the predator trophic level. This finding is interesting in two ways: First, it supports one well known theory from invasion ecology – the enemy release hypothesis – which posits that non-native introduced plants spread rapidly because they are liberated from their co-evolved natural enemies (Keane and Crawley 2002, Colautti et al. 2004). Second, it underlines the fact that exotic plants pose significant impacts at the community and ecosystem level (Vilà et al. 2011).

Conclusion

Our study demonstrates the suitability of using a continuous multi-trait approach for predicting the effects of plant communities on the diversity and structure of higher trophic levels. The effects of functional trait diversity were detectable in both a small scale study system involving aphids, mutualistic ants, and predatory ladybird beetles on a focus plant and in a broader ecological context dealing with the prediction of arthropod assemblages at different trophic levels. In addition, the evaluation of the differential importance of single traits in our study implies that the identification of key functional traits may contribute to a mechanistic understanding of different ecosystem processes. Interestingly, alongside with plant quality related traits, it was the species' attribute of being exotic or native (called floristic status throughout the manuscript) that played a major role in predicting variation of arthropod abundance and species richness. Commonly, the species' attribute of being exotic or native is not considered as a functional trait because it breaks with the strict definition of a functional trait as being any morphological, physiological or phenological feature. However, we propose that it may be seen in a functional context as well and included in the set of functional traits that are traditionally used because it may help to explain ecosystem functioning, such as bottom-up effects of plant functional diversity on higher trophic levels.

Chapter 5

Linking species invasions to environmental change: Consequences of elevated temperature and soil compaction on the composition and biodiversity of an urban plant community

Abstract

Elements of global change, such as climate change, land use intensification, and biological invasions are predicted to interact on the composition and functioning of plant communities, which may lead to new threats for biodiversity. However, few experiments have tested whether the individual elements interact synergistically together in shaping plant communities. In a mesocosm study, we altered the abiotic conditions temperature and soil compaction to elucidate the differential responses of exotic and native plant species within an urban grassland community. Since elevated temperature and soil compaction may act as environmental filters, we conducted a trait analysis to elucidate which functional traits are responsible for the plant responses. Finally, we investigated impacts of both factors on diversity, evenness, and functional trait diversity of the plant community. Elevated temperature and soil compaction had a negative and positive effect on community productivity, respectively, while no interactions between the environmental factors were found. The responses were driven by the group of exotic plant species, while the group of native plant species remained unaffected. Species diversity, evenness, and functional trait diversity were positively affected by elevated temperature but not by soil compaction. We suggest that this was likely due to a reduction of competition in the community. Our results show that global change factors can have independent and contrasting impacts on the composition and biodiversity of a grassland community. Exotics were more sensitive to the altered environmental conditions than natives which led in the case of elevated temperature to a decline of dominant exotics associated with an increase of the community's functional diversity.

Introduction

Biological invasions are an important element of global change which can change ecosystem functioning and influence biodiversity on local and global scales (Vitousek et al. 1996, Dukes and Mooney 1999, Vilà et al. 2007). Theoretical research indicates that other commonly recognized elements of global change such as climate change, land use intensification, and urbanization favor plant species invasions and that synergies between these elements may lead to a new thread for biodiversity (Dukes and Mooney 1999, Vilà et al. 2007, Hellmann et al. 2008). However, experimental studies on interactions between elements of global change and their influence on ecosystem properties such as plant community composition or functional diversity are still rare (but see Parker et al. 2006, Verlinden et al. 2013).

The global climate is predicted to increase by an average of 1.0 – 3.7 °C in the 21st century due to a human induced increase in the proportion of greenhouse gases in the Earth's atmosphere (IPCC 2013). Several experimental studies have shown that elevated temperatures cause shifts in species composition in plant communities which can be caused by species-specific growth responses to elevated temperatures, by altered species interactions, or both (Llorens et al. 2004). Temperature may have positive effects on metabolic rates, photosynthesis, or nutrient uptake (Llorens et al. 2004) and is also known to influence plant phenology by affecting the timing of life-history events (Yang and Rudolf 2010). In addition, plant growth might be affected indirectly by temperature effects mediated by enhanced nutrient availability due to an increase of soil microbial activity (Jarvis and Linder 2000, Rustad et al. 2001). Negative responses in plant growth may arise from water stress resulting from increased evapotranspiration related with higher temperatures (De Boeck et al. 2008). Concerning the connection between plant species invasions and climate change, most of the current knowledge stems from predictive or theoretical work (Hellmann et al. 2008). It was shown that many invasive species share certain characteristics such as a broad environmental tolerance and rapid growth rates (Sexton et al. 2002) that are predicted to allow them to tolerate climate change better than natives, which may lead to further changes in community composition.

Land use intensification is often accompanied by a compaction of the soil (Bouwman and Arts 2000, Raper 2005). In urban areas, soil compaction is often induced by the use of heavy machinery on construction sites but also by other human activities (Randrup and Dralle 1997). In compacted soils there is reduced volume available for air, and water as the mineral components are pressed closer together, which is a condition that can remain over several years (Raper 2005). As shown by a variety of studies, soil compaction has often detrimental effects on plant growth (Jim 1998, Watson and Kelsey 2006, Beck and Wurst 2013). As direct consequences, nutrient and water uptake, root growth and seedling emergence can be severely impeded (Unger and Kaspar 1994). Detrimental effects of soil compaction depend on soil moisture, i.e. they are in general more severe in dry soils (Buttery et al. 1998). Indirect effects on plant growth may arise as well: the soil microbial activity can be reduced (Kissling et al. 2009), and the soil meso- and macrofauna that rely on macropores may decrease in abundance or disappear completely (Capowiez et al. 2009). Soil compaction has also been brought into context with plant species invasion; however, there seems to be no consistent pattern emerging from the literature. Whereas Parker et al. (2010) report that soil compaction favors the establishment of exotic understory plant species in forest communities, Kyle et al. (2007) found that the establishment of an exotic herb (*Centaurea diffusa*) and an exotic grass (*Bromus tectorum*) on abandoned agricultural fields is impeded. On the other hand, Beck and Wurst (2013) found no effects of soil compaction on the invasion of an exotic legume (*Lupinus polyphyllus*) into a ruderal plant community.

In the present full-factorial mesocosm study, we investigated the individual and interactive effects of elevated temperature and soil compaction on an urban grassland plant community. We focused especially on the differential responses of native and exotic species grown within the community. Given that individual growth responses to both global change factors are often species or trait specific, our investigation of community composition was followed by an analysis of community-wide species diversity (Shannon index H’) and evenness (J’). Understanding and predicting changes in community composition have been also brought into context with the concept of functional traits (Díaz and Cabido 2001, Lavorel and Garnier 2002, McGill et al. 2006). A functional trait is any morphological, physiological, or phenological feature that influences the own organismal performance (Pérez-Harguindeguy et al. 2013) or is relevant to ecosystem functioning (McIntyre et al. 1999, Díaz and Cabido 2001, Violle et al. 2007). It is assumed that environmental filters exclude species lacking traits for persistence under a particular set of conditions and thus shape community composition (Keddy 1992). However, apart from conceptual studies, only a few studies directly correlated plant traits to environmental conditions (McGill et al. 2006, Vile et al. 2006, Lebrija-Trejos et al. 2010, Venn et al. 2011) and came to the conclusion that the examination of trait-environment relationships is a useful tool to understand plant community assembly and composition. Furthermore, the range of functions provided by a plant community will depend on the diversity of functional traits expressed by the species in that community (i.e., functional diversity) (Díaz and Cabido 2001, Petchey and Gaston 2002). As such, measures of shifts in functional diversity have been used to determine community responses to environmental filters (Díaz and Cabido 2001), as well as land use intensification (Flynn et al. 2009, Mayfield et al. 2010) and disturbance regimes (Ernst et al. 2006).

In the present study, it was our main goal to elucidate how the interaction of elevated temperature and soil compaction influence the community composition of an exotic-rich urban plant community and which role the group of exotic plant species within the community plays in that context. Furthermore, by interpreting temperature elevation and soil compaction as environmental filters that filter out species bearing certain set of traits and allow the dominance of others we conducted a trait analysis to elucidate if the responsiveness of certain traits can explain shifts in community composition. This was followed by a quantification of functional diversity which is linked to ecosystem functioning und functions such as productivity (Clark et al. 2012). In detail, we aimed to answer the following questions: (1) Do the combined effects of elevated temperature and soil compaction on community productivity sum up (additive effects), are stronger than the two individual effects together (synergistic effects), or counteract each other so that the combined effects are weaker than the individual effects together (antagonistic effects)? (2) Do the exotic plant species respond differently than the natives to elevated temperature and soil compaction? (3) If there are shifts in community composition (in conjunction to question 2), do these shifts cause changes in species diversity and evenness? (4) Do elevated temperature and soil compaction act as environment filters on specific plant functional traits and will this affect the functional diversity of the community?

