Biodiversity and multitrophic interactions in changing terrestrial ecosystems

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Kumulative Habilitationsschrift
zur Erlangung der *venia legendi*
für das Fach Ökologie
von

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Vorgelegt der
Fakultät für Agrarwissenschaften
der Georg-August-Universität Göttingen

Im Juli 2011

Table of Contents

Effects of tree diversity on herbivory, herbivores and predators

published as:

Sobek S, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. Oecologia 160:279–288.

Effects of tree diversity on true bugs (Heteroptera)

published as:

Sobek S, Goßner M, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera). Ecological Entomology 34: 772–782.

Effects of tree diversity on trap-nesting bees, wasps and their natural enemies

published as:

Sobek S, Tscharntke T, Scherber C, Schiele S, Steffan-Dewenter I (2009) Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? Forest Ecology and Management 258: 609–615

Chapter 1

An introduction and overview

1 General Introduction

We are all living in a changing world - rapid human global population growth, expansion and globalization of the economy, increasing global trade, revolutions in communication technology, as well as political changes, are just some of many possible indicators of change (Martino and Zommers 2007). However, population and economic growth don´t come without costs - in particular, growth always requires resources, and resource demand has been increasing dramatically over the last decades.

For living organisms, and the ecosystems which they are part of, some types of human activities are more influential than others. One major type of human activity is land-use, that is, the way in which man transforms land cover for various (often agricultural) purposes.

Understanding the effects of land-use on life on Earth is therefore one important aim of this thesis. The following subsections shall introduce some of the basic concepts, and may serve as an overview of what will be covered in later chapters of this thesis.

1.1 Components of global change

Since the onset of the 18th century, human societies have passed through several phases of **industrial revolutions** (Spilhaus 1970), all of which created their own impacts on the environment (Ellis 2011). In general, such transitions are characterized by abrupt changes in technology, communicaton or mobility, followed by increases or decreases in human population growth rate (Meyer and Turner 1992).

Over the last decades, it has become clear that some of these anthropogenic impacts have now reached a **global dimension**, affecting components of the Earth system as a whole (Zavaleta and Heller 2009), commonly referred to as "**global change**" or "**global changes**" (Turner et al. 1990).

Global change may, for example, comprise processes such as (i) increasing **atmospheric concentrations of CO_2** (carbon dioxide); (ii) anthropogenic changes in **biogeochemical** cycles, or (iii) **land-use change** (Vitousek, 1994). The term "global change" may have two distinct meanings. On the one hand, "global" may refer to the spatial scale of operation of a process; for example, an event happening very locally may have direct consequences on a global scale. On the other hand, "global" may also mean an accumulation of localized changes (Figure 1, p. 6; for details, see Turner et al. 1990).

In this thesis, some of these components of global change will be **experimentally manipulated** on a local scale, to study global change effects on ecosystems. In particular, we study the effects of

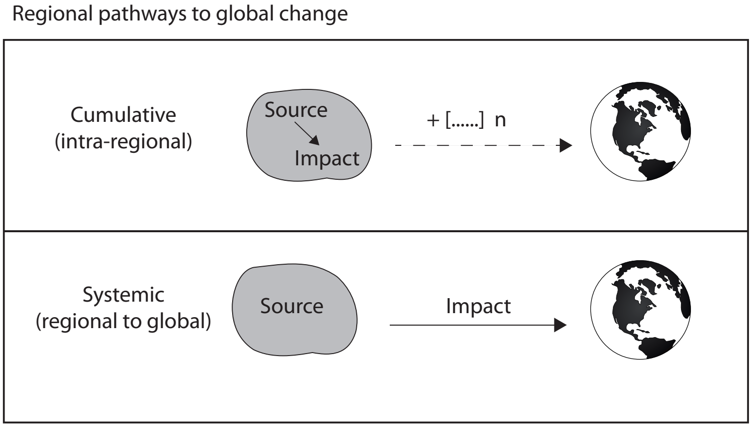

Figure 1: Pathways to global change. Global change may be either (i) a cumulative process, where individual sources have regional impact, and only have a cumulative effect on the Earth system, or (ii) a more direct process, where a single regional event has direct global consequences. Modified from Turner et al. 1990.

rising atmospheric CO_2, **warming and increased drought** on a heathland ecosystem (Chapter 5, page 85; Chapter 6, page 101). It has been shown that increasing concentrations of atmospheric CO_2 may affect plant productivity, nitrogen cycling (e.g. via changes in plant nitrogen demand) and trophic interactions (e.g. via changes in survival, growth and reproduction of herbivores). We investigate these mechanisms using two types of insect herbivores (Chapter 5, page 85 and Chapter 6, page 101).

1.2 Global losses of biodiversity

Anthropogenic changes need not be restricted to abiotic effects (such as climatic changes). In addition to changes in climate, atmospheric CO_2 concentration or land cover, humans are also altering the **dominance structure** of species in ecological communities. In particular, there is increasing concern about the **loss of biological diversity** from ecosystems (Sala et al., 2000). Recently, it has been debated whether human activities have already initiated a **sixth mass extinction** (Barnosky et al., 2011). Whether or not biodiversity loss is given the status of a mass extinction, there is little doubt that human-caused extinction rates are substantially higher than background rates from the fossil record (Rosenzweig, 2001). In this thesis, we study how changes in biodiversity can affect e**cosystem processes** (Chapter 4, page 49), with a special focus on multitrophic interactions.

1.2.1 Effects of biodiversity on multitrophic interactions

During the last decades, ecologists have increasingly moved away from two- or few-species interactions to **multi-species interactions** that span multiple trophic levels. They have also started to consider other types of interactions, such as non-trophic or indirect interactions, in their studies of ecological communities (Borer et al. 2002, Bruno et al. 2003). Interactions may be classified based on effects on population size or growth rate, or on fitness components (Abrams, 1987). Interactions between species may also be affected indirectly by additional interactions with other species (indirect interactions; Thompson, 1988). One of the most challenging areas in the study of multitrophic, nontrophic or indirect interactions is the incorporation of species richness, and the link to food web theory (Goudard and Loreau, 2008). In particular, it has remained unclear how **changes in biodiversity** at one trophic level are passed on to adjacent levels (Cardinale et al. 2006), and how biodiversity change affects different types of interactions. In this thesis, we address these issues by experimentally manipulating plant biodiversity, and studying responses of organisms and processes in a multitrophic context (Chapter 4, page 49).

1.2.2 Effects of biodiversity on biological invasions

Biological invasions have been recognised as an important cause of biodiversity loss (Sala et al., 2000), although recently the impact of biological invasions on ecosystems and their potential consequences in terms of biodiversity loss have been questioned (Hejda et al. 2009; Simberloff 2009). In this thesis, we investigate the effects of **biodiversity** and **belowground interactions** on **biological invasion** processes, using phytometer invaders (Chapter 2, page 25) and weed invaders in general (Chapter 4, page 49).

1.3 Land-use change in terrestrial ecosystems

Human-caused changes to ecosystems occur not only on large scales; at a **regional and local scale,** it is mostly the type and intensity of land-use that decides upon which species reside in a community. The history of agriculture in Europe is governed by such transitions in land use - from large stretches of natural deciduous forests to agricultural mosaic landscapes and “industrial agriculture” (Wilson, 2007). In this thesis, we study changes in biodiversity across a range of ecosystem types, from near-natural forests (Chapter 9, page 153; Chapter 10, page 179; Chapter 11, page 195; Chapter 12, page 215) to grassland (Chapter 2, page 25; Chapter 3, page 37; Chapter 4, page 49) and cropland (Chapter 7, page 117; Chapter 8, page 135).

1.4 The central role of agriculture in shaping biodiversity

The world in which we live in is certainly not in a "natural" state any more: Human land-use activities have greatly transformed the biosphere (Vitousek et al. 1997), giving rise to what has been called "**anthromes**" - biomes that are largely shaped by human activities (Ellis, 2011). In fact, even pristine rainforest ecosystems are indirectly influenced by these activities, and some authors have even

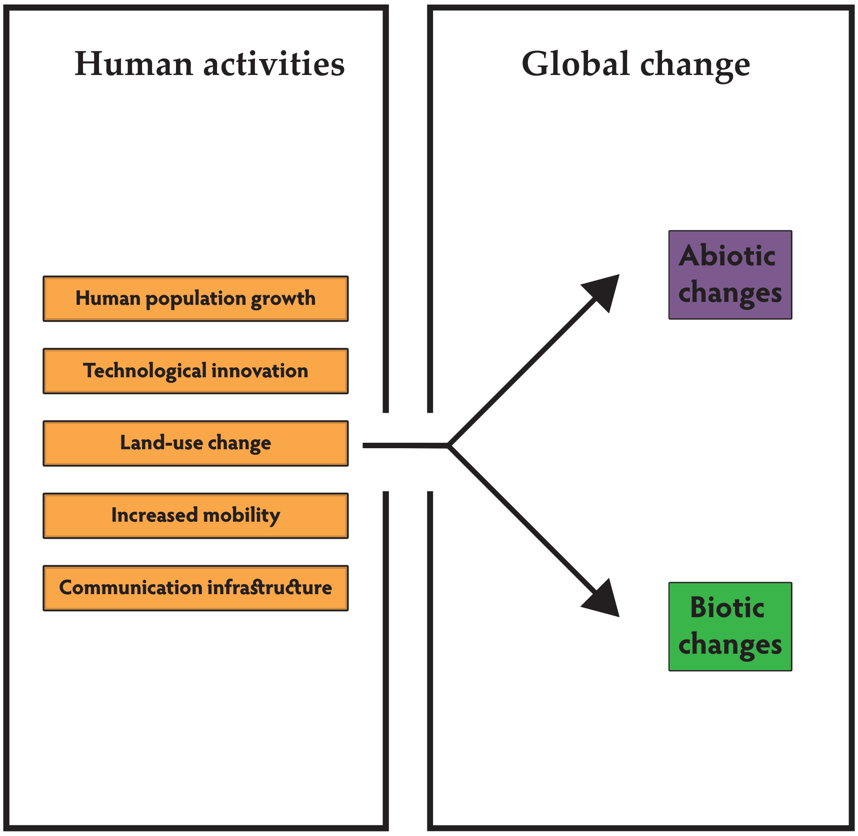

Figure 2: Overview of topics covered in this thesis. Above: Some possible anthropogenic causes of global change, resulting in either abiotic or biotic environmental changes.

claimed that a new epoch in geological time, the so-called **anthropocene**, has begun (Zalasiewicz et al. 2011).

If you look down on a piece of land from an aircraft or a helicopter, you can clearly see that agricultural land use is by far one of the most important human activities in terms of shaping the look of the Earth´s surface (c.f. Kareiva and Wennergren 1995). Unless you fly over an uninhabited area, you will almost always recognize structures that have been transformed, fragmented, reshaped, fertilized, mown, grazed, or otherwise reshaped by direct or indirect human activity. Therefore, the type of agriculture we are employing is of great influence to species, communities, and ecosystems.

In large parts of this thesis, we use **grassland ecosystems** to study how changes in plant biodiversity affect other organism types and their interactions. "**Grassland agriculture**" is an important type of agriculture in many parts of the world (Barnes et al. 2003). Especially in Central Europe, grassland ecosystems belong to the most species-rich ecosystems (e.g. Poschlod and WallisDeVries 2002). Other managed ecosystems covered in this thesis include cropland (e.g. Chapter 7, page 117) and heathland (e.g. Chapter 6, page 101). In addition, we also cover largely unmanaged ecosystems (e.g. Chapter 9, page 153).

2 The general structure of this thesis

The chapters in this thesis center around the effects of **global change** on **components of the Earth system**. Because terms such as “global change” may potentially mean many different things to different readers, the thesis follows a strict **framework** that is shown in Figure 2, p. 8 and the following page. The box on the far left shows a selection of human activities that may cause global environmental changes (through pathways shown in Figure 1, p. 6). On the opposite page, some components that may be affected by these environmental changes are shown - for example species, communities, or ecosystems. Finally, the far right of the figure lists some of the **experiments** that were conducted within the framework of this thesis. More details on the experimental approaches will be given in the next section.

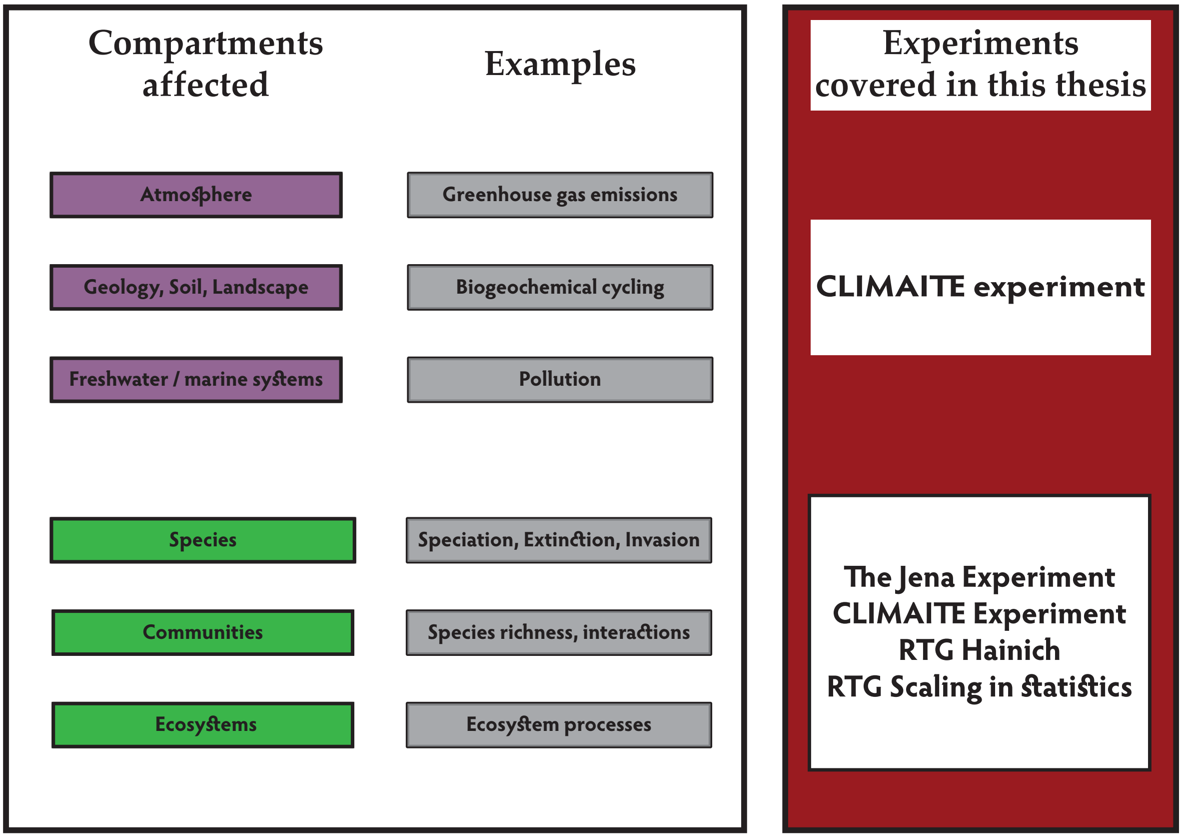

Figure 2 (continued): System compartments affected by global change, along with examples. Note that communities and ecosystems are not necessarily clearly separated compartments. The right hand side shows experiments presented within the framework of this thesis. RTG, research training group (coordinated program for PhD students funded by the DFG.

Because of the variety of experimental approaches used, the chapters of this thesis have been grouped into four sections.

2.1 Section 1

Section 1 covers the effects of changes in biodiversity on ecosystem processes and multitrophic interactions. The section consists of the following chapters:

Chapter 2 (page 25) describes the effects of plant biodiversity on invasion resistance - in particular, resistance against plant invasion.

Chapter 3 (page 37) uses an experimental approach to show how components of plant biodiversity affect the performance of insect herbivores.

Chapter 4 (page 49) combines these findings with others to synthesize plant biodiversity effects on different groups of organisms and multitrophic interactions in general.

2.2 Section 2

Section 2 moves away from biodiversity effects and covers the more general effects of global change on multitrophic interactions. In particular, some global change components are experimentally manipulated to study the effects of climate change on insect herbivores and above-belowground interactions. The section consists of just two chapters:

Chapter 5 (page 85) describes the effects of combinations of warming, drought and elevated atnospheric carbon dioxide concentration on performance of a specialist insect herbivore.

Chapter 6 (page 101) uses the same experimental system to test whether climate change effects are passed on from the aboveground to the belowground subsystem.

2.3 Section 3

In **Section 3**, the focus moves towards more intensively used ecosystems, such as oilseed rape fields and agricultural landscapes in general. In

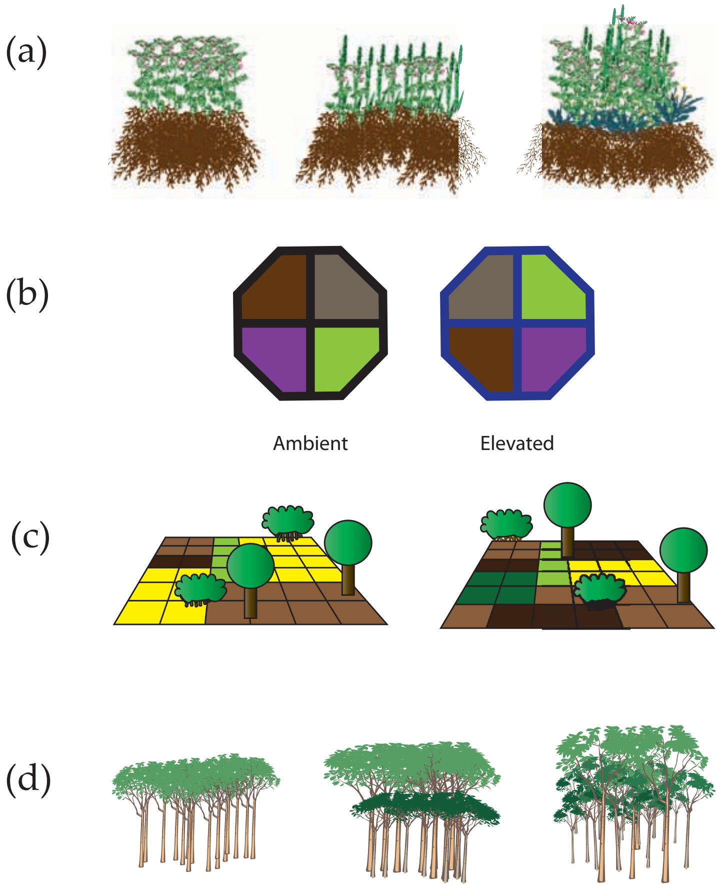

Figure 3: Main types of experimental approaches used in this thesis.

(a) Sown gradients in plant species richness (The Jena Experiment), covered in **Section 1**;

(b) Free air carbon dioxide enrichment (FACE) experiments of **Section 2;**

(c) Existing gradients in landscape structure, for example habitat amount or identity (RTG Scaling problems in statistics)., covered in **Section 3**;

(d) Natural gradients in tree species richness (RTG Forest Biodiversity, Hainich National Park), see **Section 4**.

this chapter, the effects of land-use on multitrophic interactions are investigated - with land-use changes as another prominent component of global change. This section consists of the following two chapters:

Chapter 7 (page 117) uses an experimental model system to study the effects of habitat identity and landscape composition on multitrophic interactions in wild mustard.

Chapter 8 (page 135) combines these and other findings to develop a more general view on biological control in a landscape context. This chapter is largely devoted to methodological issues, such as experimental design, sampling, and statistical analysis of studies on biocontrol at a landscape scale.

2.4 Section 4

Finally, in **Section 4**, we return to plant biodiversity effects again, but this time using an unmanaged ecosystem that shows equilibrium dynamics. This section differs from all previous ones, because the results presented here were all obtained in an unmanaged forest ecosystem. In this section, we show that many findings from agricultural systems may be transferred to natural or near-natural ecosystems. In particular, there are some striking similarities between forest biodiversity and grassland biodiversity effects on multitrophic interactions. The section consists of the following chapters:

Chapter 9 (page 153) describes effects of forest biodiversity on beetle communities

In **Chapter 10** (page 179), we study the effects of forest biodiversity on herbivory and plant-herbivore interactions.

Chapter 11 (page 195) describes tree diversity effects on true bugs, a diverse group of insects inhabiting forest ecosystems.

Finally, **Chapter 12** (page 215) uses a similar approach to study tree diversity effects on trap-nesting bees, wasps and their natural enemies.

3 Hypotheses

3.1 Hypotheses for Section 1

H 1 : Plant biodiversity and invasion resistance. Species-rich plant communities are more resistant against plant invaders than species-poor plant communities (monocultures in particular). Invasion resistance is mediated by aboveground competition for light, and/or by belowground competition for water, nutrients or space.

H 2 : Plant biodiversity and herbivore performance. Performance of specialist insect herbivores will increase with plant species richness, provided that the preferred host plant species is present in the community. The mechanism for this is dietary mixing, leading to increased herbivore performance when feeding on a diverse mixture of plant species. Dietary mixing has beneficial effects on growth, survival and reproduction of herbivores.

H 3 : Plant biodiversity and multitrophic interactions. In general, an increase in plant species richness will lead to increases in the abundances of other trophic levels, such as herbivores or carnivores. The frequency of interactions among trophic groups (and other related food web parameters) increase with plant species richness, leading to more complex interaction webs with increasing plant species richness.

3.2 Hypotheses for Section 2

H 1 : Climate change effects on herbivore performance. Increased CO_2 will have a negative effect on herbivore performance, because plant material becomes increasingly depauperate in nitrogen, an important resource for herbivores. Drought should negatively affect growth and survival of herbivores, while warming should have a positive effect on herbivore performance.

H 2 : Climate change effects on above-belowground interactions. Elevated CO_2 concentration has been shown to increase plant growth and carbon fixation, provided that the system is not nitrogen-limited. Aboveground herbivory has been shown to increase under elevated CO_2. If plants act as mediators between the above- and the belowground subsystem, it can be expected that elevated CO_2 should also affect above-belowground interactions. The effects of warming and drought are more difficult to predict.

3.3 Hypotheses for Section 3

H 1 : Effects of habitat type and landscape structure on multitrophic interactions. Both habitat identity and landscape complexity will influence plant-herbivore and herbivore-parasitoid interactions in agricultural landscapes. The proportion of oilseed rape (a host plant of the main herbivore used in this study) is predicted to influence (specialist) parasitoid abundance more than (generalist) herbivore abundance.

H 2 : Effects of landscape structure on biological control on a landscape scale. We predict that a grid sampling approach is suitable to sample arthropods in the agricultural landscape.

3.4 Hypotheses for Section 4

H 1 : Effects of tree species richness on beetle communities. We hypothesize that species rich forest communites have a greater habitat heterogeneity, leading to increasing beetle species richness with increasing tree species richness. Species turnover (b-diversity) will be higher in species-rich forest stands than in monospecific stands. Spatial turnover between trees contributes more to overall beetle diversity than temporal turnover.

H 2 : Effects of tree species richness on herbivory, herbivores and predators. The resource concentration hypothesis predicts that herbivory should be highest in monospecific tree stands. Similarly, the enemies hypothesis predicts that predator abundance should increase with tree species richness. The results may be modulated by tree species identity.

H 3 : Effects of tree species richness on true bugs. Because of greater structural diversity in species-rich tree stands, we expect a general increase in Heteropteran abundance and species richness with increasing tree species richness. Spatial turnover of species contributes more to Heteropteran diversity than temporal turnover.

H 4 : Effects of tree species richness on trap-nesting bees, wasps and their natural enemies. Richness and abundance of the studied taxa should increase with tree species richness (habitat heterogeneity hypothesis). Parasitism rates will increase with tree species richness.

4 Methods and study systems

4.1 Methods for Section 1

In this section, we present some results of an ongoing biodiversity experiment that is called "The Jena Experiment". The experiment was established on former arable land in 2001 (Roscher et al. 2004). The field site comprises roughly 10 ha and lies in the Salle valley in Thuringia (Germany), close to the town of Jena. The experiment was laid out as a randomized blocks design consisting of four blocks and about 90 plots with a size of 20 x 20 m each. The main experimental treatments applied were (i) a sown gradient in plant species richness, ranging from monocultures to up to 60-species mixtures; (ii) plant functional group identity (presence of grasses, legumes, small and tall herbs) and (iii) plant functional group richness, raning from 1 to 4 plant functional groups present per plot. The main aims of this experiment were:

(1) to assess the effects of plant species richness on biogeochemical cycling and multitrophic interactions and

(2) to identify the relative contributions of plant species and functional richness to ecosystem processes.

In the chapters presented in this thesis, we additionally performed the following experiments:

(i) We study the resistance of plant communities against invasions by other plant species (usually external, i.e. not present in the species pool of a given plot). For this purpose, we transplant a set of phytometer individuals into each plot. A "phytometer" is a plant individual whose performance is measured in every plot. The aim of such a phytometer approach is to draw inferences about how the surrounding plant community influences the phytometers´ performance. In our case, we study how the phytometers´ performance is influenced by plant species richness. Previous studies had shown that aboveground competition for light, or belowground competition for space, water and/or nutrients might be potential drivers of phytometer performance in species-poor vs. species-rich grassland. In this chapter, we experimentally manipulated aboveground competition for light to show whether this process influences community invasion resistance.

(ii) We study the effects of plant species richness, functional group richness and functional group composition on performance of an insect herbivore, the grasshopper Chorthippus parallelus Zett. (Acrididae). We transferred a set of grasshopper individuals into cages installed in every plot (N=81 plots) and studied growth, survival and reproduction of these herbivores as a function of plant species richness.

(iii) finally, we use a large dataset on multitrophic interactions collected within the framework of the Jena Experiment over a period of eight years to study how plant biodiversity influences multitrophic interactions. The analyses conducted for this chapter took several years of time, and more than 40 scientists had been involved in data collection. This chapter comprises a great variety of different methods, and the reader is referred to Chapter 4, page 49, for further details.

[**methods section** continued on page Seite 21]

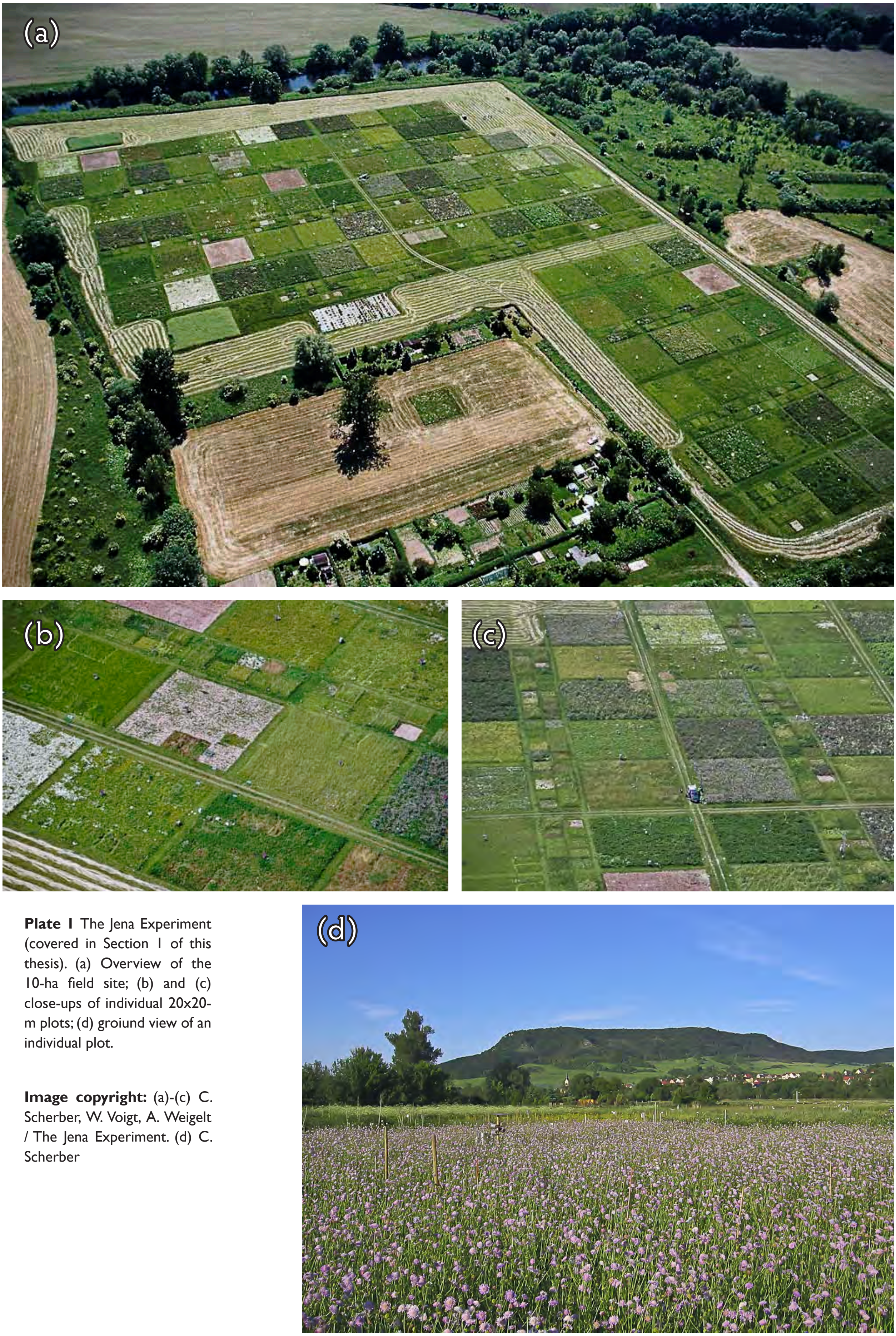

Plate 1 The Jena Experiment (covered in Section 1 of this thesis). (a) Overview of the 10-ha field site; (b) and (c) close-ups of individual 20x20-m plots; (d) groiund view of an individual plot.

Image copyright: (a)-(c) C. Scherber, W. Voigt, A. Weigelt / The Jena Experiment. (d) C. Scherber

Plate 2 Grassland plant mixtures used in the Jena Experiment (covered in Section 1 of this thesis). (a) A grass monoculture; (b) a monoculture of *Knautia arvensis*. (c) a sixty-species mixture and (d) a 2-species mixture of *Knautia arvensis* and *Leucanthemum vulgare*.

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Plate 3 Some specific experiments and sampling techniques used in the Jena Experiment (covered in Section 1 of this thesis). (a)-(c) Grasshopper experiment (see Chapter 3, page 37); (a) each plot received two cages, one of which stocked at random with 10 females and 10 males of the grasshopper *Chorthippus parallelus* Zett. (Acrididae). (b) another, smaller cage was used for oviposition experiments; (c) an individual of C. parallelus (3rd instar). (d) Trap nests used to measure parasitism rates (see Chapter 4, page 49). (e) Pitfall trap, installed in every 20x20-m plot, to capture epigaeic invertebrates. (f) Mower used for grassland management and plot maintenance.

Image copyright: (c) A. Oswald/S. Unsicker (Jena); (d) C. Scherber/C. Rothenwöhrer; all other pictures taken by C. Scherber.

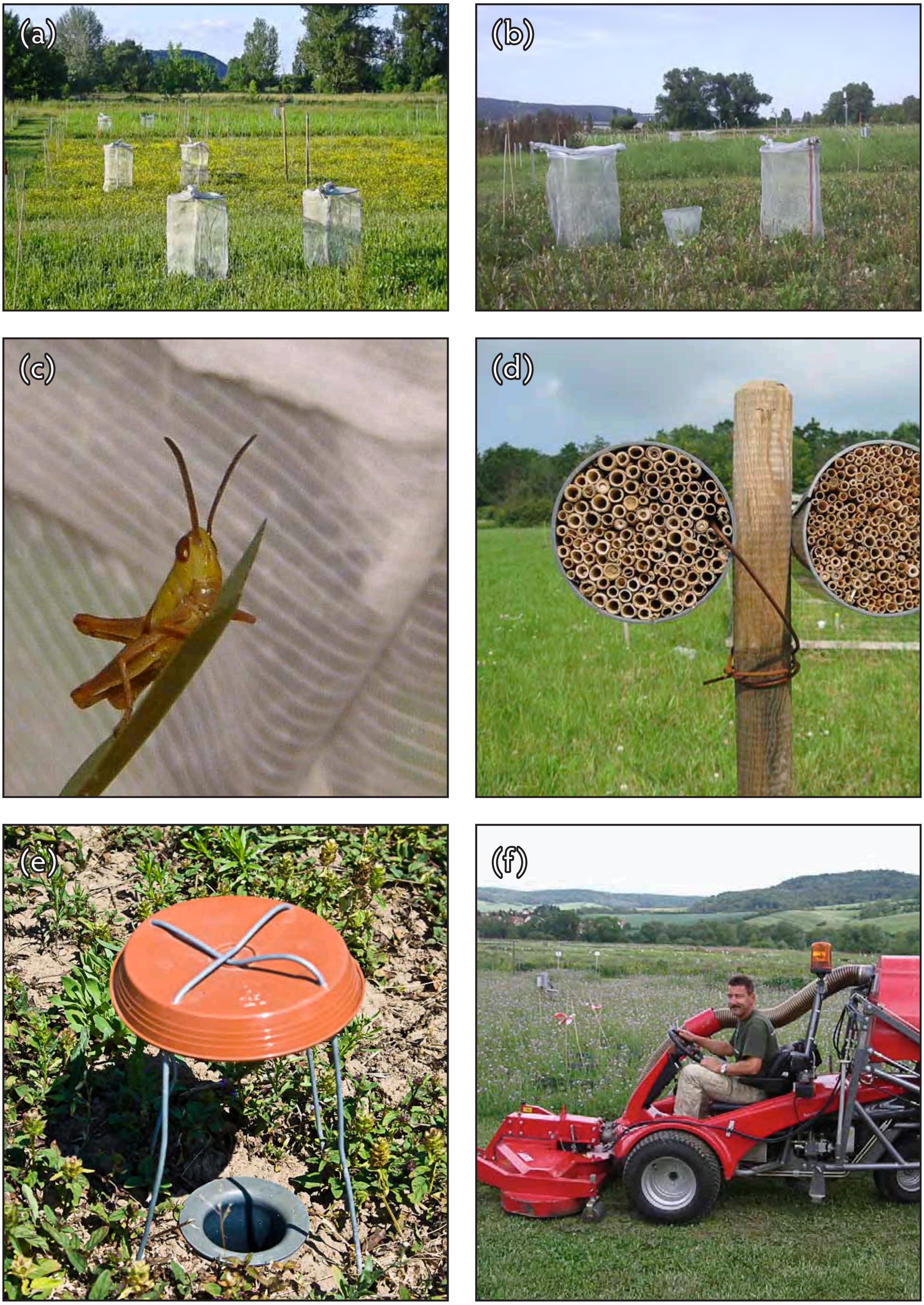
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Plate 4 Climate change experiment ("Climaite"), covered in Section 2 of this thesis. (a), (c) and (e) Overview of individual FACE rings (each measuring 7 m in diameter); Each ring is subdivided into four sectors for treatment combinations of drought and warming; (e) a drought curtain moved over half of one of the octagons. (b), (d) and (f): Experiments with the heather beetle, *Lochmaea suturalis* (see Chapter 5, page 85). (b) Cage stocked with beetle larvae; (d) adult beetle and (f) larval beetle feeding on *Calluna vulgaris*.

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Plate 5 Details on the above-belowground experiment described in Chapter 6. (a) an individual grasshopper cage, fitted around soil cores planted with the grass Deschampsia flexuosa. (b) An individual of the grasshopper Chorthiippus brunneus, ready for randomized addition to individual cages. (c) Soil cores after extraction (left: without, right: with herbivory); (d) an extracted soil monolith, ready for determination of microbial biomass and protozoan abundance in the laboratory.

Image copyright: (a) and (b) by D. Gladbach; (c) and (d) by S. Christensen / K. Stevnbak Andersen.

Plate 6 Experiments with the rape pollen beetle, *Brassicogethes aeneus* F. (Coleoptera: Nitidulidae), covered in Section 3, Chapter 7, page 117. (a) An oilseed rape field close to the city of Göttingen, Germany. (b) Rape pollen beetles (*Brassicogethes aeneus*) feeding on pollen released from the anthers of oilseed rape. (c) Sinapis arvensis phytometers and (d) Parasitoids searching for larvae of the *B. aeneus*.

Image copyright: All images taken by C. Scherber.

Plate 7 Landscape-scale sampling of organisms using a grid-based sampling scheme (described in Chapter 8, page 135). (a) Overview of a 1-km² landscape that was equipped with yellow pan traps using a regular grid. Pan-trap grid points were positioned (b) in the middle of a wheat field; c) in grassland, (d) and (e) in oilseed rape. (f) close-up of a pan trap, showing UV fluorescent colour.

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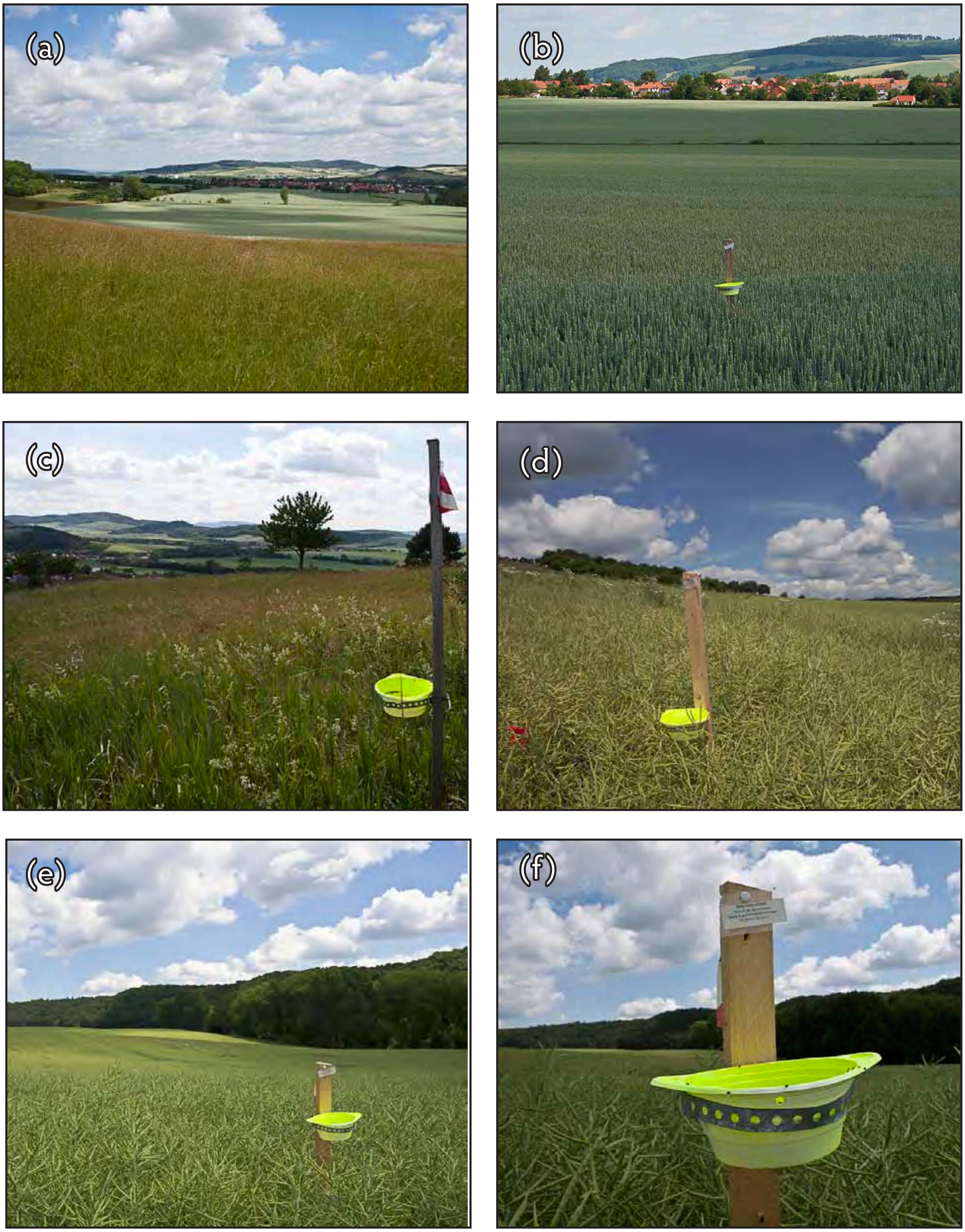
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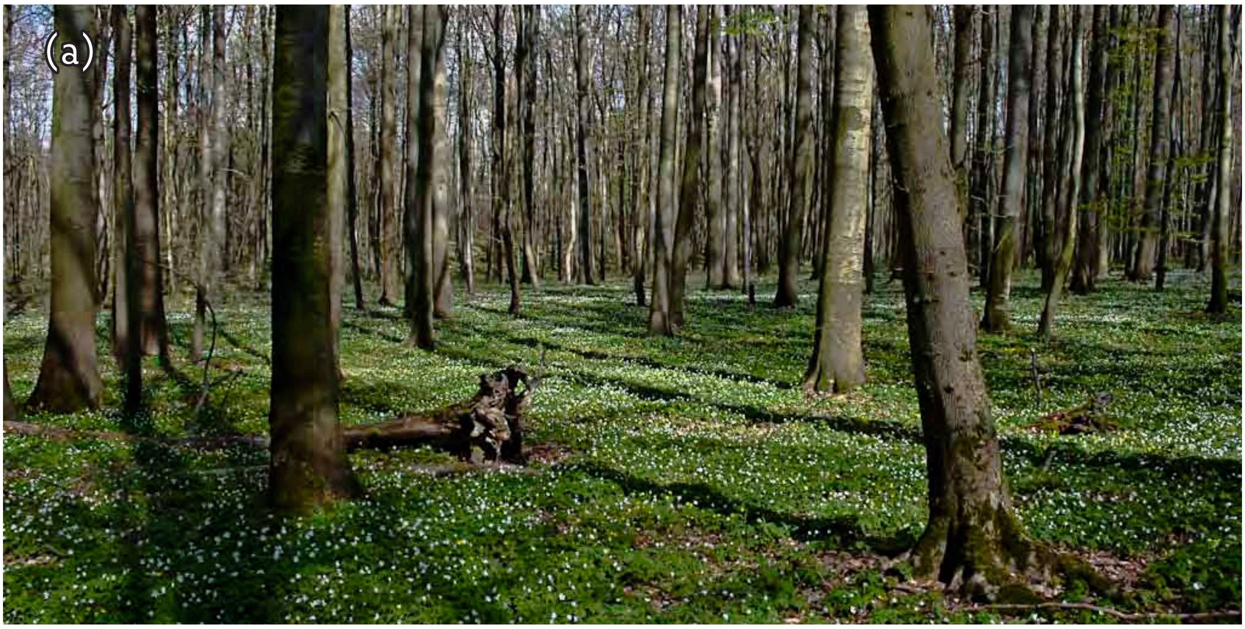
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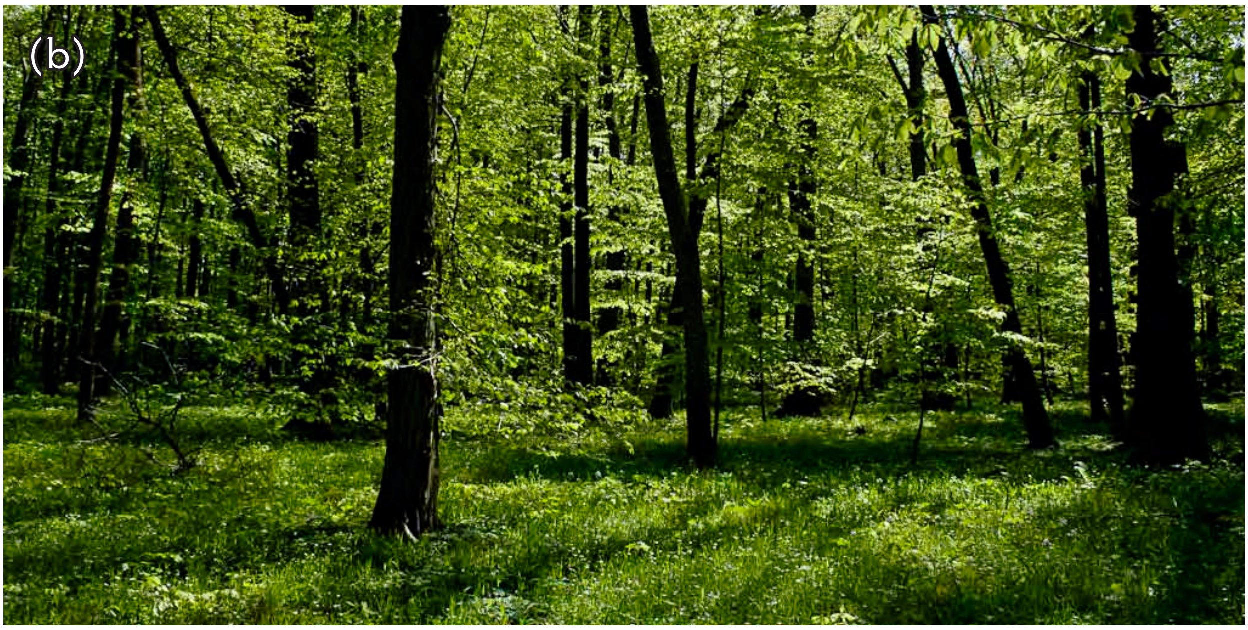
(b)


(c)


(d)

Plate 8 (Opposite page) Forest biodiversity research, described in Section 4 of this thesis (starting with Chapter 9, page 153).

(a) species-poor dorest dominated by *Fagus sylvatica* L. (Fagaceae); (b) species-rich forest, containing >5 tree species per ha, dominated by lime trees (Tilia cordata and T. platyphyllos, Tiliaceae). (c) Flight interception trap used to collect flying arthropods (see Chapter 9, page 153 and Chapter 11, page 195). (d) Herbivory on individual saplings of F. sylvatica, as described in Chapter 10, page 179.