Methods

Experimental design

We established a full-factorial mesocosm experiment with the following treatments: elevated temperature, soil compaction, elevated temperature combined with soil compaction, and a control treatment. Each treatment was replicated eight times, resulting in a total number of 32 mesocosms.

For the elevated temperature treatment, eight chambers (base 70 x 70 cm, height 96 cm) were built by using bamboo sticks (10 mm diameter) as a rectangular framework. Transparent plastic greenhouse film (LDPE, 0.150 mm thick) was mounted tightly to the four lateral faces of the chambers. Bottom and top faces remained free from the film, but the bottom sides were closed by the top surface of the greenhouse tables on that the chambers were mounted. As heat source for the temperature chambers we used heat mats (ThermoLux, 30 x 50 cm, 30 W heating power, AccuLux, Murrhardt, Germany) that were placed on the bottom of four chambers while the remaining four chambers received no heat mats. Each chamber contained four mesocosms (polypropylene pots, 7.5 l volume, 21 cm height, 26 cm upper diameter and 19 cm lower diameter); each mesocosm was positioned on a plastic plate standing on four cylindric plastic feet (height 10 cm) to prevent a direct contact between the heat source and the bottom of the pots and to ensure a heat transfer from the heating mat to the ambient air in the chamber. The heat mats were provided with a thermostat set to heat the interior chamber space up to 2 °C above the temperature of the unheated chambers. A temperature increase of 2 °C lies in the range of predicted increases of average global temperature assessed by the Intergovernmental Panel on Climate Change in its latest report (IPCC 2013). The day-time temperature was recorded twice a day, and the night-time temperature was recorded with a maximum-minimum thermometer. During the entire experiment the average difference in temperature between heated and unheated chambers was 1.5 °C on daytime and 2.5 °C in nighttime. Temperature in unheated chambers was on average 23 °C and 18 °C on day- and nighttime, respectively.

Each mesocosm was filled with a loamy sand (pH 8.1, C/N ratio of 28:1) that was collected from an abandoned urban site in Berlin (N52°28'30", E13°21'46") and sieved before the experiment (3 mm mesh size) but remained untreated otherwise. The mesocosms of the soil compaction treatment were filled with a total of 11000 ± 0.5 g of soil, while the uncompacted treatment received 7305 ± 0.5 g. For the soil compaction treatment, 2200 g soil was filled initially into the pot and was compacted by dropping a heavy weight (approximately 11000 g) 15 times from a 20 cm height onto the soil. This procedure was repeated four times to achieve the dedicated amount of soil and compaction in the mesocosm. As weight we used a non-experimental pot that was filled with soil and was prepared to have a strengthened and plane bottom. The mesocosms that received no soil compaction were simply filled with the dedicated amount of soil. Quantification of soil compaction with a pocket penetrometer (Eijelkamp, Agrisearch Equipment, Giesbeek, The Netherlands) indicated values from 0.0 – 0.5 kg m^{-2} for the uncompacted soils to 4.5 – 5.0 kg m^{-2} for the compacted soils. Apparently, the mesocosms from the soil compaction treatment received a higher amount of soil, which was done to achieve the same volume in both treatments. This difference goes along with a higher amount of soil nutrients in mesocosms with compacted soil, but it does not imply that plants necessarily profit from that, as shown by Beck and Wurst (2013) who used a comparable approach to achieve soil compaction in a mesocosm greenhouse experiment.

Plant community

Unlike other manipulative greenhouse studies that used compiled pairs consisting of one native and one exotic species (e.g. Verlinden et al. 2013) our species selection was conducted with the purpose of reflecting the composition of a ruderal plant community typical for abandoned fields and disturbed habitats in urban areas. Specific abiotic conditions and the proximity to human settlements and transport connections support the establishments of exotic plant species in these areas (Kowarik 2003). This community was further chosen because ruderal plant species may be subjected to a considerable degree of soil compaction and harsh climatic conditions (Santamouris 2001). The community was compiled after several vegetation surveys on appropriate sites across Berlin (Germany). It contained 10 angiosperm species (5 natives and 5 non-natives), of which 6 were forbs, 2 legumes and 2 grass species (Table 5.1). The major part of the plant seeds we used was collected on the urban abandoned site where we collected the soil for the experiment, a minor part of the seeds was provided by Appels Wilde Samen (Darmstadt, Germany) and by the Botanical Garden Berlin-Dahlem.

Table 5.1 Overview about the plant species that were used for the experiment and their floristic status (FS) after Klotz et al. (2002).

Plant species	**Family**	**FS**
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	Poaceae	native
Artemisia vulgaris L.	Asteraceae	native
Chenopodium album L.	Amaranthaceae	exotic
Melilotus albus MEDIK.	Fabaceae	exotic
Poa pratensis L.	Poaceae	native
Senecio inaequidens DC.	Asteraceae	exotic
Sisymbrium loeselii L.	Brassicaceae	exotic
Solidago canadensis L.	Asteraceaea	exotic
Tanacetum vulgare L.	Asteraceae	native
Trifolium pratense L.	Fabaceae	native

In November 2012, 20 equally sized seedlings (two individuals per species) that had been germinated on sterilized experimental soil were transplanted carefully into each mesocosm (day 0 of the experiment). To compensate for neighbor effects we assigned each seedling randomly to one of the 20 possible positions in each mesocosm resulting in 32 plant communities that did not differ in species composition, diversity, or initial abundance but in their spatial composition. The heat mats were turned on four days after transplanting to give the seedlings a short period of time to develop under un-heated conditions. The mesocosms were watered every second or third day, each with the same amount of water. Twice a week, the mesocosms were completely randomized, including randomization between the climate chambers. During the whole experiment the pots were kept in the greenhouse with 16 hours light a day (~ 180 µE m-2 sec-1 PAR).

Measurements

In week 12 of the experiment, we measured the soil moisture content twice a day on three consecutive days. Therefore we used a 6050X1 Trase System I (Soilmoisture Equipment Corp., Santa Barbara, USA) and 16 buriable waveguides (probes) of 20 cm length that were inserted into the soil of four mesocosms of each treatment. We treated the unmeasured mesocosms in a similar fashion to provide an equal disturbance to every mesocosm. The first soil moisture measurement was taken immediately after a watering event and the last measurement directly before the next watering event three days later. With this approach we could investigate how our treatments influence the decrease of soil moisture between two watering events.

In week 13, we harvested the aboveground part of the experiment. Plant shoots were cut at ground level and oven-dried at 55 °C for at least 72 hours. Afterwards, shoot dry weight for each species was determined with a precision balance. The roots were washed out from the soil and were dried and weighted as well. It is not possible to distinguish between roots of individual species in a long mesocosm experiment because the roots become interwoven. Therefore, we measured total root dry weight of the whole plant community.

We measured the three plant functional traits, plant height, specific leaf area (SLA), and leaf nitrogen concentration (LNC) according to international standards (Cornelissen et al. 2003) on each species from each mesocosm. Plant height was determined on both individuals on the day of harvest shortly before cutting the plants. For the calculation of SLA we sampled ten leaves per species (five from each individual, if possible) and stored them in moistened plastic bags at 4 °C. Within the next five days, these leaves were scanned with a flatbed scanner to produce digital images. Afterwards, the leaves were dried at 55 °C for at least 72 hours and weighted. For measuring leaf area from the images we used the image processing software ImageJ (Schneider et al. 2012). SLA was calculated by dividing the one-sided leaf area by its dry mass. For determining LNC, we used the ten leaves from the SLA measurement and pooled them together to one sample. These samples were ground in Eppendorf tubes by using a mixer mill (MM400, Retsch GmbH, Germany) and were dried again for at least 24 hours. LNC was determined on the dry samples by using an elemental analyser (Euro EA, HEKAtech GmbH, Germany).

Biodiversity measures

To determine whether changes in community composition affected biodiversity, we measured species diversity (H’, Shannon index), evenness (J’, Pielou's evenness), analyzed the functional trait distribution (CWM, community weighted mean), and calculated functional trait diversity (trait-based FD index). The Shannon index was calculated with the equation

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

where p_i is the proportional abundance (in our case aboveground biomass) of each species and S is the number of species in the community; the evenness was calculated with

$$J' = H'/H'_{max}$$

where H' is the number derived from the Shannon index and H'_{max} is the maximum value of H'.

To analyze the relationship between the environmental conditions and the distribution of functional traits within the community we performed a redundancy analysis analysis (RDA, Rao [1964]) following the tutorial by Kleyer et al. (2012). As trait set we used the three continuous traits that were measured by ourselves (SLA, LNC, plant height) plus four categorical traits for which we obtained trait values from the BiolFlor database (Klotz et al. 2002) and appropriate publications (Table 5.2). These categorical traits were 'association with arbuscular mycorrhizal fungi (AMF)', 'growth form', 'nitrogen-fixation' and 'floristic status'. The trait floristic status defines whether a plant is native or exotic to Germany. CWMs, which are weighted average trait values, were calculated for each mixture based on species biomass proportions according to the equation

$$CWM = \sum_{i=1}^{S} p_i \times t_i$$

where S is the number of species in the community, p_i is the species biomass proportion and t_i are the given trait values. Then, a RDA of the CWMs constrained by the environmental factors temperature and soil compaction was performed using Monte Carlo permutations (9999 repetitions) to test the significance of the association between the environment and the traits. RDA was performed by using the ade4 package (Dray and Dufour 2007) in R (version 3.0.2, R Core Team 2013).