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4.2 Methods for Section 2

In this section, we use a heathland ecosystem to study global change effects on multitrophic interactions. Thus, the main explanatory variable is now not "biodiversity loss", but rather "global change". The experiment was installed in 2005 at Brandbjerg (55°53′N, 11°58′E), about 50 km north-west of Copenhagen, Denmark. The experiment simulates a climate scenario for Denmark in the year 2075 with an increase in atmospheric CO_2 concentration to 510 ppm, an increase in air temperature of about 2°C and extended summer drought (Mikkelsen et al. 2008). The experiment consists of 12 FACE rings, each about 7 m in diameter (six elevated, six ambient CO_2 concentration). The experiment is laid out as a randomized split-plot experiment with drought and warming treatments nested within each FACE ring. In this section, we present the results of two sub-experiments:

(i) We introduce a specialist insect herbivore, the heather beetle (*Lochmaea suturalis* Thoms., Coleoptera: Chrysomelidae), into cages present in each plot, and measure insect growth and survival. This chapter is similar to Chapter 3, page 37in terms of the experimental approach used.

(ii) We use another type of herbivore, the grasshopper *Chorthippus brunneus* Thunb. (Acrididae) to induce a strong herbivory signal and study how this herbivory effect is passed on to the belowground subsystem. We then study how climate change modifies this multitrophic interaction between the above- and the belowground subsystem.

4.3 Methods for Section 3

Here, we move from grassland and heathland ecosystems to arable land. While Chapter 7 (page 117) uses agricultural areas around the city of Göttingen (Germany), the following chapter (Chapter 8, page 135) is more technical and describes methodological issues arising in the study of multitrophic interactions on a landscape scale. The experimental approach followed in Chapter 7 is similar to the phytometer approach followed in Chapter 2: We selected a set of eight landscape sectors along this gradient of land-use intensity and established a set of N=40 study plots in five different habitat types (cereal field, field margin, fallow, grassland, wood margin). Each plot received three phytometer individuals of *Sinapis arvensis* L. (Brassicaceae), a locally common wild plant occuring on arable land. We then studied colonization of these plants by a specialist herbivore, the beetle *Brassicogethes aeneus* (Coleoptera: Nitidulidae) and its parasitoids.

4.4 Methods for Section 4

In the last section of this thesis, we move to an unmanaged ecosystem to study tree biodiversity effects on trophic interactions. We use a set of 12 study sites in a 25-km² area of broad-leaved deciduous forest in the Hainich National Park in Thuringia, Central Germany that covered a natural gradient in tree species richness, ranging from almost monospecific stands to 5-species mixtures. Each of the 12 plots measured 2500 m². Plots were chosen to have comparable pedological conditions, similar annual precipitation patterns and comparable stand structure. We selected four stands of pure beech forest, four stands of beech-ash-lime forest and another four stands of beech-ash-lime-hornbeam-maple forest (see Leuschner et al. 2009 for details).

In this section, we cover the following topics:

(i) We study tree diversity effects on beetle communities across space and time. Beetles were sampled using N=72 flight interception traps (six traps per stand) installed in the centre of individual tree crowns. Beetle sampling was conducted over a period of six months in 2005.

(ii) We study herbivory in beech (*Fagus sylvatica* L.) and maple (*Acer pseudoplatanus* L. and *Acer platanoides* L.) saplings across the tree diversity gradient to test for biodiversity effects on herbivory (similar to results presented in Chapter 4). In addition, we assessed invertebrate abundance on these saplings using a variety of methods.

(iii) We investigate tree diversity effects on true bugs, using flight interception samples described in Chapter 9. In this study, we emphasize the role of beta diversity (in relation to alpha diversity) in understanding effects of tree species richness on other organisms.

(iv) Finally, we expose experimental trap nests for trap-nesting bees, wasps and their natural enemies (similar to the approach described in Chapter 4). A total of 144 trap nests was installed across all forest stands (12 trap nests per stand; 6 in the canopy, 6 in the understorey). The trap nests were exposed over a period of 6 months from May 2006 onward, collected and inspected for presence of Eumenidae, Sphecidae, Pompiliidae and other groups of Hymenoptera.

Overall, the scientific approaches and experiments covered in this thesis span a variety of different ecosystems (grassland, heathland, arable land, forest), a variety of methods (cages, phytometers, trap-nests, interception traps), and a variety of philosophical approaches (from pure technical-experimental to observational gradients chosen a priori).

5 Statistical approaches

Because most experiments described in this thesis involved some kind of spatial or temporal nesting, an important unifying approach to data analysis is the use of mixed models (incorporating both random and fixed effects; Pinheiro and Bates 2000, Zuur et al. 2009). In general, most analyses conducted within the framework of this thesis used linear statistical models and their derivatives, such as general linear models, generalized linear models, mixed effects models, or even generalized linear mixed models. Multivariate methods were used especially in Chapter 4, where it was necessary to account for spatial non-independence (multivariate linear models) and network structure of trophic interactions (structural equation models). More details on these issues can be found in the corresponding chapters.

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Chapter 2

Biodiversity, belowground interactions, and invasion resistance

published as:

Scherber C, Mwangi PN, Schmitz M, Scherer-Lorenzen M, Beßler H, Engels C, Eisenhauer N, Migunova VD, Scheu S, Weisser WW, Schulze ED, Schmid B (2010) Biodiversity and belowground interactions mediate community invasion resistance against a tall herb invader. Journal of Plant Ecology 3:99-108

Journal of
Plant Ecology

VOLUME 3, NUMBER 2,
PAGES 99–108

JUNE 2010

doi: 10.1093/jpe/rtq003

Biodiversity and belowground interactions mediate community invasion resistance against a tall herb invader

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Abstract

Aims
Species-rich plant communities are hypothesized to be more resistant against plant invasions because they use resources in a more efficient way. However, the relative contributions of aboveground competition and belowground interactions for invasion resistance are still poorly understood.

Methods
We compared the performance of *Knautia arvensis* transplants growing in plots differing in plant diversity both under full competition and with shoots of neighbors tied back to determine the relative strength of aboveground competition in suppressing this test invader without the confounding effect of shading. In addition, we assessed the effects of belowground competition and soil-borne pathogens on transplant performance.

Important Findings
Both aboveground competition and plant species richness strongly and independently affected invader performance. Aboveground biomass, height, leaf mass per area and flowering of transplanted individuals of *K. arvensis* decreased with increasing species richness of the host community. Species-rich and species-poor communities both imposed equally strong aboveground competition on *K. arvensis*. However, belowground interactions (especially belowground root competition) had strong negative effects on transplant performance. In addition, the presence of grasses in a plant community further reduced the performance of *K. arvensis*. Our results suggest that belowground competition can render species-rich host communities more suppressive to newly arriving species, thus enhancing community invasion resistance.

Keywords: aboveground competition • competitive suppression • belowground interactions • root competition • shoot exclusion • species richness

Received: 5 September 2009 Revised: 12 January 2010 Accepted: 8 February 2010

INTRODUCTION

Increasing evidence shows that the chance of establishment of newly arriving plants in grassland communities decreases with increasing plant diversity (e.g. Balvanera *et al.* 2006; Burke and Grime 1996; Crawley *et al.* 1999; Fargione and Tilman 2005; Hector *et al.* 2001; Tilman 1997; van Ruijven *et al.* 2003). Several authors attribute this phenomenon to more efficient resource use by diverse as opposed to species-poor communities (Fridley 2003; Hooper 1998; Loreau and Hector 2001; Naeem *et al.* 2000; Scherer-Lorenzen *et al.* 2003; Spehn *et al.* 2000; Symstad and Tilman 2001; Tilman 1999; Tilman *et al.* 1996). Newly arriving plants therefore find progressively fewer 'empty' niches as plant diversity increases (Elton 1958; Levine and d'Antonio 1999). For similar reasons, the presence of particular plant functional groups can affect the success of species additions to plant communities (Fargione *et al.* 2003; Mwangi *et al.* 2007). However, in some cases, even species-poor communities have been shown to be invasion resistant, and this requires additional mechanisms of invasion resistance than species richness *per se* (Levine *et al.* 2004).

The diversity–invasion resistance relationship is often explained by a larger amount of unconsumed below- or aboveground resources in species-poor than in species-rich communities, thus allowing a greater number, abundance or biomass of invading species. However, below- and aboveground interactions have not experimentally been separated in previous diversity–invasion resistance studies.

Increasing species richness may differentially affect below- and aboveground biomass production (see e.g. Spehn *et al.* 2005) and similarly below- and aboveground competition effects on invaders may have different magnitudes (see reviews by McPhee and Aarssen 2001 and Wilson 1988). In addition, belowground invertebrates such as plant-feeding nematodes may suppress establishing plant species in plant communities (De Deyn *et al.* 2003), an effect that is often not accounted for in traditional plant competition studies.

A reduction of aboveground competition in diverse communities can increase invader success, especially during early stages of invasion (Burke and Grime 1996; Diemer and Schmid 2001; Gross *et al.* 2005; Hobbs and Huenneke 1992; Levine 2000). Once successfully established, the growth of a newly added individual in a plant community may be affected both by below- and aboveground competition. Roscher *et al.* (2008) found that access to open space both above and below ground may determine invasion resistance. In addition, other components of the belowground system may affect invader growth and performance.

Not only plant species richness *per se* may mediate a plant community's invasion resistance. Specific plant functional groups, such as grasses, may also be expected to contribute to invasion resistance, e.g. because of their dense root systems and overall competitiveness. Due to niche preemption, tall herbs may be expected to increase invasion resistance against *Knautia arvensis*, which is itself a tall herb (Mwangi *et al.* 2007). Conversely, legumes may be expected to be less suppressive because of their low root biomass and provision of nitrogen through N_2 fixation.

In the experiments presented here, we used experimental plant communities ranging from 1 to 60 species to which we transplanted seedlings of a potential invader species, *K. arvensis.* Once these transplants had established, we reduced aboveground competition for half of them by tying back all aboveground parts of the surrounding plant community and compared their growth with that of the controls still experiencing full aboveground competition. Thus, if species-rich plant communities were still invasion resistant even after removal of aboveground competition, then it is likely that belowground interactions are responsible for community invasion resistance. We tested the following specific hypotheses:

(i) suppression of *K. arvensis* transplants increases with increasing diversity of the plant community,
(ii) in addition to diversity, the presence of particular functional groups can negatively (grasses, tall herbs) or positively (legumes) affect the growth of transplants,
(iii) the suppression of *K. arvensis* transplants can be reduced by reducing aboveground competition,
(iv) competition for space is more important aboveground than belowground (Roscher *et al.* 2008) and
(v) belowground competition and interactions with belowground pathogens are additional mediators of community invasion resistance. Instead of destructively harvesting all plant parts, we used shoot biomass as a predictor of overall plant performance (Howard and Goldberg 2001). We additionally assessed other aspects of the belowground system (root competition, soil pathogen abundance) to test hypotheses (iv) and (v).

MATERIALS AND METHODS

General experimental design of the Jena Experiment

This study was carried out in a grassland biodiversity experiment established in spring 2002 near Jena, Germany (50° 55′ N, 11° 35′ E, 130 m above sea level; 'The Jena Experiment'; http://www.the-jena-experiment.de). The field site is a former arable field that lies in the floodplain of the river Saale (Roscher *et al.* 2004). Because of a gradient in soil characteristics, the field site was divided into four blocks, perpendicular to the river. Experimental grassland plant communities were then sown on a total of 82 plots. Each community consisted of 1, 2, 4, 8 or 16 species drawn at random with replacement from a pool of 60 naturally co-occurring Central European grassland species. In addition, four plots were sown with all 60 species. The plant communities were established on 20×20 m^2 plots at a sowing density of 1 000 viable seeds per square meter. There were 14–16 replicates at each richness level that all differed in species composition (see Roscher *et al.* 2004 for details).

In addition to plant species richness, we manipulated plant functional group identity and -composition orthogonal to the richness treatments. All plant species were classified into four functional groups: grasses (16 species), small herbs (12 species), tall herbs (20 species) and legumes (12 species), based on multivariate analyses of species traits related to ecosystem functioning (Roscher *et al.* 2004). Each plot received 1, 2, 3 or 4 plant functional groups. For example, there were grass monocultures but also mixtures consisting of 2, 4, 8 or 16 grass species (and so on), allowing us to disentangle both species richness and functional group richness and identity effects.

Plots were weeded and mown biannually to maintain target species compositions. Mowing took place at the end of May and August each year to mimic usual pasture management. Plots did not receive any fertilization.

Cultivation and transplantation of *K. arvensis*

Knautia arvensis is a perennial herb native to Eurasia, occurring in natural and semi-natural grasslands. It is invasive in other parts of the world, e.g. in North America and Canada. *Knautia arvensis* has a well-developed taproot, opposite feather-shaped leaves and grows up to 1 m tall; consequently, it has been classified as belonging to the 'tall herbs' functional group in this experiment (Roscher *et al.* 2004) and was also present in 14 of the 82 communities. For the experiments reported here, we experimentally transplanted *K. arvensis* as seedlings into all 82 experimental plant communities to measure their performance and how it was affected by the species richness treatments, aboveground competition and other factors.

Knautia arvensis was grown from seed (Rieger-Hofmann, Blaufelden-Raboldshausen, Germany) sown on moist filter paper in March 2003 in a greenhouse. Seedlings were transferred to 125-cm^3 pots (60 × 60 mm^2) cells of a potting tray filled with a mixture of soil from the field site (Eutric Fluvisol), standard compost (Torfkultursubstrat TKS 1, DIN 11 542, 120–250 mg N and P_2O_5 per l, pH 5.5–6.5) and perlite (DIN 4102; S&B Industrial Minerals GmbH, Neuss, Germany) at ~1.2:1:0.1. Plants were grown under a 14-h light regime with 22°C:15°C day:night temperatures. In mid-April 2003, at an average size of four to seven leaves, we hardened the plants by placing them outside the greenhouse for 1 week. On each of the 82 experimental plots, we selected a 2 × 2 m^2 subplot at random and transplanted five randomly selected *K. arvensis* plants in a row at 28-cm intervals. Each seedling had the soil mixture attached to the roots and was transplanted using a manual drill machine.

In August 2003, we counted the number of leaves of each plant and harvested the aboveground parts before routine mowing of the experimental plots and oven-dried them at 70°C for 48 h.

Exclusion treatment

One year after transplantation (April 2004), the *K. arvensis* individuals had reached sufficient size to start the shoot exclusion experiment. We reduced aboveground competition around a randomly selected pair of *K. arvensis* transplants per plot by excluding shoots of neighboring plants ('target technique'; McPhee and Aarssen 2001). Two other transplants were used as controls (the additional fifth plant was not considered for this study). Neighboring shoots around each pair of transplants were bent down using mesh wire as follows: we installed a 30 × 60 cm^2 wire mesh (mesh size 1 × 1 cm^2) with two holes that were 28 cm apart (i.e. the distance between two adjacent transplants) to allow unhindered growth of the target *K. arvensis* transplants. The wire mesh was secured with two nails at ~5 cm above ground and slightly raised on the sides to (McPhee and Aarssen 2001) allow otherwise free growth of the neighbors that were tied back. Shoots of the neighboring plants that had grown through the wire mesh were pulled back under the wire mesh at weekly intervals.

In the last week of May 2004, at the peak of growth, leaf area index (LAI) per transplant pair was measured by taking, for every transplant pair, one measurement above the vegetation and three measurements on the ground exactly at mid-distance between the rooting positions of each pair using the LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE, USA). The LAI-2000 was set to one-sensor mode and measurements were taken under stable sky conditions. The LAI data were recomputed with the FV2000 Software (LI-COR Inc.) to restrict the measure to a zenith angle of 23°, corresponding to a maximum potential field of view diameter of 40 cm at 100 cm vegetation height. These adjustments assured that the LAI-2000's field of view was always confined to the 30 × 60 cm^2 exclusion area around each pair of transplanted *K. arvensis* individuals. In total, there were 82 plots, each with two 'exclusion' and two 'control' individuals of *K. arvensis*, and (2×) (1 + 3) LAI subsamples were taken per plot. These were later averaged to give one LAI reading per plant pair and plot.

In addition to LAI, we measured height, noted whether the transplant had flowered and randomly harvested 10 mature leaves from each *K. arvensis* individual. Leaves were transported to the lab in a cool box, where total leaf area was measured using an LI-3100 Area Meter (LI-COR Inc.). At the same time, all individuals were harvested and separated into stems and leaves (including the leaf samples) and then dried to a constant weight at 70°C for biomass determination. We computed leaf mass per area (LMA) by dividing the total leaf mass by the total leaf area of each 10-leaf sample. In addition, the leaf samples were analyzed for nitrogen content using an elemental analyzer (as described in Temperton *et al.* 2007).

Measurement of belowground parameters

As additional covariates, we measured soil nematode numbers and belowground plant competition on each 20 × 20 m^2 plot ($N = 82$). For practical reasons, data on nematode numbers were only collected in autumn 2005 (October). As belowground organisms generally respond to diversity treatments with a time lag (van der Putten *et al.* 2001), this difference in sampling time was considered acceptable. Soil samples for the analysis of nematode densities were taken from randomly selected subplots (1 × 1 m^2) of every plot using a metal corer (diameter 2 cm, depth 5 cm). Five soil samples were taken per subplot, pooled and stored at 5°C. Nematodes were extracted using a modified Baermann method (Ruess 1995). After an extraction time of 30 h at 20°C, nematodes were preserved in 4% formaldehyde. The number of extracted nematodes in each sample was counted and 10% of the individuals (but not <100 individuals, if possible) were assigned to the feeding groups plant feeders/plant pathogenics, bacterial feeders, fungal feeders, predators and omnivores according to Yeates *et al.* (1993). Only plant pathogenic nematodes were considered for this study.

Spatial soil exploitation by roots was assessed with the ingrowth core technique (Oliveira *et al.* 2000). In June 2003, five soil cores (4.8 cm diameter, 30 cm depth) were removed per plot and replaced by root-free soil from the field site. In September 2003, the initially root-free ingrowth cores were removed and the holes were refilled with root-free soil until the following withdrawal in July 2004. To extract the newly formed roots, each ingrowth core was first weighed and carefully homogenized. A subsample of 50 g of soil was suspended in water and rinsed over a 0.5-mm screen. Roots collected in the screen were transferred into a water-filled clear acrylic tray and scanned. Total root length was determined from images using WinRhizo (Regent Instruments, Quebec, Canada). Afterwards, root length density (cm root length per cm^3 soil volume) was calculated.

Statistical analysis

Sown and realized diversity levels were very closely correlated in our experiment (Roscher *et al.* 2004) and we therefore used sown species richness and sown functional group richness to analyze diversity effects. Since *Knautia* aboveground biomass in August 2003 was strongly correlated with number of leaves per plant in August 2003 ($r^2 = 0.86$, $n = 76$, $P < 0.001$), we used the latter as a measure of initial plant size.

Because exclusion treatments were nested within plots, we analyzed our data using mixed-effects models (MEMs) implemented in the 'nlme' and 'lme4' packages (Bates *et al.* 2008; Pinheiro and Bates 2000) in R 2.9.2 (R Development Core Team 2009) and included the 82 plots as random effects (Piepho *et al.* 2003; Schmid *et al.* 2002). Fixed effects were entered as follows: initial leaf number; block; log-linear plant species richness (LSR); plant functional group richness; grass, legume and tall herb presence; exclusion treatment plus two-way interactions between all terms except initial leaf number. We then removed terms one at a time from each maximal model and compared the resulting models using (i) Akaike's An Information Criterion (AICc) and Akaike weights (Burnham and Anderson 2002) or (ii) QAICc for overdispersed count data (Bolker *et al.* 2009), depending on whether (i) linear or (ii) generalized linear MEMs were used. Plant biomass, LMA and plant height were log-transformed and analyzed using linear MEMs. Variance functions (Pinheiro and Bates 2000) were used to model remaining heteroscedasticity. Significance in linear MEMs was assessed using sequential *F* tests (Pinheiro and Bates 2000). Number of flowers, probability to bolt and probability to flower were analyzed using Poisson or binomial generalized linear MEMs with Laplace approximation, implemented in the lme4 package in R (version 0.999375-31, 20 May 2009).

To test for effects of additional covariates (LAI, root length density, abundance of plant-feeding nematodes), we constructed a 'covariate model' and analyzed *Knautia* biomass aggregated across plots ($N = 82$; shoot exclusion effects were nonsignificant if LAI was used as a covariate). This model contained as fixed effects initial leaf number plus two-way interactions between LAI; nematodes; root length density; LSR; functional group richness; tall herb, grass and legume presence. Covariate explanatory variables were log-transformed to improve model fits. Blocks were treated as random. Variance inflation factors were all <4. Model selection was done as described above.

RESULTS

Effects of plant biodiversity on *Knautia* performance

The effects of plant biodiversity will be described in the sequence in which the terms were fitted in the sequential analysis of variance (ANOVA) tables (species richness, functional group richness, tall herbs, grasses, legumes). Increasing plant species richness had a strong negative effect on the aboveground biomass of *K. arvensis* transplants (Table 1; Fig. 1a). On average, the transplants were over eight times heavier in monocultures than in 60-species mixtures (8.5 ± 2.0 vs. 0.7 ± 0.3 g) (Fig. 1; Table 1). While plant height also declined with plant diversity (Fig. 1b), this effect was not significant.

In addition to aboveground biomass of *K. arvensis*, LMA (Table 1) and number of flowers (Poisson MEM, $chi^2 = 18.27$, df = 1, $P < 0.0001$; Fig. 1c) decreased considerably with increasing species richness. Transplants in monocultures vs. 60-species mixtures had on average 7.29 ± 1.94 vs. 0.12 ± 0.08 flowers, respectively. The probability to bolt and flower was not significantly influenced by plant species richness *per se*.

The number of plant functional groups did not significantly affect *Knautia* performance. While presence of tall herbs had no significant effect on *K. arvensis*, presence of grasses decreased the performance of *K. arvensis* significantly. On average, transplants in plots with grasses weighed only 1.74 ± 0.47 g compared to 6.09 ± 1.10 g in plots without grasses (Table 1). The same was true for plant height (without: 50.05 ± 2.81 cm, with: 33.09 ± 2.12 cm; Table 1) and number of flowers (without: 5.98 ± 1.05, with: 1.03 ± 0.22; $chi^2 = 11.20$, df = 1, $P < 0.0009$). Probability to flower ($chi^2 = 6.57$, df = 1, $P = 0.0103$) was also significantly negatively affected by grass presence (but not by legume presence). The LMA of transplants was not affected by the presence of grasses.

The presence of legumes had a significantly negative effect on aboveground biomass (without: 4.19 ± 0.97 g, with: 3.31 ± 0.71; Table 1) but a significantly positive effect on height (without: 37.34 ± 2.56 cm, with: 43.98 ± 2.61 cm). In addition, legume presence led to a strong and significant increase in plant nitrogen concentration (2.30% vs. 1.83% N; Table 1).