Functional diversity was calculated via the FD index of Petchey and Gaston (2002, 2006). FD is defined as the total branch length of a functional dendrogram, which is created from data of plant functional traits. This index has logical statistical properties and performs well in predicting ecosystem functioning when appropriate trait data are available (Flynn et al. 2009). We used the community based FD index (Petchey and Gaston 2006), which is a revised version of the plot based version introduced in 2002 (Petchey and Gaston 2002). We calculated for each mesocom two FD index values: one unweighted FD value and one weighted FD value (wFD). By calculating wFD, it is possible to load each entry of the dissimilarity matrix with a relative measure of abundance (in our terms biomass) before performing the dendrogram. The two indices were calculated to investigate whether changes in functional diversity were due to greater distances between trait values or due to a shift of species abundances within the community. The calculations of FD were performed by the R-based software FDiversity (Casanoves et al. 2011) by using Gower distance as distance measure and UPGMA (average linkage) as clustering algorithm. Gower distance has the ability to cope with mixed trait data (categorical and continuous) and missing values (Podani and Schmera 2006, Petchey and Gaston 2007) and UPGMA was shown to outperform other procedures (e.g. UPGMC, WPGMC, single linkage, complete linkage, etc.) in measuring FD indices (Podani and Schmera 2006).

Table 5.2 Trait data used for the analysis of the trait-environment relationship and the calculation of functional trait diversity.

Trait	Range or categories
Specific leaf area (SLA), $cm^2 g^{-1}$	30.1 – 65.1
Plant height, cm	6.1 – 69.5
Leaf nitrogen concentration (LNC), mg g^{-1}	19.7 – 57.0
Growth form	Herb, grass
Floristic status	Exotic, native
Association with arbuscular mycorrhizal fungi (AMF)	AMF, no AMF
Nitrogen-fixation	Legume, not legume

Statistical analysis

Differences in plant community composition were tested with multivariate analysis of variance (MANOVA) with elevated temperature and soil compaction as independent variables. We ran two MANOVAs on the aboveground biomass data: One with the proportions of native and exotic species as dependent variables and another one with the proportions of each plant species as dependent variables. When MANOVA rejected the null hypothesis of no differences in community composition ($P < 0.05$), we subsequently performed univariate analyses of variance (ANOVAs) on each dependent variables. Belowground biomass data were analysed with ANOVA only. We used a linear mixed effects model to measure the effects of soil compaction, elevated temperature, and time (fixed effects) on the soil moisture content (response variable) of the mesocosms (random effect).

The four diversity indices (H’, J’, FD, wFD) were calculated for each mesocosm. With ANOVAs we tested for significant impacts of our treatments on each index. All models were tested for the underlying assumptions (homoscedasticity, normality). All statistical analyses were performed in R (version 3.0.2, R Core Team 2013) with addition of the nlme package (Pinheiro et al. 2013) for the linear mixed effects model.

Results

Plant community composition

Soil compaction had a positive influence on the aboveground biomass of the plant community (MANOVA, *F* = 5.15, *P* < 0.05), while the elevated temperature had a strong negative effect (MANOVA, *F* = 22.30, *P* < 0.001). There was no significant interaction between both global change elements on aboveground biomass (MANOVA, *P* > 0.05), indicating that both effects are additive (Fig. 5.1a).

Elevated temperature had also a negative effect on total root biomass (ANOVA, *F* = 6.67, *P* < 0.05). Additionally, a significant interaction between soil compaction and elevated temperature was detected: The detrimental effect of elevated temperature on root growth was less severe when the soil was compacted (ANOVA, *F* = 10.28, *P* < 0.005, Fig. 5.1b).

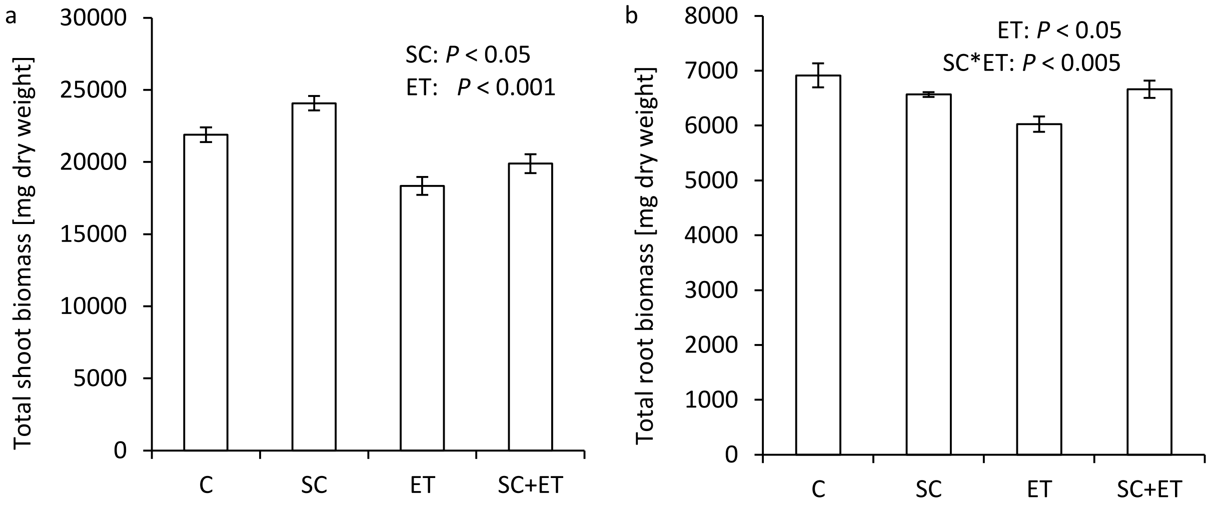

Figure 5.1 Impact of soil compaction (SC) and elevated temperature (ET) on (a) total shoot biomass and (b) total root biomass of the plant community (10 species, bars represent means ± SE, n = 8). *P*-values for main and interaction effects are derived from a MANOVA in (a) and an ANOVA in (b).

Differences in aboveground community biomass were mainly driven by responses that exotic species exhibited (Fig. 5.2). The group of exotic species produced less aboveground biomass under elevated temperature (ANOVA, $F = 27.90$, $P < 0.001$), but more in compacted soil than in uncompacted soil (ANOVA, $F = 5.33$, $P < 0.05$). Again, there was no significant interaction between both factors (ANOVA, $P > 0.05$). In contrast to the exotic species, the group of native species showed no response in biomass production, neither to elevated temperature (ANOVA, $P > 0.05$) nor to soil compaction (ANOVA, $P > 0.05$).

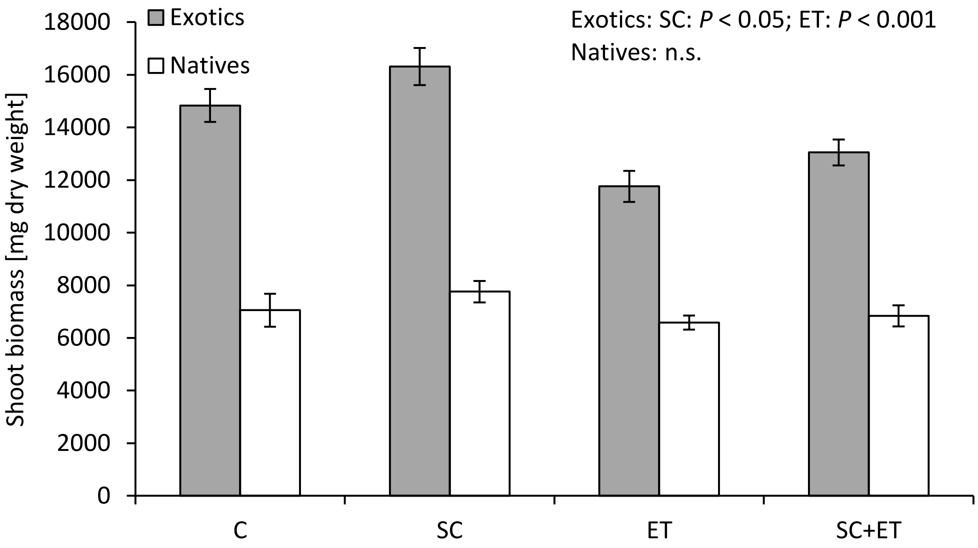

Figure 5.2 Impact of soil compaction and elevated temperature on the proportions of exotic and native plant species on total aboveground biomass of the plant community (5 exotic and 5 native species, bars represent means ± SE, n = 8). *P*-values are derived from single ANOVAs performed after a MANOVA.