Table 1: sequential ANOVA table for linear mixed-effects models with the response variables plant biomass, plant height, LMA and leaf nitrogen concentration

Response	Terms	numDF	denDF	*F* value*	*P* value
Log (plant biomass g^{-1})	Intercept	1	74	421.8461	<0.0001
	Initial leaf number (log)	1	74	178.5114	<0.0001
	Block	3	72	2.3311	0.0814
	Plant species richness (log)	1	72	9.5653	0.0028
	Grass presence	1	72	20.1977	<0.0001
	Legume presence	1	72	9.8821	0.0024
	Exclusion	1	74	0.2833	0.5962
	Legumes:plant species richness	1	72	6.1989	0.0151
	Exclusion:grasses	1	74	4.4311	0.0387
Log (plant height cm^{-1})	Intercept	1	76	4 658.411	<0.0001
	Initial leaf number (log)	1	76	18.781	<0.0001
	Plant species richness (log)	1	75	2.241	0.1385
	Grass presence	1	75	10.978	0.0014
	Legume presence	1	75	4.754	0.0324
	Exclusion	1	76	10.389	0.0019
	Legumes:plant species richness	1	75	3.894	0.0522
Log (LMA mg cm^{-2})	Intercept	1	69	38 821.88	<0.0001
	Initial leaf number (log)	1	67	27.44	<0.0001
	Block	3	69	5.33	0.0023
	Plant species richness (log)	1	69	7.06	0.0098
	Legume presence	1	69	1.14	0.2885
	Exclusion	1	67	16.03	0.0002
	Plant species richness:legumes	1	69	3.99	0.0498
	Exclusion:plant species richness	1	67	3.78	0.0562
	Exclusion:legumes	1	67	3.5	0.0658
Log (leaf nitrogen concentration)	Intercept	1	70	7 244.761	<0.0001
	Initial leaf number (log)	1	63	3.74	0.0576
	Block	3	70	3.385	0.0228
	Plant functional group richness	1	70	3.821	0.0546
	Legume presence	1	70	56.147	<0.0001
	Exclusion	1	63	2.345	0.1307

*F values show tests where every term is added sequentially to the null model. num, numerator; den, denominator, DF, degrees of freedom

Effects of shoot exclusion on plant community LAI

Shoot exclusion had a highly significant overall effect on LAI of the surrounding plant communities ($P < 0.0001$; Fig. 2), with by far the largest F value in the model ($F_{1,75} = 421.583$), compared with F values around 10–20 for the other significant terms. In addition, LAI differed slightly between blocks ($F_{3,72} = 3.02$, $P = 0.04$), increased significantly with plant species richness ($F_{1,72} = 11.41$, $P = 0.0012$) and increased significantly in presence of legumes ($F_{1,72} = 24.16$, $P < 0.0001$). Plant functional group richness and grasses were not significant.

Effects of shoot exclusion on *Knautia* performance

Plants weighed on average 3.66 ± 0.57 g and had an average height of 40.89 ± 1.85 cm. Plants grown under reduced aboveground competition were heavier (3.88 ± 0.75 g) and shorter (37.7 ± 2.54 cm) than plants growing under ambient competition (weight 3.44 ± 0.86 g, height 44.11 ± 2.65 cm; Fig. 1a and b). While shoot exclusion had highly significant main effects on plant height (Table 1; Fig. 1b), LMA (Table 1) and number of flowers ($chi^2 = 7.49$, df = 1, $P = 0.0062$; Fig. 1c), there were no significant effects on plant biomass (Fig. 1a), the probability of the transplants to bolt and to flower and leaf nitrogen concentration (Table 1).

Interactions between shoot exclusion and plant biodiversity

While there were no significant interactions between shoot exclusion and plant species richness *per se* (Fig. 1), there was a significant interaction between grass presence and shoot exclusion: if transplants grew together with grasses, their biomass was always significantly lower and unaffected by shoot

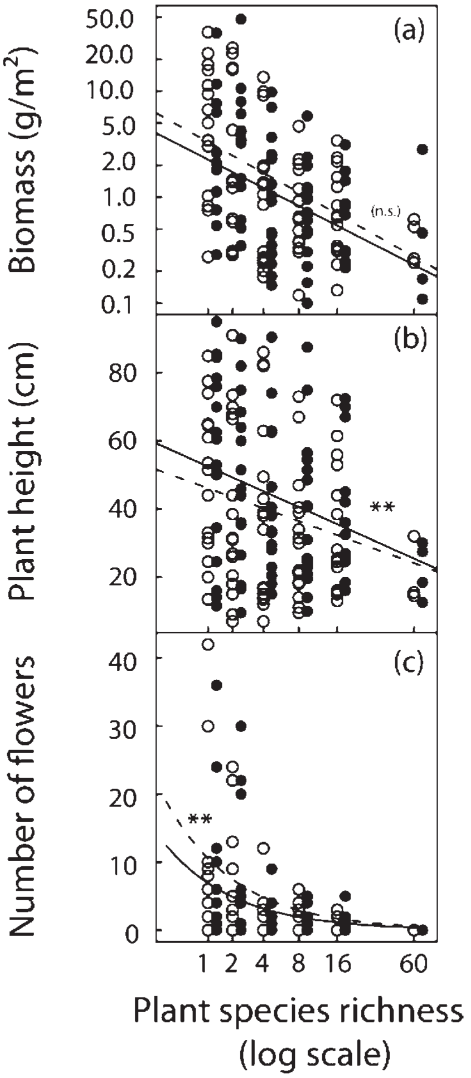

Figure 1: effects of LSR on a) aboveground plant biomass (log scale), b) plant height and c) number of flowers of *Knautia arvensis* transplants with (filled circles, solid lines) and without (open circles, dashed lines) aboveground competition. Lines in (a) and (b) show least-squares fits; (c) shows predictions from the minimal adequate generalized linear MEM at average values of all covariates. Significant effects ($P <$ 0.05) of the removal treatment are indicated by asterisks.

exclusion (Table 1). In contrast, transplants profited significantly from shoot exclusion when grasses were absent. It is likely that belowground competition with grass roots is responsible for this pattern, which is why we investigated this further (see Effects of particular functional groups and belowground parameters on transplant performance).

Effects of particular functional groups and belowground parameters on transplant performance

Because shoot exclusion effects were independent of plant species richness (Table 1; Fig. 1), we hypothesized that belowground processes might mediate invasion resistance of species-rich plant communities. For example, the plant communities contained between 0.4 and 40 plant-feeding nematodes per gram of soil (mean = 12), and root length density ranged from 0 to ~100 cm root length per cm^3 soil (mean = 41 cm × cm^{-3}). Separate analyses with LAI and belowground variables as covariates (see MATERIALS AND METHODS and Fig. 3) revealed that *Knautia* aboveground biomass was independent of belowground nematode abundance (Fig. 3a) but strongly negatively affected by plant species richness, root length density (Fig. 3b), initial leaf number (Fig. 3c) and LAI (Fig. 3d), while legume presence slightly increased *Knautia* biomass (Fig. 3f). In addition, there were several significant interaction terms (Table 2).

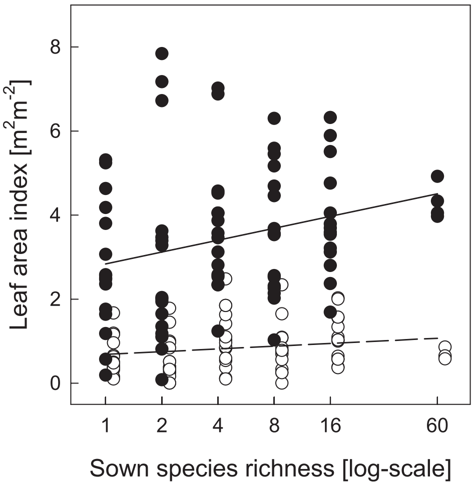

Figure 2: interaction effects between LSR and removal of aboveground competition on LAI measured next to *Knautia arvensis* transplants. Closed circles and solid line indicate LAI with aboveground competition; open circles and broken line indicate LAI without aboveground competition.

DISCUSSION

Experimental approach

Our study has clearly shown that invasion resistance of species-rich plant communities against a tall invader species is not mediated by aboveground competition for light. Rather, belowground processes—and especially belowground root competition—seem to be responsible for invasion resistance. Before we expand on this in greater detail, we will critically evaluate the strengths and weaknesses of the approach we used.

First of all, two major criticisms need to be addressed—namely—(i) is our study a valid test of invasion resistance? and (ii) does our experimental design allow a differentiation between above- and belowground competition, given that only aboveground competition was manipulated?

'Invasion resistance' is a very broad term (Rejmanek 2000) and one needs to be very clear about what part of the invasion

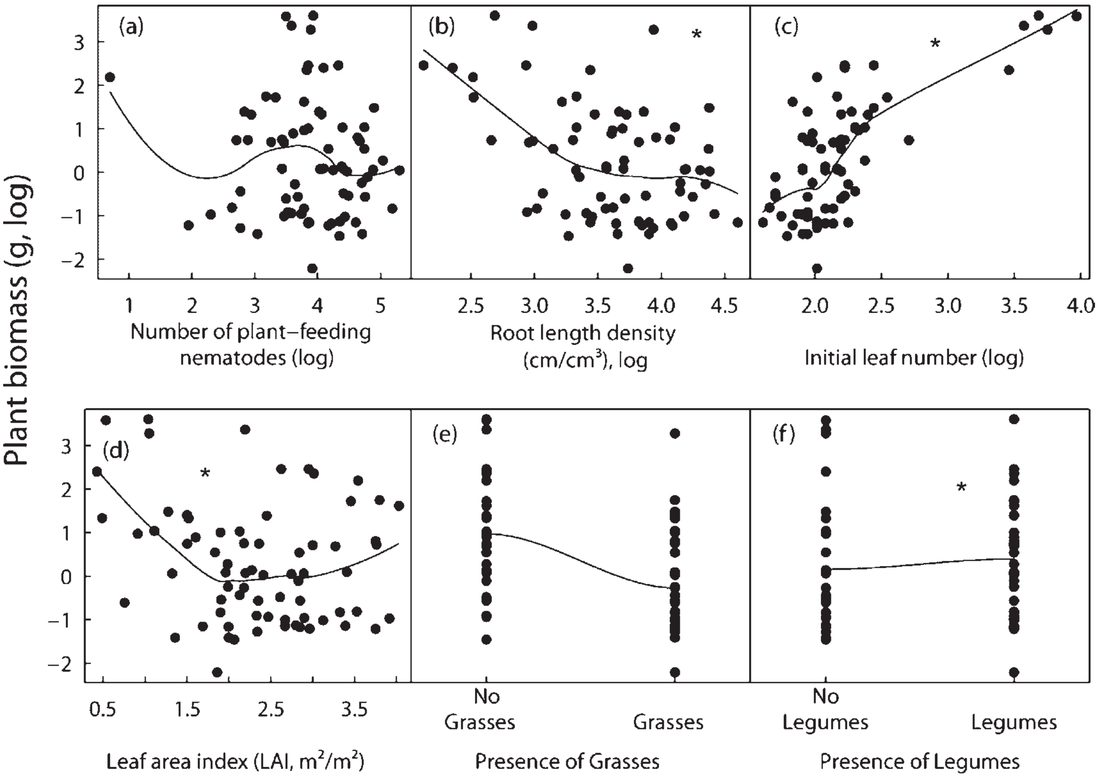

Figure 3: aboveground plant biomass of *Knautia arvensis* transplants in communities as affected by (a) number of plant-feeding nematodes, (b) belowground competition, (c) initial leaf number, (d) LAI, (e) grass presence and (f) legume presence. Variables ln-transformed if not stated otherwise. Solid lines show local regression fits (for illustration); significance in the full covariate model is indicated by asterisks.

process we focused on here (Levine *et al.* 2004). Clearly, the focus was not the dispersal stage nor was the germination stage considered. Our study explicitly only tested invasion resistance 'given that' germination had been successful and a certain initial seedling size had been reached. Hence, in the terminology of Levine *et al.* (2004), we focused on biotic resistance as a 'regulator' of invading populations. This stage is crucial for the further spread of an invading plant population.

While the plant species used in this study was native to the invaded plant community, it was part of the sown community only in 14 of 82 plots (17%). On first principles and as a null model, it seems reasonable to assume that the same mechanisms may allow invasion of native or exotic species' individuals into plant communities (Scherer-Lorenzen *et al.* 2007). Using native species as test invaders is more appropriate to understand community invasion resistance because it avoids possible confounding effects of general and potential specific invasion mechanisms which might occur with exotics (Hierro *et al.* 2005; Mwangi *et al.* 2007). Hence, with the above limitations in mind, we believe that our study allows a valid assessment of community invasion resistance.

The second major criticism, i.e. if our study allows a clear separation of above- and belowground competition, needs to be considered, too. It is clear that our experiment was originally designed to test for the effects of aboveground competition for light. Yet, it turned out that a reduction of aboveground LAI did not change the diversity–invasibility relationship. It is therefore natural to search for new explanations, even if this is done *a posteriori*. We believe that we measured at least the most important belowground variables that might be responsible for the observed decline in *Knautia* performance with increasing plant species richness. Of course, one could always ask for more—but the strong effects of root length density in addition to LAI and interactions with plant species richness show that these belowground processes have sufficient explanatory power to explain the observed species richness effect on *Knautia* performance. Interestingly, root length density did not increase significantly with plant diversity (slope: 3.41 ± 1.92, $t = 1.78$, df = 60, $R^2 = 0.03$, not significant). Hence, the observed effect is an emergent property of the systems studied, and belowground competition acts 'in addition' to plant species richness and aboveground LAI.

In our manipulations, we assumed that the main effect of bending down the neighbors of the transplants was a reduction in aboveground competition rather than affecting other aboveground interactions among plants or between plants and other organisms (e.g. Scherber *et al.* 2006). For example, differential herbivory among transplants with and without

Table 2: sequential ANOVA table for the minimal adequate model with covariates

Term	numDF	denDF	*F* Value	*P* Value
Intercept	1	52	119.36145	<0.0001
Log initial leaf number	1	52	248.57934	<0.0001
LAI	1	52	5.12618	0.0278
Log PFN	1	52	1.82839	0.1822
Log RLD	1	52	15.35572	0.0003
Log PSR	1	52	4.5866	0.0369
FR	1	52	0.14603	0.7039
TH	1	52	1.63156	0.2072
LEG	1	52	18.70211	0.0001
LAI:LEG	1	52	8.17991	0.0061
Log PFN:log RLD	1	52	0.71345	0.4022
Log PFN:TH	1	52	8.36469	0.0056
Log RLD:log PSR	1	52	3.64701	0.0617
Log PSR:FR	1	52	0.42163	0.519
Log PSR:TH	1	52	8.63724	0.0049
TH:LEG	1	52	8.85578	0.0044

F values show tests for each parameter added sequentially to the null model. FR, functional richness; LEG, legume presence; PFN, plant-feeding nematodes; PSR plant species richness; RLD, root length density; TH, tall herb presence.

aboveground competition was unlikely because own observations showed that herbivory on *K. arvensis* in the same communities was very low. Furthermore, there could have been a difference in shoot/root ratio among the bent and intact neighbors, possibly reducing the positive effects on transplants without aboveground neighbors. We think that this again was unlikely because the bent-down neighbors were still green and growing during the full course of the experiment.

Comparison with previous studies

Our results are in line with previous findings indicating that plant diversity can increase (e.g. Hector *et al.* 2001; Kennedy *et al.* 2002; Knops *et al.* 1999; Levine 2000; Naeem *et al.* 2000; Prieur-Richard *et al.* 2002; Spehn *et al.* 2000; Symstad 2000; van Ruijven *et al.* 2003) and presence of grasses further enhance community invasion resistance (Crawley *et al.* 1999; Scherber *et al.* 2006). Presence of legumes, on the other hand, can either promote (Palmer and Maurer 1997; Prieur-Richard *et al.* 2002; Temperton *et al.* 2007) or reduce (Nitschke *et al.* 2010) the growth of individuals added to a community. In our experiment, the non-leguminous test invader *K. arvensis* benefited from the presence of legumes in the plant communities. However, we could not find a significant negative effect of tall herb presence on *K. arvensis* performance, indicating that niche preemption was not a dominant effect in our study. Interestingly, the negative effects of plant diversity on the biomass of our test invader could not be explained by a diversity-related increase in LAI. The transplants did react to aboveground competition by increased plant height and reduced LMA, which can be interpreted as a typical shade response (Huber 1996), although their aboveground biomass was unaffected. This suggests that the effect of plant diversity on the transplants was not through light quantity but possibly through light quality.

Our results agree with previous findings that grasses confer high competitive suppression of invaders (e.g. Crawley *et al.* 1999; Fargione and Tilman 2005; Prieur-Richard *et al.* 2002). This negative effect of grasses may be caused by competition with grass roots: plots with grasses had significantly higher root length density than plots without grasses ($F_{1,69}$ = 41.45, $P < 0.0005$).

One might argue whether our results are general or specific to the plant species used. A comparison with existing transplant studies, with species such as *K. arvensis*, *Trifolium pratense* L., *Plantago lanceolata* L., *Festuca pratensis* L. (Mwangi *et al.* 2007), *Rumex acetosa* (Scherber *et al.* 2006) or *Centaurea jacea* (Nitschke *et al.* 2010), shows that such functional group identity effects have frequently been observed for many different plant species.

The role of belowground competition in invasion resistance

The persistence of negative effects of plant diversity on the performance of established *K. arvensis* transplants even under reduced aboveground competition suggests that belowground competition is an important driver of community invasion resistance. The most likely explanation for this type of invasion resistance is increased belowground resource preemption rather than recruitment limitation as in seed addition studies. Several competition studies with established plants found a predominance of root competition over shoot competition (Cahill 1999; Cahill 2003; Wilson 1988; Wilson and Tilman 1995) and total competition shifts from above- to belowground with decreasing soil fertility (Cahill 1999; Cahill 2002; Casper and Jackson 1997; Wilson and Tilman 1995). Following four consecutive seasons of mowing and removal of plant material without fertilization in our experimental plots, soil resources were most strongly depleted in communities that were more diverse (Oelmann *et al.* 2007). This and the cumulative effect of roots may have intensified the magnitude of belowground competition relative to aboveground competition. In addition, reducing aboveground competition did not reduce the strong negative effect on the performance of *K. arvensis* transplants of the presence of grasses in a community. This suggests that the strong negative effect of grasses was not from aboveground competition; rather, this effect might have been due to their extensive root network that makes them efficient resource users (Craine *et al.* 2002; Fargione *et al.* 2003). This assertion is backed up by a strong and significant negative effect of root length density on (log) leaf nitrogen concentration in *K. arvensis* (Linear mixed-effects model; slope = -0.182 ± 0.03, $t_{75} = -4.8$, $P < 0.0001$). Hence, belowground competition for nitrogen may be one likely explanation for the competitive suppression observed in this study.

In summary, increased aboveground space filling and light interception with increasing diversity alone do not necessarily lead to increased competitiveness as reported before in some diversity–invasion studies (e.g. Fargione *et al.* 2003). Rather, our results suggest that belowground competition, especially from grasses, can promote invasion resistance of species-rich communities.

FUNDING

German Science Foundation (FOR 456–WE 2618/6-1 to W.W.W. and B.S.); Studienstiftung des Deutschen Volkes to C.S.; Swiss National Science Foundation (31–65224.01 to B.S.); Friedrich Schiller University of Jena; Georg-August-University Göttingen; Max Planck Institute for Biogeochemistry, Jena.

ACKNOWLEDGEMENTS

We thank the team that kept the Jena Experiment going, especially Christiane Roscher and Alexandra Weigelt. Christina Fischer, Anja Dassler and Anne Fröhlich helped with field and lab work. Two anonymous reviewers and David Gladbach are thanked for helpful comments on this manuscript.

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Chapter 3

Plant functional identity and herbivore performance

published as:

Specht J, Scherber C, Unsicker S, Köhler G, Weisser WW (2008) Diversity and beyond: plant functional identity determines herbivore performance. Journal of Animal Ecology 77:1047–1055.

Diversity and beyond: plant functional identity determines herbivore performance

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Summary

1. Recent biodiversity studies have addressed various community-level effects of biodiversity change, but the number of studies on specific biotic interactions is still rather limited. An open question in the context of plant–insect–herbivore relationships is how diversity impacts the population ecology of individual species.

2. In the present study, we explored the relationship between plant species diversity and the performance and fitness of a generalist herbivore, the meadow grasshopper *Chorthippus parallelus* Zetterstedt (Orthoptera, Gomphocerinae). A total of 1620 fourth-instar nymphs of this insect were captured and transferred to cages (10 females and 10 males per cage) on 81 experimental grassland communities in plots containing one to 60 plant species within the Jena biodiversity experiment.

3. Median survival of grasshoppers in the experiment was 14·5 days. Survival was independent of plant species richness and number of plant functional groups in the communities, but increased if plant communities contained grasses. Plant species richness and plant functional group richness had no effect on the number of oothecae laid by females or the number of hatchlings in the next generation.

4. Functional group composition of the plant communities affected most fitness measures. Grass presence increased the number of oothecae laid by females from 0·78 ± 0·21 to 3·7 ± 0·41 per female, and the number of hatchlings in the next generation from 4·0 ± 1·3 to 16·6 ± 2·4. Certain combinations of plant functional groups increased grasshopper survival.

5. The findings indicate that the fitness of *C. parallelus* is influenced more by plant functional group identity than by plant species richness. In the absence of grasses, grasshoppers performed better if more than just one functional group of plants was present. We call this a 'rescue effect' of plant functional group richness.

Key-words: dietary mixing, generalist herbivore, grasshopper, plant diversity, plant functional identity, The Jena Experiment.

Introduction

While a number of recent studies suggest strong and consistent effects of biodiversity on ecosystem processes and trophic interactions (e.g. reviewed in Balvanera *et al.* 2006), the underlying mechanisms are often ambiguous. Although some of these studies have addressed various community-level effects of biodiversity change, the number of investigations on specific interactions is still limited (Balvanera *et al.* 2006; Scherber *et al.* 2006). So far the effects of plant species extinctions on insect herbivores have mainly been restricted to observational studies, where the abundance of a whole insect community has been measured (Siemann 1998; Haddad *et al.* 2001; Brose 2003), rather than investigation of species-specific herbivore abundances (Haddad *et al.* 2001). Studies focusing on the response of single species to changes in plant diversity are rare (Tahvanainen & Root 1972; Bach 1980; Risch 1981) and often restricted to specialist insect herbivores. For specialists, there are clear predictions concerning how the abundance should decrease with increasing plant diversity (Tahvanainen & Root 1972; Otway, Hector & Lawton 2005).

In contrast, there is only limited knowledge on the effects of resource abundance and diversity on generalist insect

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herbivores. While the 'dietary mixing' hypothesis (Pennings, Nadeau & Paul 1993; Bernays *et al.* 1994) predicts a better performance of generalists on a mixed vs. single-food diet, experiments to test this hypothesis have mostly been restricted to laboratory systems. In species-poor communities, a generalist consumer will be forced to feed on fewer food plants and hence its performance may be negatively affected by plant species loss from the ecosystem. Species-rich communities may, on the other hand, allow a generalist to feed on a broader range of food plants, and this in turn may positively influence its growth, survival and reproduction. There is considerable evidence in the literature that the beneficial effect of dietary mixing in generalist herbivores is mediated both by nutrient complementation and toxin dilution effects (nutrient complementation: Pulliam 1975; Westoby 1978; Rapport 1980; Bernays *et al.* 1994; Simpson & Raubenheimer 2000; Berner *et al.* 2005; toxin dilution: Freeland & Janzen 1974; Bernays & Minkenberg 1997).