Univariate analyses of variance on biomass proportion of each species revealed that the negative effect of elevated temperature on exotic species was mainly driven by the legume *Melilotus albus* (ANOVA, $F = 29.94$, $P < 0.001$) and the forb *Sisymbrium loeselii* (ANOVA, $F = 4.89$, $P < 0.05$, Table S5.1). The other three exotics showed no significant response to elevated temperature (ANOVA, $P > 0.05$). Within natives, it was the legume *Trifolium pratense* that also showed a reduction of aboveground biomass in response to elevated temperature. Soil compaction had positive effects on two exotic species, *Chenopodium album* (ANOVA, $F = 5.61$, $P < 0.05$) and *Sysimbrium loeselii* (ANOVA, $F = 22.41$, $P < 0.001$), but no effects on the native plant species.

Soil moisture

In-between the two watering events in which the soil moisture content was constantly recorded, the elevated temperature led to drier soils (LMEM: $T = 2.27$, $P < 0.05$, Fig. 5.3). A significant interaction between soil compaction and elevated temperature indicates that the compaction of the soil counterbalanced the moisture loss of the soil under elevated temperature (LMEM: $T = 4.30$, $P < 0.005$).

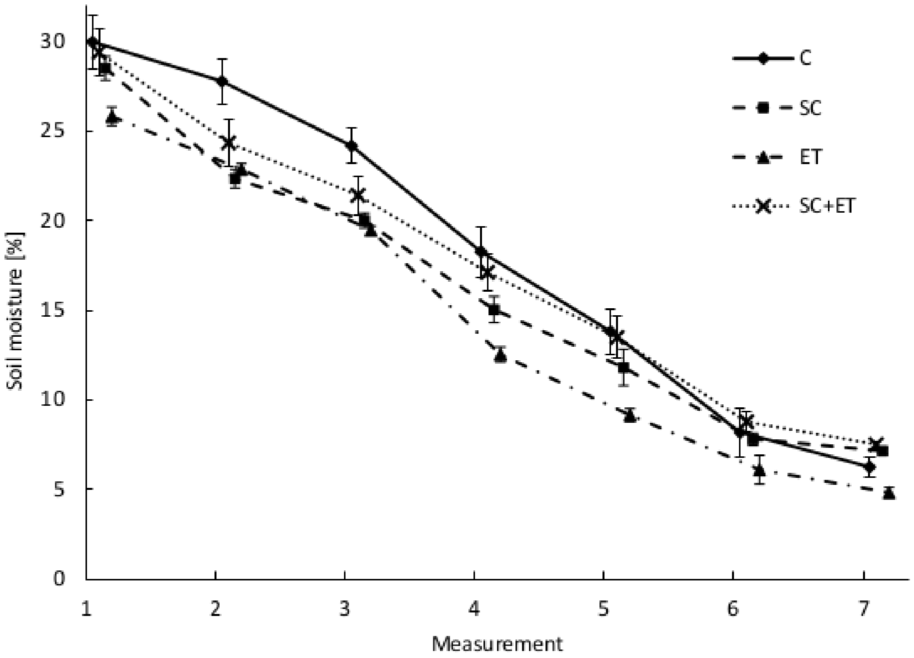

Figure 5.3 Impact of soil compaction and elevated temperature on soil moisture content on four consecutive days. Soil moisture was measured twice a day at 10 a.m. and 8 p.m. The first measurement was taken after watering the plants at 8 p.m. on the first day (means ± SE, n = 4).

Diversity and evenness

Species diversity (expressed by Shannon index H') of the plant community was significantly higher under elevated temperature (ANOVA, $F = 10.6$, $P < 0.005$, Fig. 5.4a). Neither soil compaction nor the interaction between both factors had a significant influence on species diversity (ANOVA, $P > 0.05$). The species evenness (J') exhibited the same pattern: elevated temperature increased evenness (ANOVA, $F = 9.23$, $P < 0.01$), while soil compaction and the interaction between both factors had no effect (ANOVA, $P > 0.05$, Fig. 5.4b).

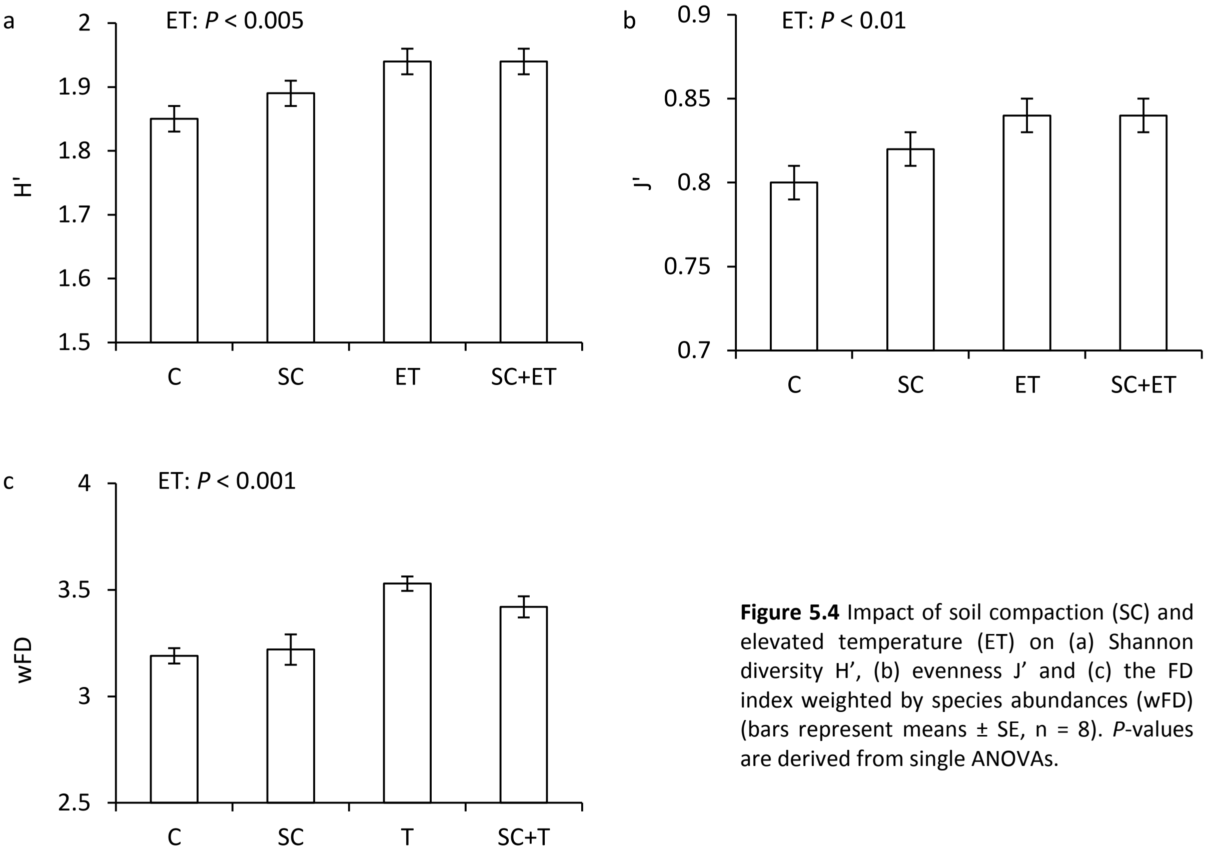

Figure 5.4 Impact of soil compaction (SC) and elevated temperature (ET) on (a) Shannon diversity H', (b) evenness J' and (c) the FD index weighted by species abundances (wFD) (bars represent means ± SE, n = 8). *P*-values are derived from single ANOVAs.

Traits-environment relationship

By means of the RDA analysis, 20.4 % of trait variation was explained by the environmental factors (Monte Carlo permutation test, $P < 0.001$), whereas RDA axis 1 and 2 explained 78.6 % and 21.4 % of this variation. The second axis clearly separates the factors elevated temperature and soil compaction (Fig. 5.5). The traits association with AMF and herbaceous growth form were negatively correlated with soil compaction, while the trait nitrogen-fixation (i.e. legumes) was negatively correlated with elevated temperature.

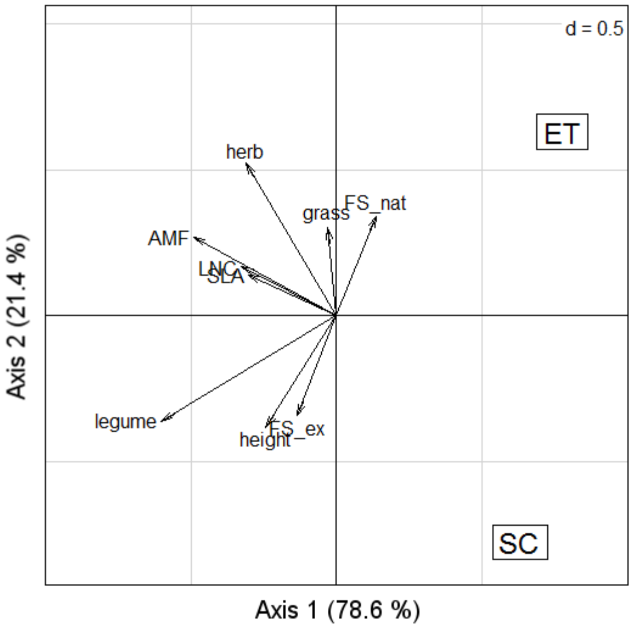

Figure 5.5 Ordination plot from the RDA showing the loadings of the environmental variables elevated temperature (ET) and soil compaction (SC), and the CWMs of the plant functional traits on both RDA axis. The scale of the graph is given by the grid in the background. The side-length (d) of a square is 0.5. Abbreviations: SLA = specific leaf area, LNC = leaf nitrogen content, AMF = association with arbusclar mycorrhizal fungi, FS = floristic status (ex = exotic, nat = native). Since N-fixation and AMF are binary variables, the negative categories (not legume, no AMF) are not included due to redundant information. FS_ex and FS_nat complement each other, so we included only one group in the analysis but depicted both in the plot to illustrate the differential response.

Functional diversity

The measure of functional diversity with the abundance weighted wFD index yielded a result which was analog to the common species diversity indices: Functional diversity of the plant community was positive affected under elevated temperature (ANOVA, F = 15.83, P < 0.001, Fig 5.4c), while soil compaction and the interaction between the factors had no effect (ANOVA, P > 0.05). The unweigthed version of FD showed no significant differences between the treatments (ANOVA, P > 0.05). Each plant species survived with at least one living individual in each mesocosm until harvest, which makes the measures of species and functional diversity accurate, because they are not influenced by changes in species richness.

Discussion

Climate change and land use intensification are two elements of global change that have major impacts on plant communities and are regarded to favor the establishment of exotic plant species. In respect to our first research question, we found no interactions on aboveground productivity of the plant community suggesting additive effects of the global change factors. While elevated temperature affected aboveground community productivity negatively, soil compaction had a positive effect. This response was driven by the group of exotic species which reacted negatively and positively to elevated temperature and soil compaction, respectively, while the group of native species remained unaffected. Because the impacts of both factors on aboveground productivity were idiosyncratic and without interaction we discuss them separately in the following paragraphs.

Effects of elevated temperature on community composition

In line with other studies (e.g. Lemmens et al. 2006, De Boeck et al. 2008), we recorded lower levels of soil moisture under elevated temperatures which is indicative for higher evapotranspiration rates. Lower soil moisture levels trigger a decrease in plant stomatal conductance (Lemmens et al. 2006), ensuring that water loss through transpiration is damped (De Boeck et al. 2006), but leading also to lower photosynthetic rates (De Boeck et al. 2007). This chain of physiological processes most likely caused biomass reductions in shoots and roots under elevated temperature in our experiment. Concerning our second research question, experimental studies that differentiated between responses of exotic and native plant species to elevated temperature and associated drought stress in an ecosystem context are rare, but consistent with our findings. Milchunas and Lauenroth (1995) applied water to shortgrass steppe communities over five years and observed positive effects on exotics while the control plots remained free from invaders. White et al. (1997) reported that biomass production of an exotic subtropical grass in New Zealand grassland communities achieved a maximum under high water availability. And, Verlinden et al. (2013), whose recent study is most comparable to ours due to a similar experimental mesocosm design, found in two out of three cases that native European grassland species dominated over exotics in two-species mixtures in heated chambers. However, our findings and also those from the cited examples above are contradictory to the many studies that are based on predictive and theoretical work (e.g. Dukes and Mooney 1999, Pyšek and Richardson 2007, Hellmann et al. 2008). In general, it is assumed that global change – and in particular, climate change as an element of global change – favors the establishment of exotic species which may increase their impact on biodiversity and ecosystem functioning (Vilà et al. 2007). Indeed, the growing body of experimental work found that exotics and native respond differently to a changing climate, but this does not necessarily mean that exotics will profit from climate change. Due to their observed sensitivity to elevated temperature, it might be suggested that as the European climate warms, the distribution ranges of exotic plant species might shift northwards, which is also supported by studies that investigated the relationship between exotic plant distributions and local variations of recent climate (Polce et al. 2011).

Effects of soil compaction on community composition

The compaction of the soil had a positive effect on aboveground community biomass, while root biomass remained unaffected which is a remarkably different finding compared to other studies (Jim 1998, Watson and Kelsey 2006, Beck and Wurst 2013). We attribute this to several properties of our study design: First, we chose plant species that are dominant on disturbed urban soils while we excluded species that could be considered as rare. Probably, most of these species are well adapted to harsh soil conditions in urban areas, which is one of the reasons why they can become dominant in these habitats. On the other hand, we took the soil, which was a loamy sand, from an abandoned urban construction site. Buttery et al. (1998), who compared the effects of soil compaction in different soil types, found that they were more severe in clay loam than in sandy soil and reported also no loss of biomass of soybean and common bean growing in a sandy soil. Consistently, Mathers et al. (1966) documented that the strength of compacted soils depends on their clay content.

Analysis of individual aboveground biomass proportions of each species revealed that the two exotics *Chenopodium album* and *Sisymbrium loeselii* grew significantly better in compacted soil, while the native legume *Trifolium pratense* exhibited a marginally significant growth promotion. One could attribute this effect to the higher amount of nutrients that was available in the compacted mesocosms due to the higher amount of soil that was filled into the pots. However, since LNC and availability of nitrogen from the soil are positively correlated (Hilbert 1990), we may refuse a connection between soil compaction and higher nutrient availability in our experiment: The LNC of *C. album* and *S.loeselii* were significant lower and marginally significant lower, respectively, in compacted soils compared to uncompacted soils (Table S5.1). So far, few studies have explicitly investigated the influence of soil compaction on the success of exotic species. Kyle et al. (2007) and Mattingly and Orrock (2013) found pronounced negative effects on growth and establishment, while (Parker et al. 2010) reported positive effects of compacted soils on exotic species richness. The potential explanations that are given in these studies seem to be rather species-specific by relating the observed effects to specific traits of the invader. In our case, we observed during various site inspections across Berlin that *C. album* is among the first plant species that colonize sites which have been abandoned quite recently which makes it a typical pioneer species. The fact that heavy soil compaction is characteristic to these sites implies that *C. album* is capable to thrive easily through compacted or disturbed soils with its root system.

Additionally, our measurements of soil moisture content suggest that the higher bulk density of the compacted sand counteracted the water loss, which was induced by the higher temperature. This pattern was mirrored in the belowground biomass indicating that higher total root biomass in compacted soil vs. uncompacted soil in the warming treatment is explained by the higher soil moisture content in the compacted soil. However, this effect did not cascade up to the aboveground compartment, i.e. the shoot biomass remained unaffected.

Diversity and evenness

Differential responses of species to elevated temperature and associated drought were responsible for the observed positive effects on species diversity and evenness. The exotic legume *Melilotus albus* was the most dominant species in all four treatments, but its biomass proportion was reduced by almost 40% under elevated temperature. The exotic forb *Sisymbrium loeselii* was the second most productive species in unheated chambers but lost this rang against the native forb *Artemisia vulgaris* in heated chambers. Since none of our species disappeared in any mesocosm the aforementioned changes in diversity and evenness relied on changes in biomass. Several previous studies reported that under warmer and drier conditions rare species are more likely to disappear due to their low densities under recent climate (Tilman and Haddi 1992, Symstad et al. 2003, Smith and Knapp 2003, Lloret et al. 2004). But it was also reported that under extreme conditions more abundant species are not necessarily the ones least affected and that these idiosyncratic responses will have probably consequences on the diversity and structure of future plant communities (Lloret et al. 2004). This is in line with our study, since we showed that the dominant species under unheated conditions responded stronger than the less abundant (in terms of biomass) which led to the observed shifts within the community.

Traits-environment-relationship

Via the calculation of CWMs of plant traits followed by a RDA we found indication that the altered environmental conditions affected certain plant traits, which can be interpreted as a filtering effect. This is consistent with other studies examining traits-environment relationship (Díaz et al. 1998, McGill et al. 2006, Lebrija-Trejos et al. 2010, Venn et al. 2011), with the difference that not community composition in terms of presence or absence of certain species but rather composition in terms of biomass proportions was affected by the filtering processes in the present experiment. While other studies report mostly relationships between environmental conditions and leaf and/or life history traits (Díaz et al. 1998, Peco et al. 2005, Lebrija-Trejos et al. 2010) we identified strong associations between the environment and certain resource-use strategy traits. Our results indicate that nitrogen-fixing plant species are negatively affected by elevated temperature and AMF dependent species are negatively affected by compacted soils. These resource-use strategy traits are related to mutualistic soil organisms, which emphasizes the importance of identifying the extent that global change drivers have on biotic interactions (Tylianakis et al. 2008).