Although coextinctions of specialists and their preferred resources have often been reported (e.g. Biesmeijer *et al.* 2006), few studies have addressed what may happen to generalists. There is only one field study that concerns these and related questions within a biodiversity–ecosystem functioning context (Pfisterer, Diemer & Schmid 2003).

Given the lack of experimental evidence for the effects of biodiversity loss on the fitness of generalist herbivores, we chose the meadow grasshopper *Chorthippus parallelus* (Zetterstedt 1821) (Orthoptera: Gomphocerinae) as a model herbivore to study growth, survival and reproduction within grassland communities ranging from one to 60 plant species over a 3-month period during 2004. In addition to plant species richness, we purposely manipulated the number and identity of plant functional groups to assess the consequences of entire plant functional groups lost from an ecosystem (Hooper & Vitousek 1997; Symstad *et al.* 1998; Hector *et al.* 1999; Haddad *et al.* 2001).

This is, we believe, the first study that attempts to tease apart pure species richness effects from functional group identity effects on insect herbivore performance. In order to do this, we have asked three basic questions for which we have tried to find empirical supporting evidence – or not, as the case may be: (i) How does plant species diversity affect the fitness of *C. parallelus*? (ii) Are certain plant functional groups affecting the performance of this grasshopper species differently? (iii) How does plant species identity affect the fitness of *C. parallelus*?

Materials and methods

STUDY ORGANISM

Grasshoppers play an important role as primary consumers in grasslands and in agricultural systems (Ingrisch & Köhler 1998). As their performance as a response to balanced and unbalanced food has been studied in considerable detail (Bernays & Chapman 1970a,b; Bernays *et al.* 1994; Simpson & Raubenheimer 2000; Raubenheimer & Simpson 2003), grasshoppers are thus most suitable organisms to examine the effects of plant species loss on herbivore performance. *Chorthippus parallelus* is a generalist species that is both widespread and abundant in European grasslands (Ingrisch & Köhler 1998). It has been reported to feed on plants within 38 genera of vascular plants, 23 of them belong to the Gramineae and four to the Juncaceae and the Cyperaceae (e.g. Gangwere 1961; Bernays & Chapman 1970a; Ingrisch & Köhler 1998; Franzke 2006; Oswald 2006; Unsicker 2006). The remaining 11 food plant genera belong to another 10 plant families (Ingrisch & Köhler 1998). *C. parallelus* hibernates as oothecae containing on average six to eight eggs (Ingrisch & Köhler 1998). The first nymphs hatch in spring, four juvenile stages being distinguishable, while adults appear from July to November. The adult females oviposit close to tussocks in the top soil layer above or inside the rootstock. *C. parallelus* is the most abundant grasshopper species in the vicinity of the sites investigated in this study (Pratsch 2004).

EXPERIMENTAL DESIGN

The Jena Experiment

The Jena Experiment was established in 2001, on 10 ha of former arable land. The site is located in the floodplain of the River Saale near Jena, Germany (altitude 130 m, 50°57′ N 11°37′ E). The species pool in the experimental grassland site consists of 60 herbaceous plants that also occur naturally in hay meadows surrounding the study site (*Arrhenatherion* grasslands; for details see Roscher *et al.* 2004). Plant species were assigned to the four functional groups grasses, small herbs, tall herbs and legumes (Roscher *et al.* 2004). The definition of these functional groups is based on life-history and morphological characteristics. Eighty-two experimental grassland plots each with a size of 20 × 20 m were sown with one, two, four, eight, 16 or all 60 plant species, and contained one, two, three or four functional groups. The plant species compositions were chosen at random to ensure that all possible combinations of species richness and number of functional groups occurred (Roscher *et al.* 2004). To account for heterogeneity in abiotic site conditions such as sand content in the soil with increasing distance from the River Saale, all plots were grouped into four blocks each comprising about 20 plots. In order to maintain the plant composition in the Jena Experiment, the plots were weeded and mown twice a year.

Caging experiment

In July 2004 two metal cages with a 10-cm border at the bottom, 1 m in height and of 0·5 m diameter, and wrapped with aluminium mesh (3 × 2 mm mesh size) that was coiled up at the top, were installed on each of 81 20 × 20-m plots. The plot with a monoculture of daisy *Bellis perennis* L. was excluded because of insufficient cover of the target species. A 2 × 4-m subplot within each 20 × 20-m plot was selected randomly to install the grasshopper cages. One of the two cages per subplot was randomly selected to serve as a grasshopper-containing cage, while the other served as a control (without grasshoppers).

Shortly before the start of the experiment, both cages per subplot were cleared of terrestrial invertebrates using a vacuum cleaner (1400-W vacuum cleaner, Kärcher A2801 plus, Alfred Kärcher GmbH & Co. KG, Winnenden, Germany).

For oviposition measurements, an extra cage was installed per plot. In blocks four and three, commercial colanders with a diameter of 22 cm, height of 15 cm and 2 mm mesh size were used. Because of delivery difficulties of the manufacturer, the oviposition cages in blocks 1 and 2 were slightly modified. These cages, 30 cm in height, were made from aluminium mesh fixed using adhesive to a plastic frame of the same diameter as the colanders. Both types of oviposition cage were located between the two larger cages and attached to the ground using long nails. We accounted for potential effects of these different cage types on any of the grasshopper fitness measures, by including them as blocking effects in all statistical analyses.

Grasshopper sampling

Between 6 and 15 July 2004, about 2000 fourth-instar *C. parallelus* nymphs were sampled using sweep-nets on meadows in the floodplain of the Saale adjacent to the study site. After the nymphs had been separated according to sex, initial body mass was determined by weighing five individuals per sex at a time in one jar using an analytical balance (Sac 51, Scaltec Instruments GmbH, Heiligenstadt, Germany). Grasshoppers were transferred to the cages in groups of 10 individuals (five females and five males) on two consecutive days so that each cage received 10 females and 10 males altogether. In total, 1620 grasshoppers were introduced to the plots.

FITNESS MEASUREMENTS

Survival

As an estimate of survival, the number of grasshoppers present in each cage was noted every second day. Survival measurements started on 16 July and ended on 1 September. After the final moult leading to maturity (= maturity moult), it was possible to visually determine the sex of the grasshoppers and thus by this time exact sex ratios in the cages could be determined. For each time interval, the survival data were corrected in the following way: if the number of grasshoppers on a given census day was higher than the number of individuals in the previous census, it was assumed that individuals had been overlooked previously and the number of grasshoppers at that census was adjusted accordingly. Median survival time of grasshoppers was calculated from a Kaplan–Meier survivorship curve fitted separately for each grasshopper cage. Survival data from grasshoppers in both cage types (grasshopper and oviposition cages) was pooled for further analysis.

Body mass

In addition to weight measurements at the beginning of the experiment, the body weight of adult grasshoppers was determined once in July and twice during August. For adult body weight measurements, three adult females and three adult males were randomly selected from the grasshopper cages. In some cages, where there was high grasshopper mortality, fewer than three adult individuals per sex survived and thus only these individuals could be weighed. Weight gain was calculated with the following formula, using the average of the two adult measurements:

$$\text{Weight gain} = \ln(\text{adult mass}) - \ln(\text{initial mass}).$$

Fecundity

C. parallelus females deposited into the top soil layer. As it was not possible to extract the top soil layer of the large grasshopper cages without causing extensive damage to the vegetation in the experimental plot, smaller oviposition cages were installed to measure fecundity (see 'Caging experiment'). Two females and one male from the herbivory cage were transferred to these smaller cages after the maturity moult. A plastic cup (10 cm diameter) filled with a mixture of sand and soil (1 : 1) was provided for oviposition in each oviposition cage. At the end of the experiment, these cups were removed and the substrate inside sieved to extract the oothecae. Additionally, the top soil underneath the oviposition cages was dug out by taking soil cores of 22 cm diameter and 10 cm depth. In the laboratory, oothecae were extracted from the soil cores by carefully washing soil off the root balls, and collecting all particles the size of the oothecae in a sieve underneath the water jet. After washing, roots were torn apart to find further egg pods. The number of oothecae from the oviposition pot and the top soil were added together to obtain the number of oothecae per plot as a measure of grasshopper fecundity.

After counting, oothecae were buried into a mixture of sand and soil (1 : 1) and transferred to a refrigerator (*c.* 5 °C) to initiate diapause. After 7 months, oothecae were removed from the refrigerator and separated in plastic cups (again filled with a mixture of sand and soil) for later measurement of hatching per individual ootheca. Cups, which were covered with fly screen to prevent the hatching grasshoppers from escaping, were checked daily for hatchlings. For data analysis, both the total number of hatched grasshoppers from each oviposition cage (total hatchlings), as well as the mean number of hatchlings per ootheca were used.

PLANT PARAMETERS

The number of plant species in all cages was determined before grasshoppers were released therein. Grass and legume cover was estimated visually prior to the start of the experiment using an integer cover scale. We used realized species richness and grass and legume cover as covariates in all analyses of grasshopper fitness parameters. A more detailed description of grasshopper effects on the vegetation is given elsewhere (Scherber 2006).

STATISTICAL ANALYSIS

The data were analysed using SPSS for Windows 13·0. Regression analyses, analyses of variance (ANOVA) and correlations were performed. Assumptions of normality and heteroscedasticity were tested. There were two basic statistical models that were used for all analyses.

First, a standard Analysis of Covariance model (ANCOVA) was used to test for effects of the design variables. This model had the following sequence of terms: grass cover (covariate), block (random factor), number of plant species, number of functional groups, presence of grasses and presence of legumes, grass: legume interaction term.

Second, additional models were used to test for effects of plant functional group composition. These models only contained block (random factor) and functional group composition as a fixed effect. Functional group composition was a factor with six levels: G, GLH, GH, L, LH, H, where mixtures were characterized by containing G = grasses, L = legumes or H = large or small herbs. Thus, in these additional models, we did not differentiate between large and small herbs to facilitate interpretations and comparisons with previous studies.

For the analysis of body mass data, initial grasshopper weight was included as a covariate in the basic ANCOVA model. A reduced ANCOVA model was constructed to test the effects of functional group composition, as described above.

Count data were analysed using generalized linear models (GLIM) with quasi-Poisson errors implemented in R 2·4·0 (R Development Core Team 2005), with terms added sequentially to the null model, and significance for these models was assessed using *F*-tests.

Results

PLANT SPECIES RICHNESS IN THE CAGE

The realized plant species richness in the cages was closely correlated with the number of sown plant species on the entire plot ($n = 81$; d.f. = 1; $P < 0·001$, $r = 0·93$). For this reason, sown plant species rather than realized species richness was used for all further analyses.

GRASSHOPPER SURVIVAL

One hundred and ninety-three individuals of the 1620 grasshoppers introduced into the cages at the beginning of the experiment survived until the experiment was terminated after 50 (blocks 1 and 2) and 56 days (blocks 3 and 4). The median survival of all grasshoppers was 14·5 days.

The survival of the grasshoppers was not influenced by the number of plant species in the plot, despite a trend to longer survival at higher levels of species richness ($F_{5,58} = 2·3$; $P = 0·051$; Fig. 1a). Survival tended to be higher in plots with three and four functional groups than in those with only one or two functional groups, but the relationship was not significant ($F_{3,58} = 2·6$; $P = 0·057$; Fig. 1b). The interaction between number of plant species and number of functional groups had no significant effect on grasshopper survival ($F_{7,58} = 0·703$; $P = 0·669$).

The most striking result was the overall positive influence of the grass functional group on grasshopper survival. Individuals of *C. parallelus* caged on plots without grasses survived for 7·5 days (median), whereas the median for survival of those on plots containing grasses was 18 days (separate model without grass cover as covariate: $F_{1,58} = 39·33$; d.f. = 1; $P < 0·001$). The higher the grass cover in the cages at the beginning of the experiment (July 2004), the higher the survival of *C. parallelus* ($F_{1,41} = 46·9$; $P < 0·001$). The presence of legumes did not affect survival ($F_{1,58} = 1·5$; $P = 0·216$) while the interaction between the presence of grasses and legumes was not significant ($F_{1,58} = 1·9$; $P = 0·166$).

Although grasshopper survival was highest in cages containing only grasses (29 days), the functional composition of grassland mixtures had a significant influence on grasshopper survival ($F_{5,72} = 15·741$; $P < 0·001$; Fig. 2a). There were high rates of survival of *C. parallelus* in all plant mixtures containing

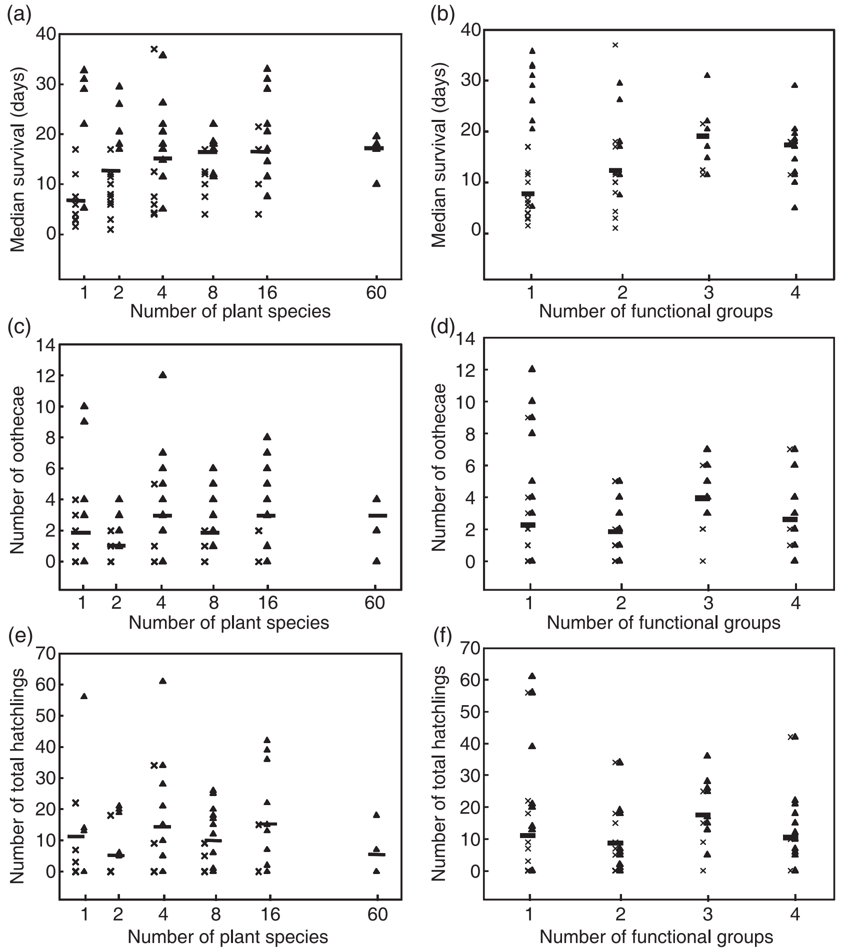

Fig. 1. The effects of plant species richness (1a, 1c, 1e) and the number of plant functional groups (1b, 1d, 1f) on various measures of grasshopper fitness. Black triangles: plots with grasses, Crosses: plots without grasses. (a, b) Grasshopper survival in days. Horizontal bars represent median survival. (e, d) Number of oothecae per grasshopper female. Horizontal bar represents the mean numbers. (e, f) Total number of hatchlings per female. Horizontal bars represents the mean number of total hatchlings per plot.

grasses. Survival was poor in plots containing only herbs or legumes (see bars L and GLH, LH in Fig. 2a). In the absence of grasses, the presence of two functional groups, namely legumes and forbs, increased survival of grasshoppers, compared with only one functional group present (see bar LH in Fig. 2a).

The relationship between the number of plant species and grasshopper survival remained nonsignificant ($F_{5,23}$ = 0·284; P = 0·917, Fig. 1a) when only plots with grass species were considered.

Owing to the staggered beginning of the experiment, grasshopper survival showed significant differences between the four blocks (ANOVA: $F_{3,58}$ = 5·7; P = 0·002). Grasshoppers survived between 8·7 days (block 1) and 19·5 days (block 3) on average.

GRASSHOPPER BODY MASS

The initial body mass of female and male grasshopper nymphs in the experiment differed between the four blocks due to the staggered beginning of the experiment. Males introduced into blocks 3 and 4 weighed 0·065 ± 0·01 g, significantly more than those caged in block 1 and 2 with a mass of 0·05 ± 0·01 g (males: $F_{3,58}$ = 53·78; P < 0·001). The same was true for females that had body mass differences of 0·02 g on average between the blocks (females: $F_{3,58}$ = 39·102, d.f. = 3; P < 0·001). This significant difference in initial body mass found between the blocks made it necessary to use initial body mass as a covariate factor in the ANOVA regarding body mass.

Approximately 10–14 days after caging, grasshoppers went through maturity moult and were weighed again. Body mass in adult grasshoppers could be determined in 497 individuals (239 males and 258 females) coming from 58 of 81 cages. At this time, there was no remaining block effect (males: $F_{3,32}$ = 2·232; P = 0·102; females: $F_{3,35}$ = 1·942; P = 0·43). Both females and males had substantially gained biomass by the time of maturity, and females weighed significantly more (0·18 g ± 0·01 g) than males (0·09 g ± 0·01 g) (paired *t*-test: d.f. = 47; P < 0·001).

There was no effect of plant species richness on weight gain in both sexes of *C. parallelus* (males: $F_{5,32}$ = 0·547; P = 0·739; females: $F_{5,35}$ = 0·913; P = 0·484). Functional group richness also had no effect on weight gain in females or males (males: $F_{3,32}$ = 1·9; P = 0·134; females: $F_{3,35}$ = 0·233; P = 0·873). The interaction between number of plant species and number of functional groups had no significant effect on grasshopper weight gain (males: $F_{7,32}$ = 0·946; P = 0·486; females: $F_{7,35}$ = 0·286; P = 0·955). Similarly, neither the presence of grasses (males: $F_{1,32}$ = 0·284; P = 0·598; females: $F_{1,35}$ = 0·93; P = 0·762) nor the initial percentage of grass cover (males: $F_{1,33}$ = 1·277; P = 0·275, females: $F_{1,35}$ = 1·6; P = 0·23) or the presence of legumes (males: $F_{1,32}$ = 0·001; P = 0·973; females: $F_{1,35}$ = 3·227; P = 0·081) affected grasshopper weight gain. The interaction between presence of grasses and legumes was also not significant (males: $F_{1,32}$ = 2·01; P = 0·159; females: $F_{1,35}$ = 0·143; P = 0·708). Finally grasshopper weight gain was also not influenced by functional group identity and

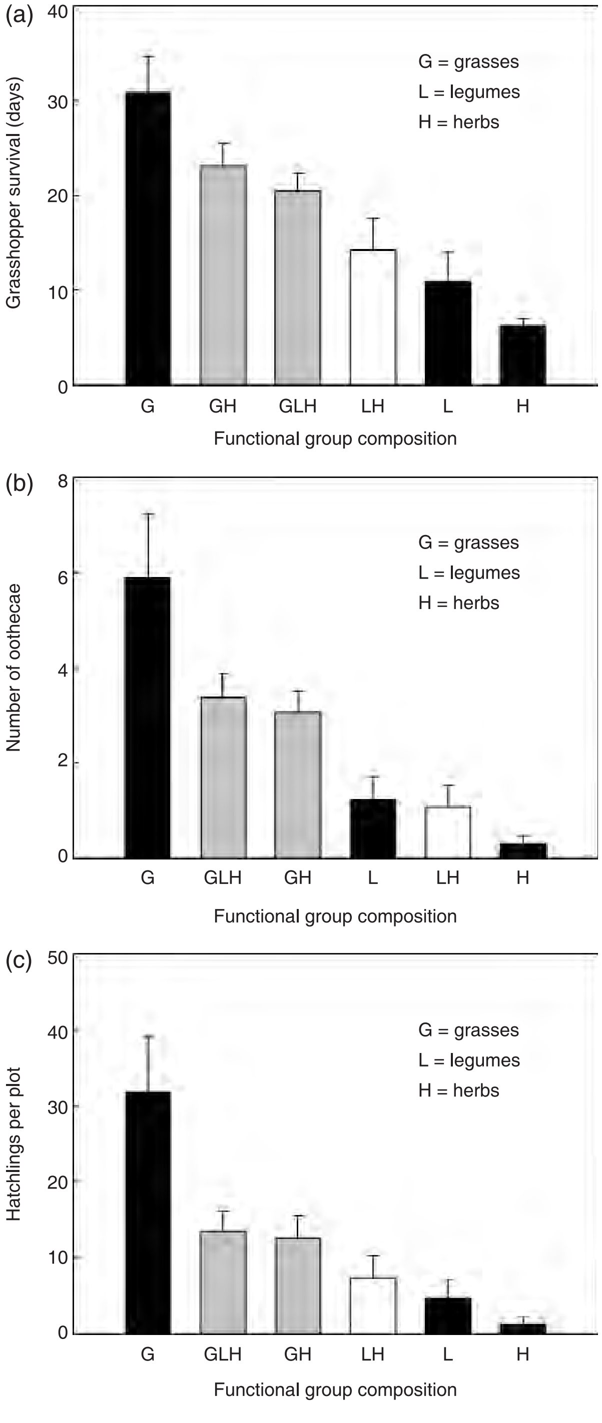

Fig. 2. (a) Relationship between the functional group compositions and the survival of *C. parallelus* (black bars = only one functional group alone, grey bars = mixtures with grasses, white bar = mixtures without grasses) (N: G = 9, GH = 15, GLH = 19, LH = 12, L = 9, H = 17). (b) Relationship between the functional group compositions and the number of oothecae (black bars = only one functional group alone, grey bars = mixtures with grasses, white bar = mixtures without grasses) (N: G = 9, GH = 15, GLH = 19, LH = 12, L = 9, H = 17). (c) Relationship between the functional group compositions and the number of hatchlings per plot (black bars = only one functional group alone, grey bars = mixtures with grasses,white bar = mixtures without grasses) (N: G = 9, GH = 15, GLH = 19, LH = 12, L = 9, H =17)

functional group composition (males: $F_{5,32} = 0{\cdot}735$; $P = 0{\cdot}601$; females: $F_{5,35} = 1{\cdot}022$; $P = 0{\cdot}415$). In terms of their effect on female weight gain, grasses came only fourth in functional group ranking, in contrast to their overall prominent effect on survival. When plots with grasses only were considered, the relation between number of species and grasshopper weight gain remained nonsignificant (males: $F_{5,20} = 0{\cdot}1$; $P = 0{\cdot}973$; females: $F_{5,17} = 1{\cdot}6$; $P = 0{\cdot}208$).

GRASSHOPPER FECUNDITY (NUMBER OF OOTHECAE/ NUMBER OF HATCHLINGS)

In total, 192 egg pods were laid in the oviposition cages on 53 plots. In many plots, no egg pods were laid and thus the data did not follow a normal distribution. A standard quasi-Poisson model for overdispersed count data (McCullagh & Nelder 1989) was sufficient to include these zero observations, as zero inflation was not severe.

A maximum of up to 12 oothecae was laid per female grasshopper in the cages, with nymphs hatching from oothecae in 47 plots. The number of hatched nymphs ranged from 1 to 61 nymphs per plot and the number of hatchlings per ootheca between 1 and 9 nymphs, with an average of 4·4 ± 0·35.

The number of plant species did not influence the number of oothecae (GLIM, $F_{5,71} = 2{\cdot}1$, $P = 0{\cdot}07$; Fig. 1c). Similarly, the total number of hatchlings was not influenced by the number of plant species present in the plots (GLIM, $F_{5,71} = 1{\cdot}1591$, $P = 0{\cdot}34$; Fig. 1e).

The number of functional groups did not affect the number of oothecae (GLIM, $F_{3,68} = 1{\cdot}9$, $P = 0{\cdot}13$; Fig. 1d). For cages where at least one ootheca had been laid, the relationship was marginally nonsignificant (GLIM, $F_{3,32} = 14{\cdot}9$, $P = 0{\cdot}058$). Likewise, the relationship between total hatchlings and the number of functional groups was not significant (GLIM, $F_{3,68} = 0{\cdot}7$, $P = 0{\cdot}52$; Fig. 1f) and also the interaction between number of plant species and number of functional groups had no significant effect on number of oothecae (GLIM, $F_{7,59} = 0{\cdot}6$, $P = 0{\cdot}72$) or on total number of hatchlings (GLIM, $F_{7,59} = 0{\cdot}8$, $P = 0{\cdot}51$).

The presence of grasses increased the number of oothecae (GLIM, $F_{1,68} = 32{\cdot}8$, $P < 0{\cdot}001$): the mean number of oothecae in cages without grasses was 0·78 ± 0·21, while cages with grasses had 3·7 ± 0·41. On average, only 4·0 ± 1·3 grasshoppers hatched in cages where grasses were absent, compared with 16·6 ± 2·4 when grasses were present (GLIM, $F_{1,68} = 15{\cdot}3$, $P < 0{\cdot}001$). With increasing initial cover of grasses, the numbers of *C. parallelus* oothecae significantly increased (regression with square-root transformed number of oothecae: $F = 25{\cdot}5$; $P < 0{\cdot}001$). The total number of hatchlings also increased significantly with increasing grass cover (regression: $F = 34{\cdot}1$; d.f. = 1; $P < 0{\cdot}001$). The presence of legumes did not affect number of oothecae (GLIM, $F_{1,66} = 1{\cdot}6$, $P = 0{\cdot}2$) nor the total number of hatchlings (GLIM, $F_{1,66} = 0{\cdot}3$, $P = 0{\cdot}54$). Similarly, the interaction between presence of grasses and legumes had no effect (GLIM number of oothecae, $F_{1,58} = 2{\cdot}7$, $P = 0{\cdot}1$; GLIM total number of hatchlings, $F_{1,58} = 2{\cdot}5$, $P = 0{\cdot}11$).

The mean number of oothecae (GLIM $F_{5,75} = 13{\cdot}3$; $P < 0{\cdot}001$; Fig. 2b) and the total number of hatchlings (GLIM $F_{5,75} = 8{\cdot}5$; $P < 0{\cdot}001$; Fig. 2c) were significantly affected by functional group composition, while the number of oothecae was highest in plots containing only grasses (see G bar in Fig. 2b). Plant mixtures containing grasses (GLH, GH Fig. 2b) showed on average fewer oothecae compared with cages containing only grasses, but more than cages without grasses at all (L, LH, H; Fig. 2b). Exactly the same pattern was found for the total number of hatchlings (Fig. 2c).The total number of hatchlings decreased on plots without grasses (L, H, LH, Fig. 2c), but, if the grasshoppers could mix legumes and herbs in their diet, their fitness was seen to increase (LH; Fig. 2c).

Assuming that a grasshopper population of *C. parallelus* will be sustained when there are at least two hatchlings per cage present, populations would persist in the following combinations of functional groups: G (116 hatchlings, averaged over all plots with only grasses), GH (38 hatchlings), GLH (33 hatchlings), L (15 hatchlings) and LH (24 hatchlings).

The relationship between the number of plant species and the number of grasshopper oothecae as well as total number of hatchlings was nonsignificant (GLIM number of oothecae, $F_{5,35} = 0{\cdot}8$, $P = 7{\cdot}4$; GLIM total number of hatchlings, $F_{5,35} = 1{\cdot}1$, $P = 0{\cdot}37$) when only plots with at least one grass species are considered. Finally, the number of oothecae differed between blocks (GLIM $F_{3,77} = 1{\cdot}1$, $P = 0{\cdot}37$) and therefore, the total number of hatchlings also showed a significant block effect (GLIM $F_{3,77} = 3{\cdot}2$, $P = 0{\cdot}02$).

Discussion

The results from this experiment clearly show that, contrary to expectation, the performance of a generalist insect herbivore is independent of the number of plant species present in the system. Of course, it is debatable what degree of polyphagy is needed to detect species richness effects. However, we have shown that *C. parallelus* can survive and reproduce even in plant communities that do not contain the preferred host plant functional group grass at all. This reveals that at least for the response variables measured in this study, it should have been possible to detect plant diversity effects. Additional observations on grasshopper feeding damage to all plant species present in the cages showed that grasshoppers indeed consumed herbs and legumes, but the quantities eaten were rather low.

Thus, from a theoretical point of view, a clear species richness effect on grasshopper survival, body mass and fecundity may have been expected. Nevertheless in our study, other variables proved much more important. Indeed, the design used in this experiment allows such a statement. This is because plant species richness, plant functional group richness and plant functional group identity were manipulated separately from one another as far as possible.

It can therefore be stated with some confidence that plant functional group identity was the most important parameter of those investigated for grasshopper survival, body mass and fecundity in this experiment. The presence of grasses had an overall positive influence on grasshopper performance. For grasshopper survival, not only was the presence of grasses important but also the number of plant functional groups present in the food plant community.

In the absence of grasses, combinations of particular plant functional groups (e.g. legumes and herbs) increased survival and fecundity compared with treatments with only one of these functional groups, which can be seen as a synergistic effect of the functional groups with regard to grasshopper fitness.

EFFECTS OF PLANT SPECIES RICHNESS

The effect of plant species richness on grasshopper fitness parameters was not significant, even though this was only marginally nonsignificant for some fitness parameters. Similar to the effects shown for the grasshopper *Parapleurus alliaceus* (Germar 1817) (Pfisterer *et al.* 2003), survival of *C. parallelus* in our study was not influenced by the number of species in the plant community. In our experiment, fecundity, measured both as the number of oothecae laid by females and the total number of hatchlings, was also independent of plant species richness.

EFFECTS OF FUNCTIONAL GROUP RICHNESS

By observing the effect of functional group richness, only survival of the grasshoppers increased with increasing number of plant functional groups present in the plant communities. Fecundity, however, was independent of functional group richness. One possible explanation for the increased survival of grasshoppers in cages with three and four functional groups compared with one or two (Fig. 1b) is that with an increasing number of functional groups, the likelihood that grasses were present increased. Figure 1(b) shows that cages in plots with three and four functional groups where survival was high were those where mixtures contained grasses. Another indication for this is the positive effect of initial grass cover on survival (see below).

EFFECTS OF GRASSES AND OTHER PARTICULAR FUNCTIONAL GROUPS

While, as mentioned earlier, grasshoppers feed mainly on grasses, legumes and to a lesser extend other forbs are also important components of their diet (Bernays & Chapman 1970a; Ingrisch & Köhler 1998; Gardiner & Hill 2004; Unsicker *et al.* 2006). In our experiments, the insects survived much longer when grasses were part of the plant community compared with the situation in which they were absent from cages, and their fecundity was also much higher in the presence of grasses.

It was also found that not only was the presence of grasses important for grasshopper life span, but their survival was also positively correlated with initial grass cover. Survival did not depend on herb or legume presence as long as grasses, as superior food plants, were available, which is in principle consistent with the study of Miura & Ohsaki (2004) in which they showed that the fitness of the grasshopper *Parapodisma subastris* (Huang, Chunmei 1983) was not affected when it was fed with two qualitatively inferior plants, as long as the superior food plant was provided. However in our study, although grasses were the preferred food plants of *C. parallelus*, there was high variation in survival and fecundity between grass-containing plots (see black triangles in Fig. 1a,c,e). This was especially true for monocultures. Possible reasons for these differences could be the nutritional quality of food plants (e.g. differences in nitrogen content), the presence of defensive compounds, such as silica (Massey, Ennos & Hartley 2007) or mechanical differences in leaf tissue, such as leaf texture or toughness.

GRASSHOPPERS AND DIET MIXING

Laboratory studies have shown a positive influence of diet mixing for generalist grasshoppers, thereby underlining the importance of nutrient balancing and/or the toxin dilution hypothesis (Bernays & Chapman 1970a; Chapman & Joern 1990; Waldbauer & Friedman 1991; Bernays *et al.* 1994; Gardiner & Hill 2004; Miura & Ohsaki 2004; Simpson *et al.* 2004; Unsicker *et al.* 2006). In our study, *C. parallelus* showed a significantly increased fitness in the presence of grasses, which can be interpreted as a clear preference for grasses. In the absence of grasses, survival and the total number of hatchlings were higher in particular functional group mixtures (e.g. a combination of legumes and herbs) than on plots with either of these functional groups alone. This synergistic effect of the superior functional groups match with findings of Miura & Ohsaki (2004) who detected that dietary mixing is particularly important when only low-quality plants are available. As we have no precise data on the feeding behaviour of *C. parallelus* in our field experiment, we cannot, however, rule out the possibility that the positive effects of plant functional richness observed are mediated by microclimatic or other rather indirect effects.

EVOLUTIONARY IMPLICATIONS

While the results here have shown that *C. parallelus* is a particular type of a generalist, the species has a preference for one functional group but can fall back on alternative foods when and if necessary. Therefore, potentially evolutionary implications of the pattern of diet utilization by *C. parallelus* may be inferred. It is probable that the distinct preference for grasses in contrast to other functional groups is an evolutionary trend towards becoming a grass specialist (hence living up to their common name!). The subfamily Gomphocerinae (slant-faced grasshoppers to which *C. parallelus* belongs) in Europe is believed to be mostly of Angarian origin, where grasshoppers belonging to this subfamily have evolved in tundras, mesophilous grasslands and xerophilic steppes (Uvarov 1929). Their extremely rapid population spread must have taken place as a direct consequence of their ecological adaptation to grassland, i.e.

from herb to grass feeders; indeed, in interglacial periods, they spread with increasing grassland cover all over Europe. According to Bernays (1991), such grass feeding adaptation has possibly evolved independently eight times during the course of their evolution. But as it was also shown in our experiment, the ability to survive and reproduce on inferior food is a stable trait in this species and could serve as an insurance policy against extinction in unpredictable environments. There is ample evidence for the beneficial aspect of diet mixing, to mention only the most two prominent mechanisms, that is: on the one hand, the balancing of nutrients (Pulliam 1975; Westoby 1978; Rapport 1980; Bernays *et al.* 1994, 2005; Simpson & Raubenheimer 2001) plus on the other, the dilution of toxins (Freeland & Janzen 1974; Bernays & Minkenberg 1997). Although the implications are of course speculative, *C. parallelus* may well also mix diets because the relative quality of food types changes over time (e.g. Singer & Bernays 2003) or, because food mixing may minimize exposure to other environmental risks.

IN THE CONTEXT OF PLANT SPECIES LOSS

Theoretical treatments on the effects of decreasing diversity on insect herbivore performance have generally proposed different mechanisms for so-called specialists and generalists. For specialists, Root (1973) suggested that specialists should be expected to be more strongly influenced by the loss of particular food plants than by general plant species loss. In contrast, for generalists, Pfisterer *et al.* (2003) argued that declining plant species richness has a negative influence on the fitness of a generalist herbivore due to a decreased likelihood of dietary mixing. As a consequence, random species loss in grassland vegetation poses a threat to generalist herbivores. Because of this, we hypothesize that the loss of particular plant species is a threat for specialist herbivores, while random loss of plant species is also a threat for generalist herbivores. Such a scenario would lead to shifts in the relative abundances of herbivores from large populations of generalist to large populations of specialist. A number of studies have indeed found higher abundances of specialist insects in less diverse plant communities, although the results are equivocal (Elton 1958; Pimentel 1961; Root 1973; Kareiva 1983; Risch, Andow & Altieri 1983; Strong, Lawton & Southwood 1984; Andow 1991; Haddad *et al.* 2001; Otway *et al.* 2005).

The results from a number of experiments on ecosystem services in the past have strongly suggested that it is not the number of plant species but rather the number of plant functional groups, and moreover the diversity of these groups in a plant community, that explain patterns in response to biodiversity loss (Haddad *et al.* 2001; Hooper & Vitousek 1997; Tilman 1997; Symstad *et al.* 1998; Hector *et al.* 1999). If this is true, it may also be useful for theoretical speculations on the relationship between biodiversity and generalist herbivore abundances to include the effects of plant functional groups.

In conclusion, we have demonstrated that in the present study, the performance of *C. parallelus* is highly dependent on the functional group grasses. Although the species could be considered as a generalist herbivore with a preference for grasses, the effects of particular grass species on fecundity and survival were not that similar. Furthermore, we have shown that the observed grasshopper population was able to survive and reproduce in the presence of food plants from other functional groups, such as legumes and herbs. We call this a 'rescue effect' of plant functional groups. Such functional groups together doubtless have synergistic effects on individual grasshopper fitness in the absence of grasses.

Acknowledgements

We thank Bernhard Schmid and Ernst-Detlef Schulze for help in setting up the Jena experiment, Christiane Roscher and Jens Schumacher for coordinating the field site, and the Institute of Ecology gardeners, many student helpers, including some Ph.D.-students, for assistances in weeding the plots. We also thank Sylvia Creutzburg, Ilka Egerer and Nadine Mitschunas for their help while setting up and running the experiment, Falk Bieling for building the grasshopper cages, Hugh Loxdale and two anonymous reviewers for reading and commenting on the manuscript. The study was supported by the Deutsche Forschungsgemeinschaft (DFG) within the research unit FOR 456.

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Received 13 September 2007; accepted 28 January 2008
Handling Editor: Simon Leather

Chapter 4

Effects of plant diversity on multitrophic interactions

published as:

Scherber C et al. (2010) Bottom-up effects of
plant diversity on multitrophic interactions in a
biodiversity experiment. Nature 468:553-556

Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment

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Biodiversity is rapidly declining[1], and this may negatively affect ecosystem processes[2], including economically important ecosystem services[3]. Previous studies have shown that biodiversity has positive effects on organisms and processes[4] across trophic levels[5]. However, only a few studies have so far incorporated an explicit food-web perspective[6]. In an eight-year biodiversity experiment, we studied an unprecedented range of above- and below-ground organisms and multitrophic interactions. A multitrophic data set originating from a single long-term experiment allows mechanistic insights that would not be gained from meta-analysis of different experiments. Here we show that plant diversity effects dampen with increasing trophic level and degree of omnivory. This was true both for abundance and species richness of organisms. Furthermore, we present comprehensive above-ground/below-ground biodiversity food webs. Both above ground and below ground, herbivores responded more strongly to changes in plant diversity than did carnivores or omnivores. Density and richness of carnivorous taxa was independent of vegetation structure. Below-ground responses to plant diversity were consistently weaker than above-ground responses. Responses to increasing plant diversity were generally positive, but were negative for biological invasion, pathogen infestation and hyperparasitism. Our results suggest that plant diversity has strong bottom-up effects on multitrophic interaction networks, with particularly strong effects on lower trophic levels. Effects on higher trophic levels are indirectly mediated through bottom-up trophic cascades.

The loss of biodiversity from terrestrial ecosystems has been shown to affect ecosystem properties, such as primary productivity[7], nutrient cycling[8] and trophic interactions[2]. In recent biodiversity experiments, focal organism groups (usually plants[7]) were used to establish gradients in species richness, and biodiversity effects were then measured at one or a few trophic levels[5,9]. Traditionally, studies have focused on the effects of horizontal biodiversity loss, that is, loss of species within a single trophic level[10]. Biodiversity loss at a given trophic level has been predicted to affect the abundance, biomass and resource use of that trophic level[5]. However, horizontal species loss may also affect other trophic levels, organism groups and processes, and, hence, vertical species loss and the associated multitrophic structure of ecosystems[10]. For example, declines in plant species richness may cause losses to herbivores, true predators, parasitoids, hyperparasitoids and omnivores, and may also alter mutualistic interactions such as pollination[11] or mycorrhizal association[4]. Overall, there is an increasing awareness that the network nature of ecological systems needs to be incorporated into studies of biodiversity–ecosystem functioning[12].

Recent meta-analyses[4,5] and experiments at individual study sites[13,14] have shown plant diversity effects on a wide range of different groups of organisms, including primary producers, first- and second-order consumers, detritivores, fungal diseases and mycorrhizae. Additional studies have addressed components of the below-ground subsystem and their linkages with above-ground biota[15]. However, interpretation and progress has been clouded by differences in study systems and by a general lack of an overarching theory incorporating both trophic and non-trophic interactions as well as direct and indirect interactions[16,17]. So far, subcomponents of food webs have often been studied in isolation, for example primary producers, the decomposer subsystem[18], soil nematodes[19], soil microbes, plant pathogenic fungi[20], above-ground invertebrates[13], pollinators[21] and so on. Here we present data from one of the most comprehensive biodiversity experiments so far, and show that diversity effects on higher trophic levels are mostly indirect and mediated through bottom-up trophic cascades. We use structural equation modelling approaches to develop comprehensive above-ground/below-ground biodiversity food webs. Finally, we link our results to recent interaction web models and provide explicit parameter estimates that can be used in future modelling exercises.

We experimentally manipulated plant species and functional group richness in 82 sown grassland plots (Methods), and recorded abundances and species richness of all relevant organism groups and biotic interactions between 2002 and 2009 (Supplementary Table 1). All data were analysed on a standardized scale[22] from zero to one and the relationship between plant species richness and the different response variables was modelled using a power function[18] to allow comparisons and extrapolation to other systems (see Supplementary Table 1 and

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Supplementary Fig. 3 for untransformed data). Analyses consisted of three steps. First, every response variable was analysed separately using a common set of linear, saturating and exponential models with untransformed plant species richness as the main explanatory variable. The presence of legumes and grasses and the number of plant functional groups were fitted as additional covariates. Variance heterogeneity was modelled using variance functions. Model selection was based on the Akaike information criterion for small sample sizes (AICc). Then, for parsimony, models were refitted using a power function. This allowed comparisons between the abundance and species richness of herbivores, carnivores and all other functional groups. Finally, multivariate techniques (multivariate linear models and structural equation models) were used to account for non-independence of variables measured on the same field plots.

Plant species richness had highly significant overall effects on the abundances of other organisms ($T_{\mathrm{PB}} = 0.56$ (Pillai–Bartlett trace), approximately F-distributed with $F_{10,37} = 4.741$, $P < 0.001$; Fig. 1a, c), the species richness of other organism groups ($T_{\mathrm{PB}} = 0.788$, approx. $F_{9,38} = 15.69$, $P < 0.001$; Fig. 1b, d) and on trophic interactions ($T_{\mathrm{PB}} = 0.733$, approx. $F_{10,22} = 6.04$, $P < 0.001$; Supplementary Fig. 1; see Supplementary Methods for definitions of interactions). The abundance and species richness of organisms and biotic interactions were affected in broadly similar ways by changes in plant species richness (Fig. 1 and Supplementary Fig. 1).

Model selection using the complete range of linear, saturating and exponential models (Supplementary Tables 2 and 3) showed that 90% of all relationships could be approximated by a power model of the form $y = a + bS^z$ (ref. 18), where the exponent z can take any real value (in particular zero and one as special cases). Only five out of 38 organism groups declined with plant species richness (abundances of hyperparasitoids, fungivorous nematodes and mites, and abundance and species richness of plant invaders; Supplementary Table 4). Responses of the below-ground subsystem were consistently smaller (average power model exponent of 0.11) than above-ground responses (exponent of 0.14).

Although most responses were saturating, closer inspection (Supplementary Table 5a–c) revealed consistent differences between the responses of herbivores, carnivores, omnivores and other trophic groups that are likely to reflect a general pattern (Fig. 2): with increasing trophic distance and for omnivores, species richness effects dampened—as indicated by the magnitude of the exponent of the common power function (Supplementary Table 4). This effect was found both for organism abundances and organism species richness, both above and below ground, and it was further supported by structural equation models (Fig. 3 and Supplementary Tables 6–10). Together, these findings indicate that species richness effects are generally dampened along trophic cascades.

If plant species richness acts on other organisms along trophic cascades, and plant species richness is the only experimentally manipulated variable, then the simplest conceptual model in our case is a bottom-up model of plant species richness effects; that is, plant species richness effects are passed from one trophic level to the next. Several authors have suggested such a 'bottom-up template' perspective for terrestrial food webs[23]. Both decomposers and predators have long

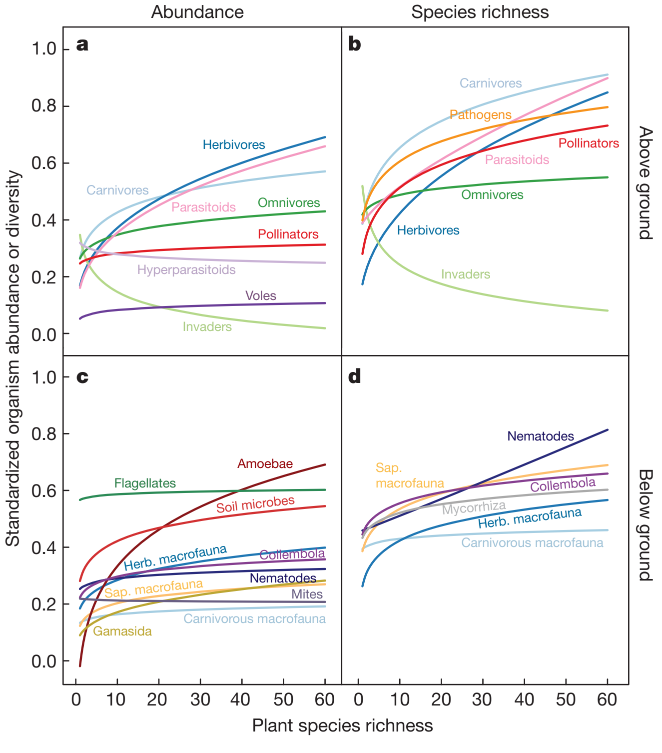

Figure 1 | Effects of plant species richness on above- and below-ground organisms in temperate grassland. **a**, **b**, Abundance (**a**) and species richness (**b**) of above-ground organisms. **c**, **d**, Abundance (**c**) and species richness (**d**) of below-ground organisms. All response variables scaled to [0, 1]. Every curve is fitted using a power function with covariates (Methods). Identical colours in each pair of panels indicate identical groups of organisms. For sample sizes, see Supplementary Table 1. Herb., herbivorous; Sap., saprophagous.