Under elevated temperature, both legume species within the community (the exotic and the native) suffered biomass losses, which may indicate that their capacity of fixing nitrogen is reduced under warmer conditions. Previous studies that examined legume growth and temperature have shown that the growth response to temperature can be positive or negative, depending on the legume species and/or the rhizobia strain (Lira Junior et al. 2005, Whittington et al. 2012). Studies on closely related legume species (*Trifolium subterraneum* and *Medicago sativa*), that are members of the same tribe as the legumes from the present study (Trifolieae), documented also a negative temperature growth response (Lilley et al. 2001, Aranjuelo et al. 2007). In the case of *Medicago sativa*, Aranjuelo et al. (2007) showed that elevated temperature reduced the nodule activitiy, and drought diminished the nodule dry mass production, which may have contributed to the observed growth reduction. In the present study, nitrogen-fixation was not the main focus, but by considering the importance of nitrogen-fixation for ecosystem functioning of grasslands, we highly recommend further studies on the interplay between nitrogen-fixing bacteria, legumes, and other interacting plant species under warming conditions.

Further, the analysis of the trait-environment relationship suggests that soil compaction negatively affects AMF dependent species and/or promotes the abundance of non-AMF dependent species within the community. Indeed, analysis of individual aboveground biomass proportions revealed that the two non-AMF dependent species *Chenopodium album* and *Sisymbrium loeselii* grew significantly better in compacted soil. Consistent with this finding, Nadian et al. (1996), who investigated the effects of soil compaction on mycorrhizal root colonization in a pot experiment, found that the plant mycorrhizal growth responses of *Trifolium subterraneum* decreased proportionally as soil compaction was increased. On the other hand, Beck and Wurst (2013) documented that the root colonization with AMF of an AMF dependent species (*Plantago lanceolata*) can be even higher in compacted soils, but does not have to lead to positive growth responses. And, Li et al. (1997) showed that AMF hyphae are more efficient in obtaining phosphorus from compacted soil than mycorrhizal or non-mycorrhizal roots of *Trifolium pratense*. Because of the variety of results from previous studies and a lack of data on mycorrhizal performance in the present study, we cannot draw a proper conclusion whether the non-AMF *C. album* and *S. loeselii* profited from their status of being non-AMF dependent and responded therefore positively to soil compaction. Further work is needed to assess the impacts on the mycorrhizal symbiosis in compacted soils, including consequences for plant community composition, also in regard to the soil type, since our study was the only one among the mentioned studies that used a sandy soil.

Functional diversity

In the present study we try to relate temperature induced changes in community composition to changes in ecosystem functioning. Concerning the appropriateness of FD (and wFD), there has been a lot of discussion whether changes in FD correspond to changes in species richness (Mason et al. 2013) or, in other words, whether species richness can be used as a predictor of FD (Flynn et al. 2009). However, since species richness was kept constant in our experiment, we presume that we captured the *de facto* changes in functional diversity that were uncoupled from changes in species richness.

Via calculating wFD, which is computed on a weighted species dissimilarity matrix, we found an increase in functional trait diversity associated with elevated temperature, but in case of FD, which is basically the same index but unweighted, we did not find any differences. Therefore, we conclude that the reduced dominance of some species in terms of biomass was responsible for the higher distance in the trait space, i.e. functional diversity. To investigate if there was a certain trait-by-species association responsible for the change of the index, we recalculated wFD several times with one trait omitted each time (data not shown), but wFD was still significant different between both temperature regimes in each case. Hence, we conclude that the change of wFD was not caused by the biomass decrease of one or two dominant species with specific traits but by a shift of the dominance patterns of the whole community. Theoretically, habitat filtering assumes that coexisting species are more similar to one another in their traits than would be expected by chance. This, contrary to our results, found recently support by field studies (Flynn et al. 2009, Pakeman 2011, Mason et al. 2012), that documented a decrease of functional diversity in stressed communities. Other potential mechanisms are given by Mouchet et al. (2010): competitive exclusion and limiting similarity principles predict the stable coexistence between functionally dissimilar species which may enhance functional diversity. On the other hand, neutral theory (Hubbell 2001) posits that species coexist and persist in a system independently of their traits and responses to environmental factors. Moreover, recent findings suggest that these three mechanisms (i.e. habitat filtering, limiting similarity, neutral theory) may co-occur simultaneously and obscure patterns or may occur sequentially along environmental gradients (Mason et al. 2007, Helmus et al. 2007). Coming back to the results of the present study, we postulate that habitat filtering by elevated temperature on certain functional plant traits caused a decline of species that were dominant under unheated conditions. This led to a reduced competitive ability of the dominants connected with an overall reduction of competition in the mesocosms, resulting in an increase in functional diversity. The assumption that the temperature treatment reduced competition among plants is plausible, since evenness was increased in the community, and a former study by Lamb et al. (2009) showed that lower competition levels were accompanied by a higher evenness in a mesocosm experiment. Additionally, the stress-gradient hypothesis, which was supported by field data many times (He et al. 2013), predicts decreasing competition among plants under increasing environmental stress. Theory also predicts a more extensive use of resources in communities with higher functional diversity due to the principle of complementarity (Díaz and Cabido 2001). However, beneficial complementarity effects were likely overshadowed by the strong negative effect of the elevated temperature and associated soil drought in our study.

Conclusion

Invasions by exotics are commonly recognized as an important element of global change, but exotics also play important roles within the ecosystems they have invaded by showing different responses than native species to changing environmental conditions. Our study shows that elements of global change work together on different levels: First, communities are affected externally by changes in environmental conditions (that may act as filters) as shown in the cases of elevated temperature and soil compaction. On the other hand, communities are internally affected by the roles that exotic species pose and their responses to global change factors. By including trait measurements, our community-level approach allowed the identification of specific functional traits that are responsible for the composition of the community. In case of elevated temperature, we showed that environmental filtering affects not only the composition but also the functional diversity which was most likely caused by a reduction of competition within the community. The role of competition should be taken into account by future studies on the relationship between functional diversity and the environment.

Supporting information

Table S5.1 Upper part: Shoot biomass, mean trait values (+/- SE) of the measured traits, and trait values of the categorical traits of each species within the community, grouped by our treatments. Lower part: Statistical results of univariate analyses of variance (ANOVAs), which were performed on each single species after the MANOVAs (see main text for MANOVA results) on the dependent variables shoot biomass and the three measured traits SLA, LNC and plant height (n = 8, df = 29). Note: The interaction term 'soil compaction x elevated temperature' was excluded for the subsequent ANOVAs if the MANOVA found no significant interaction.