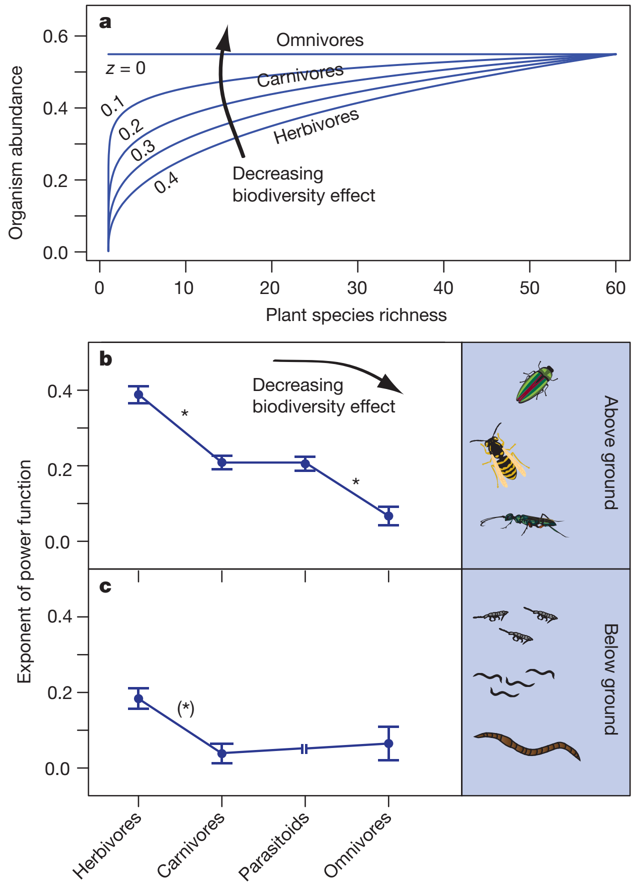

Figure 2 | Dampening of plant species richness effects with increasing trophic level. **a**, Conceptual figure showing how different values of z may influence biodiversity effects (x axis shows example range of 1–60 plant species). **b**, Estimates of z for above-ground herbivores, carnivores, parasitoids and omnivores. **c**, As in **b**, but for below-ground organisms. The y axes in **b** and **c** show estimated exponents of power functions fitted to data scaled to [0, 1]. Significant differences in z values are indicated by asterisks (*$P < 0.05$, $N = 50$ for above-ground organisms; (*)$P = 0.06$, $N = 82$ for below-ground organisms). Estimates are model predictions ± s.e.

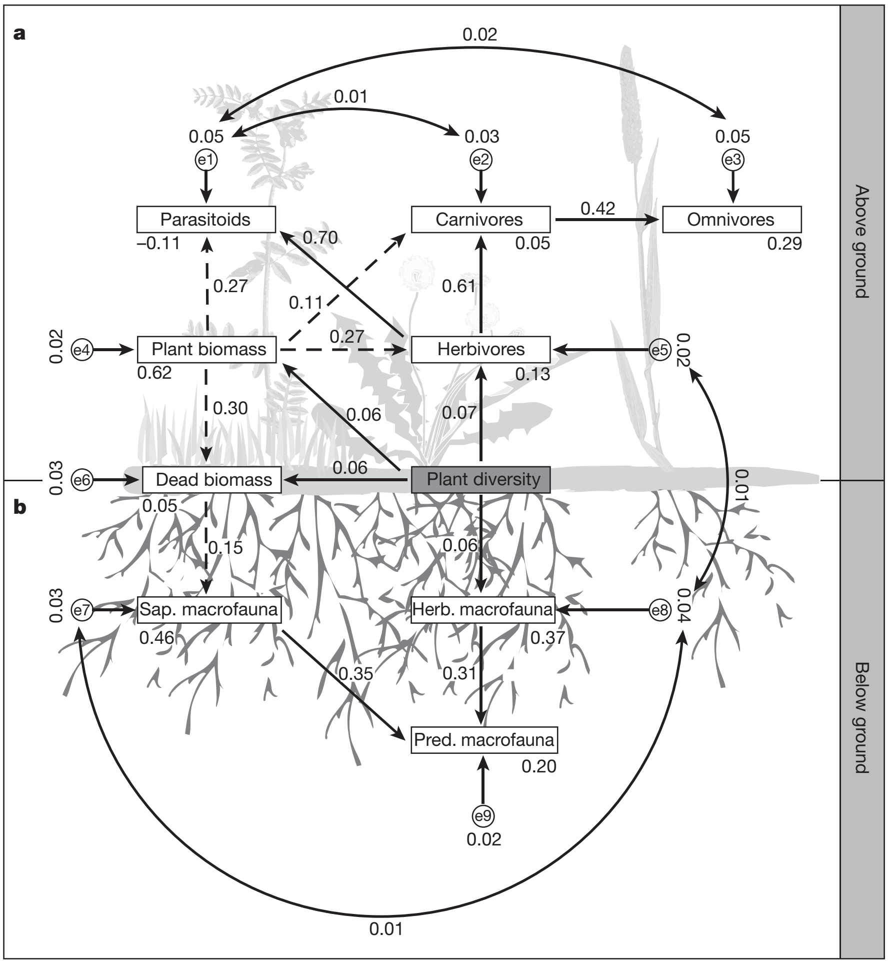

Figure 3 | Food web of above- and below-ground biodiversity. Results of a structural equation model with $N = 50$, $\chi^2 = 32.56$, $P = 0.212$, 27 degrees of freedom and a root mean squared error of approximation of 0.065 (90% confidence interval, [0, 0.135]). A model with top-down control of herbivores by carnivores had $\chi^2 = 32.07$, $P = 0.156$ and 25 degrees of freedom. **a**, Above-ground compartment; **b**, below-ground compartment. Unshaded rectangles represent observed variables (organism abundances). Circles indicate error terms (e1–e9). Solid and dashed arrows connecting boxes show significant and non-significant effects, respectively. Numbers next to arrows and boxes are unstandardized slopes and intercepts, respectively. Double-headed arrows indicate correlations between error terms. Plant species richness was experimentally manipulated and has no error term. For details, see Supplementary Tables 6–10. Herb., herbivorous; Pred., predatory; Sap., saprophagous.

been proposed to be controlled essentially from the bottom up[24]. However, top-down effects may also be expected, in particular if herbivores are not food limited[24].

Using structural equation models, we constructed a minimal adequate above-ground/below-ground biodiversity food web and found that plant species richness had almost exclusively bottom-up effects on higher trophic levels, both above and below ground (Fig. 3 and Supplementary Fig. 2). Three different theoretical constructs were used: a full model with bottom-up paths only; a full model with bottom-up and top-down paths; and all possible sets of reduced models, generated by single deletions of connections from full models (Supplementary Methods). These analyses showed that top-down control of herbivores by predators was not supported by the data. Other models (for example assuming direct effects of plant species richness on predators or omnivores) were rejected; that is, their implied covariance matrix differed significantly from the observed covariance matrix. In addition, we were able to reject hypotheses that assume positive responses only for specific trophic levels[25]. Although plant biomass was indirectly linked to changes in predator or parasitoid abundance, these effects were not significant. This indicates that plant species richness effects are generally not mediated through vegetation density or biomass (Fig. 3a).

In a separate structural equation model for below-ground organisms, the amount of above-ground dead plant biomass entering the below-ground system was generally less important than plant species richness per se (Supplementary Fig. 2). Hence, plant species richness had direct effects mainly on primary consumers, for example herbivorous macrofauna or herbivorous nematodes. In addition, there were strong direct effects of plant species richness on soil microbes and protozoans (Supplementary Fig. 2). It is likely that many of these below-ground responses are mediated either through changes in root production or through root exudates, but not through dead biomass or the amount of litter input (Supplementary Fig. 2). The direct plant species richness effects on microbes and protozoans could be mediated by changes in litter chemistry, litter diversity[18] or root exudates[26].

Although structural equation models can be used to infer causality[27], strong inference requires experimental manipulation of trophic levels in addition to manipulations of plant diversity. We therefore exposed experimental nesting sites for prey (wild bees) and measured parasitism rates (Supplementary Fig. 1) as proxies for top-down control (Supplementary Methods). Parasitism increased with plant species richness, resulting in enhanced potential for biological control in species-rich systems.

One of the most fascinating developments in the theory of biodiversity and ecosystem processes is the inclusion of trophic and non-trophic interactions into generalized Lotka–Volterra models[16]. These models have theoretically predicted a bottom-up control of carnivores by plants, with carnivore biomass indirectly controlled by plant and herbivore biomass, and top-down control of herbivores by carnivores. Structural equation models are a powerful tool for detecting such mutual dependencies, greatly enhancing our understanding of biodiversity effects in multitrophic systems. Overall, our results from a wide variety of organism groups provide strong support for a prominent role of plant species richness (rather than productivity or other covariates) in shaping multitrophic interactions.

Our results present the intriguing possibility that the effects of the species richness of one trophic level on others decrease with trophic distance. This hypothesis merits exploration by means of experimental manipulations of species numbers on other trophic levels. Because even an experiment as large as ours (82 plots) limits how many variables can reasonably be included in a multiple regression or structural equation model, future studies should be designed explicitly with a particular network of trophic interactions in mind. These studies could also be combinations of observational and experimental approaches.

We scaled all response variables to allow us to seek generalizations across different types of organism and trophic levels, but note that unscaled analyses might offer other types of insight. We also note that detailed collection of data at the level of each individual species, although prohibitively time consuming in a broad survey such as ours, is also likely to offer added insight. Our study should therefore be seen as a starting point rather than as an end point for further analyses of other data sets.

We have shown that the consequences of biodiversity loss are consistently negative for most organism groups and interactions, with particularly far-reaching feedback effects on basal trophic levels. Below-ground organisms will be less affected by biodiversity change (or will respond more slowly) than above-ground ones. Changes in plant species richness will affect neighbouring trophic levels and cascade up to higher trophic levels. Exponents of power functions ($y = bS^z$) will decline with trophic level. Our results highlight the importance of a diverse resource base[28] for trophic interactions in terrestrial ecosystems.

METHODS SUMMARY

Experimental design. In a 10-ha former arable field near Jena (Germany), we controlled the number of plant species, functional groups and plant functional identity in 82 plots, each 20 m × 20 m, in a randomized block design[29]. Plots were seeded in May 2002 with 1, 2, 4, 8, 16 or 60 perennial grassland plant species, with 16, 16, 16, 16, 14 and 4 replicates, respectively. Plot compositions were randomly chosen from 60 plant species typical for local *Arrhenatherum* grasslands. Plots were maintained by mowing, weeding and herbicide applications.

Ecosystem variables. Sown and realized plant species richness were highly correlated (2006: Spearman's rank correlation coefficient, 0.995; $t = 91.94$; 80 degrees of freedom; $P < 2.2 \times 10^{-16}$); hence, sown richness was used for analysis. Above-ground invertebrates were collected on $N = 50$ plots using pitfall traps and suction sampling. Below-ground macro- and mesofauna were extracted from Kempson soil cores. Special sampling protocols were used for microorganisms (fungi, bacteria). Decomposition was measured using litter bags. Flower visitation was a count of pollinator visits. Parasitism was measured using a trap-nest technique. Hyperparasitism was measured from aphid mummy counts in 6.25-m^2 replicate plots. Pathogen damage above ground and herbivory were estimated visually. Plant invasion was a count of the numbers of an invader plant species per unit area. Microbial biomass was measured using glucose as an artificial substrate. A full description is available in the Supplementary Methods.

Statistics. Explanatory variables in linear models were block, plant species richness, plant functional group richness, and grass and legume presence. Nonlinear models contained plant species richness, with legume and grass presence and functional richness as covariates. Models were simplified and compared using AICc. To test for differences between slopes, multivariate linear models were constructed, and orthogonal contrasts were used to test linear hypotheses. Structural equation models were fitted to test specific hypotheses on causal relationships.

Received 3 August; accepted 9 September 2010.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank J. M. Tylianakis, P. Batáry, Y. Clough, M. J. Crawley, J. Fox, J. Fründ, D. Gladbach and A. Hector for comments that improved this manuscript. The gardeners, technicians, student helpers and managers of the Jena Experiment are acknowledged for their assistance. This work was supported by the Deutsche Forschungsgemeinschaft (FOR 456).

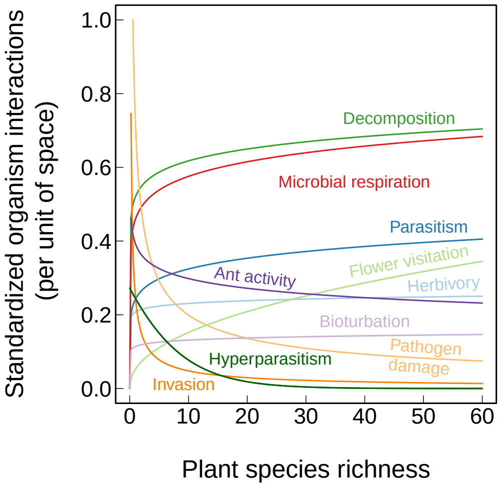
Author Contributions C.S., C.M. and J.S. assembled all data. N.E. contributed data for the below-ground food webs. C.S. performed all analyses and wrote the manuscript. C.S. and T.T. are the principal authors, N.E. to A.W. are listed in descending order of the importance of their contributions, and the remaining authors contributed equally. All authors contributed their own data sets, discussed the analysis and results, and commented on the manuscript text.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to C.S. (christoph.scherber@agr.uni-goettingen.de).

SUPPLEMENTARY INFORMATION

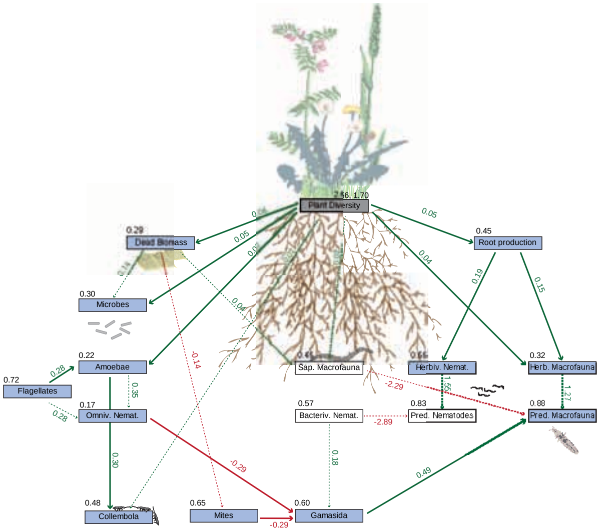
doi:10.1038/nature09492

Supplementary Figures and Legends



Supplementary Figure 1 | Biodiversity effects on organism interactions. Sample size: N=82 except for hyperparasitism (extrapolated from smaller plots).

doi:10.1038/nature09492



Supplementary Figure 2 | Effects of plant species richness on organism abundances in the belowground food web. Sample size: N=82 (missing values replaced by the mean), Chi²= 108.424, df=91 (61 estimated parameters), P=0.103; RMSEA= 0.049, 90%CI=[0;0.08]. The model is the result of a specification search over 50 models that started off with a maximal model (containing all hypothesized relationships), with subsequent deletions of arrows not supported by the data. The model shows unstandardized parameter estimates. The Supplementary Figure shows the minimal adequate model (defined by lowest AIC, BIC and lowest difference between observed and implied covariance matrices). Arrows connecting boxes show structural relationships; parameters next to solid arrows are significant at P≤0.05. Parameter estimates next to dashed arrows are not significant but were retained in the minimal adequate model. Green arrows show significantly positive relationships, red arrows significantly negative ones. Grey arrows and text show error terms. Plant species richness (grey box) was experimentally manipulated. Light blue boxes indicate variables that are linked by at least one solid arrow.

Supplementary Methods

Sampling of aboveground organisms

The population density of **small rodents** was estimated by placing two Ugglan multiple capture live-traps in each plot, with trapping between June and October 2005 (11 trapping sessions). Each trapping session lasted for two trap nights with traps activated in the morning of day 1, and three trap checks in the morning and evening of day 2 and the morning of day 3. Traps were baited with standard rodent feeding pellets and weather-protected by a metal cover. Every individual captured for the first time in a trapping session was etherized and marked individually using transponders (Trovan®). Individuals weighing less than 20 g did not receive a transponder, but were marked using fur-clipping. For every individual capture, we recorded species, body weight, sex, and breeding condition.

The population density and species richness of **aboveground invertebrates** (including herbivores, carnivores, parasitoids, omnivores and pollinators) were measured in N=50 plots (1, 4, 16, 60 plant species) using an electric suction sampler combined with a biocenometer that covered a base area of 0.75 x 0.75 m. In contrast to other approaches (e.g. sweepnetting), the biocenometer method allows **volume-specific sampling** (i.e. exactly the same biovolume is sampled on every plot, similar to taking a soil core). Thus, our data on aboveground and belowground organism abundances/species richness are highly comparable. Every plot received six suction samplings that were randomly placed without replacement. Samples were taken five times per year from May to October (2003 and 2005).

Pollination was estimated as the number of flower visits in subplots per main plot. Flower visits were quantified by counting flower-visiting insects in randomly placed quadrats of 80 x 80 cm per 20x20 m plot. Only N=73 plots containing forbs were observed (i.e. excluding plots containing only wind-pollinated grasses). Flower visitors were counted during six observation periods: 24-25 May 2005, 15-16 June 2005, 18-19 August 2005, 6-9 June 2006, 17-18 June 2006 and 1-5 August 2006. Observations were restricted to sunny days characterized by at least 18°C air temperature, with no or little wind (<2 m s-1), between 09:00 and 17:00 h. Observations within a block were carried out within two days, assuring constant weather conductions within blocks. The sequence of plot observations was independent of plant richness. We observed pollinating insects for 6 minutes per quadrat, plot and observation period, resulting in a total of 36 minutes per plot. Pollinators were identified directly in the field to genus or morphospecies and species level in the field. After each observation period we collected all unknown species for further identification in the laboratory.

In addition, we exposed N=164 standardized trap nests made from reed internodes in the exact centre of every plot (N=82). This allowed us to calculate **parasitism rate** of trap-nesting bees and wasps.

To measure the activity density and species richness of **epigeic invertebrates** (mainly Carabids, Staphylinids and spiders), two **pitfall traps** were placed near the centre of each plot (N=50) and replaced six times per year from May to October (2003 and 2005). All species were identified and their relative population densities (per unit of space) estimated.

Sampling of belowground organisms

Belowground meso- and macrofauna were sampled twice a year in 2004, 2006 and 2008 from N=82 plots. The subplot positions (2 x 4 m) for sampling were drawn at random. Samples were taken using soil cores of a diameter of 5 and 21 cm for extraction of meso- and macrofauna, respectively. Because most soil animals populate the upper soil layers, the upper 10 cm of the soil cores were used for extraction. Soil animals were extracted over a period of 10 days by heat[30].

Earthworm sampling was performed each year in April and October between 2003-2006 on N=46 plots (1, 4 and 16 plant species mixtures) using an electroshocking method[31], employing a combination of four octet devices (DEKA 4000, Deka Gerätebau, Marsberg, Germany). Positions for earthworm sampling were randomized once at the beginning of the experiment (2003). Earthworms were extracted from an area of 1 x 1 m.

Nematodes were sampled in autumn 2005 from 5 soil cores (2 cm in diameter, 5 cm deep) taken at a randomized subplot position (2 x 4 m) per plot (N=82). Samples were homogenized, nematodes extracted by a modified wet extraction technique[32], counted and determined to species level.

For the quantification of **Protozoa (Amoebae and Flagellates)**, five soil samples were taken on a randomized position on N=12 plots using a metal corer (diameter 5 cm, soil depth ~10 cm) in October 2009. The soil was homogenized and stored at 5 °C until usage. Amoebae and Flagellates were counted using a modified most probable number method[33]. Briefly, 5 g fresh weight of soil was suspended in 20 mL sterile Neff's modified amoebae saline (NMAS; see ref.[34]) and gently shaken for 20 min on a vertical shaker. Threefold dilution series with nutrient broth (Merck, Darmstadt, Germany) and NMAS at 1:9 v/v were prepared in 96-well microtiter plates (VWR, Darmstadt, Germany) with four replicates, each. The microtiter plates were incubated at 15 °C in darkness and the wells were inspected for presence of protozoa using an inverted microscope at x 100 and x 200 magnification (Nikon, Eclipse TE 2000-E, Tokyo, Japan) after 3, 6 ,11, 19 and 26 days. Densities of protozoa were calculated according to ref.[35].

Microbial biomass and respiration were measured from five cores (diameter 5 cm, depth 5 cm) taken on randomized subplot positions (2 x 4 m) per plot in May 2002, 2003, 2004, 2006, 2007 and 2008. Soil samples were homogenized from each plot and microbial respiration and microbial biomass were measured using an O_2 microcompensation apparatus[36]. Microbial biomass was determined by the substrate-induced respiration method (SIR; see Ref. [37]).

Diversity of **arbuscular mycorrhizal fungi** was determined by amplification of DNA derived directly from soil on a subset of 23 plots. Plots were selected at random, constrained of equal representation of levels of plant species richness. DNA was extracted under utilization of FastDNA Spin Kit for Soil (MP Biomedicals, Illkirch, France) according to manufacturers' protocol. The internal transcribed spacer (ITS) within the rDNA was amplified by nested PCR (see Ref. [38]) using the primer pair LSU-Glom1/ SSU-Glom1 for the first PCR reaction and ITS4/ ITS5 for the second PCR step, Between the PCR steps, an intermediate AluI digestion was performed to exclude non-mycorrhizal DNA after the first PCR. Cloning, clone fingerprinting by RFLP and sequencing were performed as in Ref. [39]. Sequences were pre-sorted into syngeneic clusters using the contig-tool as implemented in

Sequencher 4.8 (Gene Codes Corp., Ann Arbor, USA).Closest matches to each sequence cluster were determined using the BLASTN sequence similarity search tool in GenBank[40] and used as references. Sequences were pre-aligned in MultAlin[41], alignments were corrected by hand. The phylogenetic relations were inferred based on the Kimura 2-parameter method[42] with the neighbour-joining analysis[43] as implemented in PAUP 4.0b8 (see Ref. [44]). The confidence of branching was assessed using 1000 bootstrap resamplings. Sequences falling into one clade, and showing sequence identities of at least 92% were regarded as distinct taxa. The cutoff value of 92% was chosen according to Ref. [45] in order to reflect the natural sequence diversity found within and between the spores of the same AMF species[46].

Spatial **soil exploitation by roots** was assessed with the ingrowth-core technique[47]. In June 2003, five soil cores (4.8 cm diameter, 30 cm deep) were removed per plot and replaced by root-free soil from the field site. In September 2003, the initially root-free in-growth cores were removed and the holes were re-filled with root-free soil until the following withdrawal in July 2004. To extract the newly formed roots, each in-growth core was first weighed and carefully homogenized. A subsample of 50 g of soil was suspended in water and rinsed over a 0.5-mm screen. Roots collected in the screen were transferred into a water-filled clear acrylic tray and scanned. Total root length was determined from images using WinRhizo (Regent Instruments, Quebec, Canada). Afterwards, root length density (cm root length per cm^3 soil volume) was calculated.