		Biomass		**Continuous traits (measured)**						**Categorical traits**			
Treatment	**Species**	**[mg]**	**+/-**	**SLA**	**+/-**	**LNC**	**+/-**	**Height**	**+/-**	**FS**	**AMF**	**NF**	**GF**
C	Arrhenaterum	999.4	157.2	65.1	3.4	30.2	1.5	15.8	1.1	nat	yes	no	g
	Artemisia	3027.6	523.4	45.2	2.3	35.3	0.9	45.5	3.5	nat	yes	no	h
	Chenopodium	2621.7	387.6	33.9	1.8	22.6	1.6	52.1	3.6	ex	no	no	h
	Melilotus	7424.0	637.5	40.1	1.4	55.5	1.0	60.9	2.3	ex	yes	leg	h
	Poa	84.7	9.1	51.7	4.6	24.6	1.0	9.2	1.2	nat	yes	no	g
	Senecio	1691.5	115.1	52.6	2.2	39.7	2.4	34.0	3.6	ex	yes	no	h
	Sisymbrium	2967.1	350.7	34.8	1.4	45.4	2.7	13.5	1.2	ex	no	no	h
	Solidago	129.4	32.5	61.9	1.9	32.9	1.1	7.5	1.0	ex	yes	no	h
	Tanacetum	582.0	84.3	58.1	2.8	35.1	0.9	19.4	2.4	nat	yes	no	h
	Trifolium	2361.9	81.6	34.2	1.2	47.7	0.7	32.3	2.5	nat	yes	leg	h
SC	Arrhenaterum	1025.7	185.7	58.4	2.4	28.5	1.0	15.8	2.1	nat	yes	no	g
	Artemisia	2837.1	252.8	46.6	1.3	41.7	1.5	40.9	2.2	nat	yes	no	h
	Chenopodium	3257.6	456.2	32.1	2.2	19.7	0.9	54.1	3.1	ex	no	no	h
	Melilotus	7138.5	512.8	38.3	1.8	57.0	1.0	59.0	2.3	ex	yes	leg	h
	Poa	89.0	10.6	42.0	2.2	23.8	0.6	8.4	0.7	nat	yes	no	g
	Senecio	1708.3	205.7	46.7	2.6	36.6	0.7	36.6	4.2	ex	yes	no	h
	Sisymbrium	4091.7	260.0	33.7	1.4	39.7	3.3	13.9	1.0	ex	no	no	h
	Solidago	116.1	24.2	57.7	2.1	31.0	1.2	7.3	1.0	ex	yes	no	h
	Tanacetum	831.8	151.8	48.7	2.5	32.5	0.7	23.1	2.8	nat	yes	no	h
	Trifolium	2978.0	307.4	37.1	1.6	49.7	1.0	37.4	3.1	nat	yes	leg	h
ET	Arrhenaterum	903.9	101.1	59.0	3.8	31.3	1.1	16.0	2.2	nat	yes	no	g
	Artemisia	3342.3	140.5	39.3	1.3	37.0	1.0	44.6	2.2	nat	yes	no	h
	Chenopodium	2827.2	369.4	34.0	1.4	31.0	1.5	50.5	2.9	ex	no	no	h
	Melilotus	4819.0	396.4	41.9	1.2	56.0	1.3	50.9	1.9	ex	yes	leg	h
	Poa	77.5	8.4	42.2	1.5	25.0	0.6	9.3	0.6	nat	yes	no	g
	Senecio	1635.4	134.2	41.8	1.3	36.7	0.6	30.6	2.9	ex	yes	no	h
	Sisymbrium	2372.1	201.3	32.0	1.0	40.6	1.8	12.4	0.9	ex	no	no	h
	Solidago	106.6	14.6	53.3	1.2	28.7	1.5	6.1	0.6	ex	yes	no	h
	Tanacetum	665.4	120.7	46.0	1.5	32.9	0.8	19.8	1.7	nat	yes	no	h
	Trifolium	1593.5	174.7	32.2	0.8	45.5	1.4	23.8	4.6	nat	yes	leg	h
SC+ET	Arrhenaterum	889.3	52.5	61.8	1.0	31.6	1.0	16.2	1.1	nat	yes	no	g
	Artemisia	3335.6	286.3	41.5	1.1	36.2	0.7	45.4	2.4	nat	yes	no	h
	Chenopodium	4004.8	318.3	33.5	1.4	24.3	1.7	69.5	9.8	ex	no	no	h
	Melilotus	3925.0	575.6	42.1	1.0	56.0	1.2	49.4	2.6	ex	yes	leg	h
	Poa	74.9	10.2	41.3	4.0	23.5	0.5	8.4	0.6	nat	yes	no	g
	Senecio	1382.8	216.8	47.1	2.3	36.8	1.4	29.4	3.2	ex	yes	no	h
	Sisymbrium	3591.8	150.2	30.1	1.1	36.6	3.1	10.9	0.7	ex	no	no	h
	Solidago	145.6	19.2	51.9	1.1	30.9	0.8	7.2	0.8	ex	yes	no	h
	Tanacetum	718.2	123.4	45.7	2.0	34.4	0.9	16.3	1.9	nat	yes	no	h
	Trifolium	1819.5	197.9	33.7	1.8	43.5	1.7	27.3	2.3	nat	yes	leg	h

		Biomass		SLA		LNC		Height	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
SC	Arrhenaterum	0.002	0.965	0.18	0.675	0.40	0.532	0.00	0.956
	Artemisia	0.09	0.765	0.67	0.420	6.89	**0.014**	0.50	0.487
	Chenopodium	5.62	**0.025**	0.20	0.660	10.70	**0.003**	3.32	0.079
	Melilotus	1.23	0.277	0.09	0.765	0.38	0.543	0.54	0.469
	Poa	0.01	0.933	3.35	0.078	2.54	0.122	1.11	0.302
	Senecio	0.47	0.500	0.24	0.632	1.08	0.308	0.04	0.837
	Sisymbrium	22.41	**0.000**	2.39	0.134	3.74	0.063	0.30	0.591
	Solidago	0.29	0.592	3.40	0.076	0.03	0.861	0.26	0.615
	Tanacetum	1.55	0.224	7.13	**0.013**	0.44	0.510	0.00	0.947
	Trifolium	4.17	0.050	1.58	0.220	0.00	0.979	1.80	0.190
ET	Arrhenaterum	0.77	0.387	0.58	0.452	3.11	0.089	0.03	0.869
	Artemisia	1.55	0.223	10.91	**0.003**	3.30	0.080	0.46	0.501
	Chenopodium	1.55	0.223	0.04	0.843	19.26	**0.000**	1.42	0.243
	Melilotus	29.94	**0.000**	3.34	0.079	0.04	0.842	18.80	**0.000**
	Poa	1.26	0.272	1.72	0.200	0.00	0.984	0.00	0.969
	Senecio	1.22	0.278	4.84	**0.036**	0.87	0.360	2.34	0.137
	Sisymbrium	4.89	**0.035**	5.84	**0.023**	4.01	0.055	4.59	**0.041**
	Solidago	0.02	0.890	19.73	**0.000**	3.73	0.064	0.76	0.390
	Tanacetum	0.02	0.902	10.11	**0.004**	0.03	0.854	1.93	0.176
	Trifolium	21.82	**0.000**	2.90	0.100	10.59	**0.003**	8.46	**0.007**
SCxET	Arrhenaterum	-	n.s.	1.99	0.169	0.71	0.408	-	n.s.
	Artemisia	-	n.s.	0.30	0.588	11.87	**0.002**	-	n.s.
	Chenopodium	-	n.s.	**0.03**	0.862	1.66	0.208	-	n.s.
	Melilotus	-	n.s.	0.29	0.593	0.41	0.525	-	n.s.
	Poa	-	n.s.	2.42	0.132	0.26	0.615	-	n.s.
	Senecio	-	n.s.	9.42	**0.005**	1.13	0.297	-	n.s.
	Sisymbrium	-	n.s.	**0.01**	0.930	0.01	0.904	-	n.s.
	Solidago	-	n.s.	0.73	0.402	3.40	0.076	-	n.s.
	Tanacetum	-	n.s .	6.25	**0.019**	6.47	**0.017**	-	n.s.
	Trifolium	-	n.s.	0.10	0.749	2.52	0.124	-	n.s.

Abbreviations: Traits: SLA = specific leaf area (cm^2 g^{-1}), LNC = leaf nitrogen content (mg g^{-1}), Height = plant height (cm), FS = floristic status (ex = exotic, nat = native), AMF = association with arbuscular mycorrhizal fungi, NF = nitrogen-fixation (leg = legume, no = no legume), GF = growth form (h = herb, g = grass). Treatments: C = control, SC = soil compaction, ET = elevated temperature. Bold numbers indicate significant effects (P < 0.05) from our applied treatments (n.s. = non-significant).

Chapter 6

General discussion

In this thesis, I studied how exotic plant species influence and are influenced by the biotic and abiotic environment in their new range. I did so by integrating several different approaches in my thesis. The plant-soil feedback concept from Chapter 2 focused on the feedback responses of individual plant species to their soil biota community in comparison to a soil biota community of heterospecific plants. I found that a native plant species may benefit from the presence of a dominant co-occurring exotic invader which was mediated by changes of the soil biota community. In distinction from the taxon specific approach of the first experiment, I focused in subsequent experiments on the group of exotics within a plant community. I related the species attribute of being native or exotic to the functional trait concept and used it alongside morphological and resource capture related traits to predict plant community productivity (Chapter 3, first objective) and the abundance and diversity of higher trophic levels (Chapter 4). Furthermore, I investigated the effects of global change related abiotic stresses (Chapter 5), and found that exotic plant species show stronger responses to these stresses than their co-existing native counterparts. Finally, I demonstrated that the seed germination rate and seedling survival of an exotic plant species can be related to the functional trait diversity of the recipient community (Chapter 3, second objective), which is a reciprocal approach because it focuses on the invaded community itself and not on the invaders like the aforementioned approaches.

Mechanisms that explain invasion success of exotic plant species

It was pointed out several times (e.g. Richardson and Pyšek 2006, Catford et al. 2009, Kowarik 2010, Keller et al. 2011) that every invasion process in itself must be understood as highly context-dependent and linked to a combination of both abiotic and biotic factors, and multiple underlying mechanisms, which is also one of the main conclusions of this thesis. For example, plant-soil feedback processes are thought to explain the invasion success of many exotic plant species (Klironomos 2002, Callaway et al. 2004, van der Putten et al. 2013). However, these mechanisms do not sufficiently explain the strong dominance of exotic invader *Solidago canadensis* in urban grassland communities since this species showed only a slightly positive soil-feedback that depended on the habitat type (see Chapter 2 for details). Consistently, Bezemer et al. (2006) showed that effects of soil biota communities on feedback effects are not only plant species-specific but also may vary in different soils. Although the study of Bezemer et al. (2006) was not conducted in an invasion context, it indicates that abiotic and biotic factors do not only affect the performance of exotics directly but also indirectly via the alteration of important soil feedback processes.

In general, exotic plant species showed stronger responses to abiotic stresses such as elevated temperature and soil compaction than native species did (Chapter 5). However, staying with the example of *S. canadensis*, I found no indication that the growth of this particular species was affected by both abiotic stresses, although other exotic species showed strong responses in my experiment, which leaves the question on the mechanisms of its dominance in its new range still open. This is also interesting in view of the fact, that *S. canadensis* is native to North American prairie habitats, in which plants are frequently subjected to high temperatures, drought periods (Helzer 2009) and grazing induced soil compaction (Naeth et al. 1990). The 'adaptation theory' from invasion ecology predicts that invaders possess certain traits that make them pre-adapted to the new environment (Duncan and Williams 2002, Catford et al. 2009). Indeed, *S. canadensis* did not responded, for example, to the elevated temperature and associated soil drought, while other species suffered dramatic losses, but it also did not become a more dominant component of the entire plant community under elevated temperature in my experiment.

From other studies on *S. canadensis* in its new ranges it is known that it maintains its dominance in local communities through its pronounced clonal growth (Dong et al. 2006, Kowarik 2010). However, this asexual reproduction mode can only become effective after *S. canadensis* is already established in a local community, which makes its sexual reproduction via seeds an important factor for its long-distance dispersal and establishment. I showed that the seedling establishment of *S. canadensis* decreases with increasing functional trait diversity of the recipient community (Chapter 3, second objective) which is a confirmation of the 'biotic resistance hypothesis' (Levine et al. 2004, Parker and Hay 2005, Alpert 2006). However, consistent with studies that tested the biotic resistance of communities with increasing plant species diversity (see Levine et al. [2004] for a meta-analysis), it is remarkable that *S. canadensis* seedlings still established in the most diverse communities to a significant extent in my experiment. Thus, recipient community diversity (no matter whether functional or species diversity), is able to reduce invasion success, but is not strong enough to categorically prevent invasion. This is a crucial point in the case of *S. canadensis* because this species is known to become a strong competitor once it is established in a community (Kowarik 2010).

In summary, this example of *S. canadensis* clearly demonstrates how several ecological mechanisms act together in affecting the invasion success of an exotic plant species. Furthermore, I showed by the example of *S. canadensis* that different mechanisms can be more relevant than others in certain stages of the life cycle of a plant. In Chapter 5, I showed that plant responses to abiotic stresses are often species-specific which underlines the view that invasion processes must be considered as highly context-dependent. However, this high degree of context dependency makes it difficult and challenging to predict plant invasions from theory, which is a crucial aspect for invasion ecologist, since there is no sign that the human caused introduction of species into new ranges will decline in future (Keller et al. 2011).

Species invasions and ecosystem functioning

In Chapter 3, 4, and 5, I worked on questions that are relevant for biodiversity-ecosystem functioning research, even without the context of species invasions. By confirming previous results (Petchey and Gaston 2006, Roscher et al. 2012), I showed that plant community productivity can be explained by functional trait diversity. Although species richness is still the most common measure of biodiversity used by scientists, conservationists, and policy makers, here I show that the loss of functional diversity can be more severe than would be predicted if functional diversity simply reflected species richness, since I kept the number of species the same in my mesocosm studies. Similarly, other researchers have found that species richness is an inadequate measure of biodiversity in general (Wilsey 2005, Flynn 2008), and recommend using indices that account for abundance and composition of organisms.

In general, the field of species invasions can be related to biodiversity-ecosystem functioning research. So far, most studies focused on the impacts that exotics have on processes such as plant diversity and community composition, plant productivity, decomposition, microbial activity or nutrient cycling. Contrary to the common studies that focus on single exotic species or groups of them, I considered in this thesis the attribute of being native or exotic as a component of plant functional diversity (Chapter 3, 4, and 5). I based this approach on several leading hypothesis from invasion research such as the ‘enemy release hypothesis’, which posits that an invader may lose its natural enemies upon entry in a new range (Keane and Crawley 2002, Colautti *et al.* 2004), the ‘new associations hypothesis’, which posits that an invader may form new relationships with organisms in the new range (Callaway et al. 2004, Colautti et al. 2004), or the ‘missed mutualism hypothesis’, which posits that the invader may lose its beneficial relationships from its home range (Mitchell et al. 2006, Alpert 2006). These theories have in common that they characterize the interactions of an invader with its biotic environment. Based on these theories, I hypothesized, that species with different biogeographical histories differ in the number of associations they form with their biotic environment and that this will not only affect the species’ own performance but also community-wide ecosystem properties. I showed, that this trait is second most important (behind N-fixation) in explaining the relationship between functional diversity and productivity, and functional diversity and arthropod abundance and diversity (Chapter 3 and 4), which is a remarkable result of this thesis. That an abundant number of exotic species within a plant community is negatively related to its herbivore abundance and diversity (Chapter 4) has also implications for the biotic resistance of this community against new arriving invaders: Levine et al. (2004) showed in a meta-analysis on the 'biotic resistance theory' that herbivory has a significant and strong negative effect on invader establishment and individual performance. In invasion ecology there is already one theory existing, which captures this phenomenon: the theory of 'invasional meltdown' (Simberloff and Holle 1999, Mack 2003). This theory posits that direct or indirect symbiotic or facilitative relationships among invaders cause an 'invasion domino effect', i.e. already established exotics can make the habitat more accessible for other invaders by altering ecosystem properties. I assume that this invasional meltdown is not only a relevant mechanism for single taxa of exotics (as was shown before), but also for whole trophic levels. I did not test this relationship in my thesis, but I think, it is appropriate to speculate about a potential feedback mechanism: A high proportion of exotic plant species in a community promotes lower herbivore abundance and diversity (Chapter 4), which negatively affects the biotic resistance of the community (Levine et al. 2004), which may lead to the establishment of new invaders in turn. Such a feedback loop may be another good example how different mechanisms of invasion success may act in concert and this is something that needs to be investigated by future studies.

Specific suggestions for future research

As mentioned above, I found that a native plant species may benefit from the presence of a dominant co-occurring exotic invader mediated by changes in the soil biota community (Chapter 2). Facilitative interactions in plant communities were neglected for a long time in ecology; only in the last two decades they have received considerable attention (Brooker et al. 2008). However, in the field of plant-plant interactions the focus in invasion ecology is still on negative impacts that exotics have on native plants. Nevertheless, there are a few other examples of exotics that facilitate native plants present in the literature (Rodriguez 2006, Perkins and Nowak 2013). Future research should evaluate how widespread these facilitative interactions are and how relevant they are compared to competitive interactions.

I showed by the example of *S. canadensis* (Chapter 2, 3, 5, and 6) how several ecological mechanisms act together in affecting the invasion success of an exotic plant species. Invasions are complex processes, and simple approaches that focus on one factor at a time (such as the traits of invaders or recipient communities) have had limited success (Moles et al. 2012). I believe that the best way to further increase our understanding of invasions will be to adopt more holistic approaches that incorporate several different types of information simultaneously, especially information about the ways conditions have changed.

I showed that the effects of global change related abiotic stresses on plant communities are mainly species-specific and context-dependent (Chapter 5). Furthermore, my results are consistent with a growing body of experimental work, which found that exotic plant species are not necessarily the ones that benefit from global change as it is predicted from theory. This underlines the fact how important it is, to conduct experiments to better understand the impact of global change on present and future plant communities.

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Contribution to the manuscripts

Schittko, C. and Wurst, S., 2014. Above- and belowground effects of plant-soil feedback from exotic *Solidago canadensis* on native *Tanacetum vulgare*. *Biological Invasions*, 16(7), pp.1465–1479.

My contributions: I conceived and designed the experiment, performed the experiment, analyzed and interpreted the data, wrote the manuscript, and submitted it to *Biological Invasions*.

Schittko, C., Hawa, M. and Wurst, S., 2014. Using a Multi-Trait Approach to Manipulate Plant Functional Diversity in a Biodiversity-Ecosystem Function Experiment. *PloS one*, 9(6), p.e99065.

My contributions: I conceived and designed the experiment, performed the experiment, analyzed and interpreted the data, wrote the manuscript, and submitted it to *PloS one.*

Schittko, C. and Wurst, S., 2014. Bottom-up effects of plant functional trait diversity on arthropod abundance and diversity in an urban grassland plant community.

My contributions: I conceived and designed the experiment, performed the experiment, analyzed and interpreted the data, and wrote the manuscript.

Schittko, C., Forstreuter, M. and Wurst, S., 2014. Linking species invasions to environmental change: Consequences of elevated temperature and soil compaction on the composition and biodiversity of an urban plant community.

My contributions: I conceived and designed the experiment, performed the experiment, analyzed and interpreted the data, wrote the manuscript, and submitted it to *Global Change Biology*.

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Curriculum vitae

For reasons of data protection,

the curriculum vitae is not included in the online version