Classification of organisms into groups

All organisms collected were classified into functional groups (guilds) based on extensive literature and database searches. Functional groups were defined based on trophic position (feeding guild) and interaction type (consumers, mutualists, pathogens, decomposers).

Aboveground herbivores: Phytophagous beetles (mainly Chrysomelidae and Curculionidae), Leafhoppers (Cicadina), gall-forming and other phytophagous Hymenoptera, phytophagous Heteroptera, Grasshoppers (Saltatoria: Acrididae), phytophagous Diptera.

Aboveground carnivores: Zoophagous Hymenoptera (excl. Parasitica), zoophagous beetles (mainly Carabidae and Staphylinidae), Zoophagous Heteroptera, Zoophagous Diptera, Spiders (Arachnidae).

Aboveground omnivores: Omnivorous beetles (mainly Staphylinid beetles) and Diptera

Parasitoids: Parasitoid Hymenoptera and Diptera. No parasitoid Coleoptera were found.

Hyperparasitoids: Hyperparasitoid Hymenoptera (mainly *Alloxysta* sp., Hymenoptera: Cynipidae) and mummy parasitoids (*Dendrocerus* sp., Hymenoptera: Megaspilidae)

Pollinators: Hymenoptera (mainly Apidae), Diptera (mainly Syrphidae).

Pathogens: Plant-pathogenic fungi of the groups Peronosporaceae (Downy Mildews), Erysiphales (Powdery Mildews), Ustilaginales (Smut diseases) and Uredinales (Rust fungi). Further, we included Bacteria and Fungi causing Leafspot diseases.

Invaders: Abundance (dry weight/m²) and species richness of (weedy) plant species not present in the pool of 60 plant species present in the Jena Experiment (so-called external invaders).

Belowground microfauna: Amoebae and Flagellates.

Belowground mesofauna: Collembola, Herbivorous Nematodes, Bacterivorous Nematodes, Fungivorous Nematodes, Omnivorous Nematodes, Oribatid mites, pro- meso- and astigmatic mites.

Saprophagous Macrofauna: Earthworms (Lumbricidae), Isopoda, Diplopoda, Enchytraeidae

Predatory Macrofauna: Araneida, Geophilidae, Lithobiidae, Carabidae, Staphylinidae, Elateridae, zoophagous insect larvae, Hymenoptera

Herbivorous Macrofauna: Gastropoda, Curculionidae, herbivorous larvae iof Diptera, Symphyla, herbivorous Hemiptera groups.

Definition and quantification of organism interactions

We included only those interactions between organisms that were directly and quantitatively observed in the field (as opposed to correlative approaches where interaction partners are generally unknown). Hence, every interaction considered here contains information about the exact process rates. For example, “decomposition” is the amount of material of known quantity decomposed over a given period of time per unit area.

The specific definitions for each interaction are:

Herbivory: The percentage of intact leaf area of an average sample of each plant community consumed by invertebrate herbivores over a given period of time on subplots of 2 x 4 m, averaged across time. Plant community herbivory was visually estimated in May and August 2003, 2004 and 2005 by sampling a given number of plant individuals along transects through each of the 82 experimental plots and noting the percentage of leaf area eaten by invertebrate herbivores (insects and molluscs).

Parasitism: The percentage of wildbee (Hymenoptera: Apidae) cells parasitized in artificially exposed trap nests (measured in 2005 and 2006). Trap nests consisted of reed internodes cut to a standardized length and enclosed in plastic tubes of c. 14 cm diameter. There were 4 trap nests installed on a wooden post in the middle of each plot; trap nests were installed in early spring each year and removed in autumn, and all reed internodes were checked for colonization by trap-nesting bees, wasps and their natural enemies. We used parasitized wildbee cells because these measurements were performed in all N=82 large plots. Qualitatively similar results were obtained using parasitism rates estimated from aphid mummies.

Hyperparasitism: The percentage of aphid mummies that were parasitized by Hymenopteran hyperparasitoids. All stationary aphids (including alates within colonies) were counted 4 times (twice before the first mowing, twice after) in c. 3 m x 20 cm transects in 47 small extra plots on all sown plant species (plant species richness here ranged from 1 to 9 plant species). All mummies (parasitized aphids) were collected in the same transect at the same 4 dates and checked for parasitoids and hyperparasitoids. Analyses were performed separately from all other data, and lines in Fig. 1 show predicted values extrapolated to more species-rich mixtures. Hyperparasitism was additionally measured in 23 large plots (20 x 20 m) and a binary regression analysis showed qualitatively the same result.

Pollination: The number of flower visits by Dipteran and Hymenopteran pollinators per time interval (6 minutes) visually counted on 0.64 m^2 subplots in each plot (excluding those plots containing only grasses) in May, June and August 2005 and 2006, averaged over time.

Pathogen severity: The mean percentage of leaf area damaged by plant pathogenic fungi across the whole plant community of every plot. Pathogen infection was visually assessed in 2006 for all species in all 82 large plots. Screening focussed on the pathogen groups downy mildew, powdery mildew, rusts and smuts. In addition, infection of fungal-caused leaf spots was assessed. Fungal pathogen infection was registered for each species per plot as the mean percentage infected individuals per species.

Bioturbation: The number of burrowing holes of the Common Vole (*Microtus arvalis*) found in June and September 2005 in an area of 20 x 20 m on every plot, averaged across time. Activity of other bioturbators (e.g. earthworms) was not assessed, but data on earthworm densities are available upon request.

Decomposition: The percentage of litter remaining in standardized exposed litter bags per plot after four months of time. Litter of three plant functional groups (grasses, herbs and legumes) was used to establish four litter treatments [grasses (G), herbs (H), legumes (L) and mixed (M)]. Each litterbag contained 3 g dry weight of plant material. Litter of each functional group was obtained by mixing 1 g of senesced litter of three plant species: grasses (*Festuca rubra*, *Lolium perenne*, *Poa pratensis*) (N 2.0%, C:N 22.6), herbs (*Cirsium oleraceum*, *Daucus carota*, *Plantago lanceolata*) (N 2.3%, C:N 19.6), legumes (*Lathyrus pratensis*, *Lotus corniculatus*, *Trifolium repens*) (3.0%, C:N 15.5). For the mixed litter treatment we used 3 g dry weight litter (N 2.4%, C:N 19.3) from a homogenous mixture created by mixing all 9 plant species. The litter material was collected from the Jena Experiment field site in the previous season (2003), sorted, dried for 3 days at 60 °C and cut into pieces ~ 3 cm in length. Litterbags were built using 4 mm mesh to allow access of soil animals including large earthworms such as *Lumbricus terrestris*. Litterbags of each of the four litter treatments were placed on the soil surface of four decomposer treatments (reduced and increased earthworm density, ambient and reduced springtail density) of the 1, 4, 16 plant species diversity plots in February 2004. The litterbags were collected in June 2004, after 4 months of exposure, dried three days at 60 °C and weighed. The percentage of litter remaining in the mixed litter treatment after these four months was used as a measure of decomposition rate. Measurements were performed on plots containing 1, 4 and 16 plant species.

Biological invasion: The population density (individuals per 4 m^2) of an invading weedy plant species (*Cirsium arvense*), measured in 2004 on randomly placed positions in the core area of every plot.

Microbial respiration: Microbial respiration was measured from five cores (diameter 5 cm, depth 5 cm) taken on randomized subplot positions (2 x 4 m) per plot in May 2002, 2003, 2004, 2006, 2007 and 2008. Soil samples were homogenized from each plot and microbial respiration was measured using an O_2 microcompensation apparatus[36].

Ant activity: Between 4th July 2006 and 16th August 2006, ant colonies were counted in each plot in an area of 4m^2. The surface of the plots was searched visually. Every entrance was counted as a measure of colony number. An entrance was defined by the observation of ants passing in and out and by recruiting behaviour occurring when the entrance was disturbed using tweezers.

Statistical Methods

We used R 2.11.0 (see Ref. [48]) for data analyses. In addition, we calculated structural equation models using AMOS 16.0 (SPSS, Inc.). Code printed below refers to R 2.11.0.

General approach

For most of our analyses, we present results on a unified scale [0;1]. This allows direct comparisons of slopes, intercepts and other model parameters across all taxonomic groups.

A small example dataset shall serve to introduce the methodology used; let $y_1$and y_2 be carnivore and herbivore abundance, respectively; let x_1 be the explanatory variable (plant species richness). $y_1'$and y_2' are the transformed versions of the response variables y_1 and y_2. A possible dataset may then look like this:

x_1	y_1	y_2	y_1'	y_2'
1	10	100	0	0
2	22	220	0.4	0.4
3	34	340	0.8	0.8
4	40	400	1	1

The slopes of corresponding regression lines are then 10.2 for carnivores or 102 for herbivores. On the transformed scale, however, both slopes are exactly 0.34. Thus, standardizing the response variables to [0;1] reveals that both groups actually respond in exactly the same way to plant species richness. Such a conclusion would, however, not have been possible on the original scale.

Our approach to data analysis consists of four steps:

(1) Standardization of response variables to a unified scale [0...1]
(2) Separate analysis of every response variable using a common set of 572 linear and nonlinear models per response variable
(3) Combined analysis of all response variables using a common power law function
(4) Combined multivariate analyses of groups of response variables using (i) multivariate linear models and (ii) structural equation models.

We chose a transformation to range [0,1] rather than a z transformation because (i) the resulting values are easier to compare and to interpret, (ii) because this transformation is more robust than the z transformation [49], and (iii) because information about the variation of variables is lost with the z transformation (all variables having a standard deviation of 1 after transformation).

Note that scaling variables to [0;1] may introduce a bias when dividing by the maximum observed value for each variable, especially if the underlying distributions are skewed. In particular, a large maximum:median ratio could lead to lower values of the exponent z reported in power functions. However, the z values calculated by us were based on highly aggregated data, for which the arithmetic mean is likely to be an unbiased estimater of the true population mean.

We additionally ran our analyses using a z transformation and found no principal differences.

Univariate linear and nonlinear models

The set of linear and nonlinear models was carefully chosen from biologically meaningful models:

(1) **Linear models** containing block, plant species richness, number of plant functional groups, grass and legume presence
(2) **Saturating** non-linear models (Michaelis-Menten, asymptotic regression models, logistic regression models)
(3) **Exponential** non-linear models (including biexponential models)
(4) **Power law models** covering a wide range of possible shapes of responses

To make linear and non-linear models comparable, legume presence, grass presence and number of functional groups were included as covariates into the nonlinear models.

If model diagnostic plots showed variance heterogeneity or non-normality of variance, we updated our models using variance functions. In two cases (vertebrate herbivore abundance and hyperparasitism rates) we additionally used generalized linear models for analysis[50].

Blocks were treated as fixed rather than random effects because there were only four levels of blocks, and because treatments were unequally represented within blocks (see Ref. [51] for a similar approach).

We used AICc (Akaike´s Information Criterion, corrected for small sample sizes; see Ref. [52]) for model simplification and model selection. Manual deletions of terms from models (comparing models using conditional F-tests) lead to qualitatively very similar results.

Abundances and numbers of distinct species per sample were summed during data aggregation. For non-count data (organism interactions), we calculated mean values for every plot. The total sample size was at least 50 for abundance and species richness data, and 82 for organism interactions. For practical reasons, hyperparasitism and belowground protozoa had a smaller sample size. These variables were therefore not included into the multivariate linear models. Every response variable was transformed using a transformation to [0;1] prior to analyses to allow comparisons of model parameters. Vertebrate herbivore abundance was log-transformed before transformation to [o;1] to reduce non-constancy of variance. For every response variable, we set up a set of linear and nonlinear candidate models. In generalized non-linear least squares models, we used variance functions to account for heteroscedasticity. For every response variable, the set of candidate models considered was created using linear and nonlinear models.

To give every model the same chance of being selected, the same principal set of initial models was considered for every response variable in turn.

This makes the overall model selection process entirely reproducible.

The R code for the general model selection function was:

```
evaluate.all=function(response=quote(response),DF=quote(DF),i){
require(MASS)
require(pgirmess)
require(nlme)
options(width=500,show.error.messages=T)

DF <- cbind(response = DF[[response]], DF)
options(show.error.messages=F)
L=list(
        modelname1=try(model.formula1,DF)),
        modelname2=try(model.formula2,DF)),
        modelname3=try(model.formula3,DF))
        #the full list of model formulae is available upon request
        #[...]
        )

L2=Filter(function(x) !inherits(x, "try-error"), L) #to select only those models that converged
without error
nn=names(L2)

# actual model selection based on AICc:
        df=data.frame(selMod(L2))
        nn=nn[as.numeric(row.names(df))]
        df=cbind(nn,df)

# return the i´th selected model
selected=which(seq(1:length(nn))==as.numeric(rownames(selMod(L2)))[i])

# return the model formula (this has the structure response~...,data=DF)
called=lapply(L2[selected],function(x)x$call)

# Some text replacement to have the correct response variables and dataframes in there:

called=sub("response",response,called)
replacevec<-c("newsynthesis.ranged")

called=sub("DF",replacevec,called)

# Finally, return the selected models

returnlist=list(response=response,models=df,selected.model=called,all.models=L2)

return(returnlist)
}
```

The full list of model formulae used inside the function is available on request.

The `gnls()` function from the `MASS` library in R[53] was used to fit generalized nonlinear least-squares models that allow for covariates in nonlinear models, and variance heteroscedasticity can be modelled using variance functions.

The `try()`command prevents the function to exit with an error if initial parameter values do not lead to model convergence. Initial parameter values for nonlinear models were based on previous manual model fitting approaches.
The index `i` allows the i´th model to be extracted from the resulting list of models (ordered by AICc) for manual inspection and modification.

For all models we calculated the number of parameters, log-Likelihood, Akaike´s An Information Criterion, corrected for small sample size (AICc), delta-AICc values and Akaike weights. The five models with lowest AICc values were inspected in detail by plotting model predictions and model diagnostic plots to inspect the variance structure. The model with lowest AICc and highest Akaike weight was taken to be the best model of the subset, with some exceptions where biological knowledge made competing models more likely (for example if theory predicted saturating rather than exponential kinetics).

To allow the reader a full assessment of all competing models, we supply two Excel tables containing all models considered. Model convergence was different for every response variable, and we provide these outputs to allow a precise judgement of which patterns are strongly supported by the data, and which not.

Fitting a more parsimonious unified power law model

Using the `evaluate.all()` function defined above revealed that 25 out of 54 response variables (i.e. 46%) showed clearly nonlinear relationships with plant species richness (8 exponential, 7 Michaelis-Menten, 10 power law relationships).

For parsimony, we decided to fit a **common power law function** to all response variables (Adler 1998), covering a broad range of possible non-linear and linear biodiversity effects.

The common power law function used was

$$y = a + b \times \text{sowndiv}^{c}$$

Where y is the response variable, sowdiv is sown plant species richness, and a, b and c are parameters to be estimated from the data.

Note that this model also allows linear models (for c=1) and null models (for c=0).

Because many response variables can be assumed to be zero for zero plant species richness, we excluded the intercept from the model in cases where the c parameter was compared across different response variables (model named `Pa4` below).

The power law models were fitted using the following R code:

```
evaluate.small=function(response=quote(response),DF=quote(DF)){
require(MASS)
require(pgirmess)
require(nlme)
options(width=500,show.error.messages=T)

DF <- cbind(response = DF[[response]], DF)

L=list(
      Pa1=try(nls(response~a+b*sowndiv^c,start=list(a=1,b=1,c=1),DF)),
      Pa2=try(nls(response~a+b*sowndiv,start=list(a=1,b=1),DF)),
      Pa3=try(nls(response~a+sowndiv^c,start=list(a=1,c=1),DF)),
      Pa4=try(nls(response~b*sowndiv^c,start=list(b=1,c=1),DF)),
      Pa5=try(nls(response~sowndiv^c,start=list(c=1),DF))
)

L2=Filter(function(x) !inherits(x, "try-error"), L) #to select only those models
that converged without error
nn=names(L2)

called=lapply(L2[1],function(x)x$call)

params=lapply(L2[1],function(x)summary(x)[10])

summary=lapply(L2[1],function(x)summary(x))

called=sub("response",response,called)
replacevec<-c("newsynthesis.ranged")

called=sub("DF",replacevec,called)

returnlist=list(response=response,selected.model=called,all.models=L2,params=par
ams,summary=summary)
return(returnlist)
}
```

Multivariate linear models

Measurements collected on the same 82 plots cannot be considered statistically independent; for example, herbivory and decomposition can be indirectly correlated via faeces of herbivorous insects or induced leaf abscission. Hence, we used multivariate linear models[54] to compare the responses of different variables to biodiversity.
For parsimony, multivariate linear models consisted of a matrix of response variables, and log (plant species richness) as the only explanatory variable.

We used the log of plant species richness to linearize individual relationships between each response and explanatory variable, and to reduce leverage. The model was fitted like this:

```
model1<-lm(cbind(response.variable1,response.variable2...)~logdiv)
```

We constructed three multivariate models, one for organism abundances, one for organism species richness, and one for biotic interactions. The overall output from these models yielded Pillai´s trace and approximate F values cited in the manuscript text.

For every model, we further constructed a matrix of contrast coefficients for the response variables that was used to compare the slopes of the response variables with one another. In all cases, we used so-called successive difference contrasts[53].

For example, the successive difference contrasts for a set of 8 response variables was specified using

```
require(MASS)
contr.sdif(8)
```

In this case, the first comparison is between herbivores and carnivores, the second comparison is between parasitoids and carnivores, and so on.

F- and P-values for each comparison were calculated from the diagonal elements of the resulting hypothesis and error sum of squares-and products matrices (here termed `SSPH` and `SSPE`; see also Ref. [54]) using the following formulae:

```
f.value=diag(linhyp$SSPH)/(diag(linhyp1$SSPE)/res.df)
p.value=1-pf(f.value,1,res.df)
```

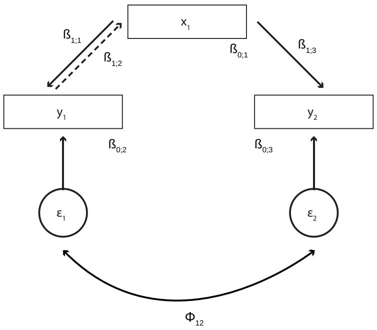
where `linhyp` is the linear hypothesis constructed using the matrix of contrast coefficients, and `res.df` are the residual degrees of freedom of the multivariate linear model under consideration.

Structural equation models

As effects of plant species richness on organism abundances or diversity may also be mediated indirectly, we decided to employ structural equation models (SEMs; see Refs. [55,56]) to allow multiple pathways for the effects of plant species richness.

SEMs are particularly well suited also in an experimental context, i.e. where some variables are deliberately manipulated experimentally (Grace 2006, pp. 233 ff). Further, SEMs "can be used to develop accurate and meaningful final multiple regression models when collinearities among explanatory variables are thought to be present" (see Ref. [57]).

We use the following terminology for graphical representations of structural equation models:



x_1, y_1 and y_2 are observed variables; ß$_{0;1}$, ß$_{0;2}$ and ß$_{0;3}$ are intercepts, ß$_{1;1}$, ß$_{1;2}$ and ß$_{1;3}$ are path coefficients representing directed effects of x_1 on y_1, y_1 on x_1, and x_1 on y_2. ε_1 and ε_2 are residual errors, and ϕ_{12} represents the residual co-variance between ε_1 and ε_2. The corresponding structural equations are:

$\varepsilon_1 \sim N(0, \sigma_1)$
$\varepsilon_2 \sim N(0, \sigma_2)$

$y_1=$ß$_{0;1}+$ ß$_{1;1}$ $x_1 + \varepsilon_1$
$x_1=$ß$_{0;2}+$ ß$_{1;2}$ y_1
$y_2=$ß$_{0;1}+$ ß$_{1;3}$ $x_1 + \varepsilon_2$,

where x_1 is treated as an "explanatory" variable measured without error, and ε_1 and ε_2 follow standard normal distributions N with mean 0 and standard deviations $\sigma_{1 \dots 2}$.

Because plant species richness was our main experimentally manipulated variable, all SEMs started off with plant species richness and further trophic groups were added both above- and below ground. All "response" variables were log-transformed and scaled to [0;1] before analysis to avoid non-positive definite residual covariance matrices. Plant species richness was log-transformed before analysis to reduce leverage. In essence, we therefore fitted log-log models that were essentially linearized versions of the individual non-linear regression models. Missing values were replaced by the mean. The total sample size was N=50 data points.

This allowed us to use up k<49 degrees of freedom for all SEMs. Hence, with a total of about 50 variables for all above- and belowground organism groups, it was not possible to fit a "complete" above-/belowground food web model.

We therefore present two types of SEMs:

(1) An above-/belowground SEM incorporating only organism groups with a size of >2mm (macrofauna).

(2) A belowground SEM incorporating only belowground organism groups.

For both types of SEMs, we decided on the initial model by considering published food webs (e.g. Coleman et al. 2003) and collecting expert opinions before the actual model-fitting process. The resulting initial models were then simplified using the "Specification search" command in AMOS 16.0 for Windows XP (SPSS, Inc). The minimal adequate model was considered to be the one that minimized Akaike´s An Information Criterion [58]. For the minimal adequate model, the 95% confidence interval of the root mean square error of approximation (RMSEA) was further required to include 0 (see Ref. [59]).

Supplementary Tables

Supplementary Table 1 | Summaries of response variables on original scale. Statistical summaries and units of measurement for the response variables used in this study on their original scale. The values of each observation y_i on the transformed scale can easily be computed using this table and the formula: $y' = (y_i - y_{min})/(y_{max} - y_{min})$. For example, a herbivory value of 3% corresponds to (3-0.02)/(9.48-0.02) = 2.98/9.46=0.32 on the transformed scale. N is the number of plots with non-missing values (sample size).

	Minimum	**Median**	**Mean**	**Maximum**	**N**
Design variables					
Grass presence (1=absent, 2=present)	1	1	1.46	2	82
Legume presence (1=absent, 2=present)	1	1	1.48	2	82
Small herb presence (1=absent, 2=present)	1	2	1.52	2	82
Tall herb presence (1=absent, 2=present)	1	2	1.54	2	82
Plant functional group richness (1-4)	1	2	2.12	4	82
Sown plant species richness (1-60)	1	4	8.59	60	82
Organism abundances					
Microbial biomass (µg C/g soil)	5.40×10^2	9.41×10^2	9.43×102	1.62×10^3	82
Amobae abundance	1.95×10^3	1.42×10^4	3.60×10^4	1.78×10^5	12
Flagellate abundance	2.09×10^3	9.58×10^3	1.23×10^4	1.98×10^4	12
Saprophagous macrofauna abundance	0	7	8.94	51	80
Saprophagous mesofauna abundance	0	4	7.51	64	80
Herbivorous macrofauna abundance	0	4	4.76	19	80
Predatory macrofauna abundance	0	11.5	15.49	101	80
Bacterivorous nematode abundance	0	16	18.22	86	73
Fungivorous nematode abundance	0	13	17.17	78	73
Plant-feeding nematode abundance	2.07	47	60.47	201	73
Predatory nematode abundance	0	1	1.84	24.47	73
Omnivorous nematode abundance	0	8	10.19	46	73
Collembola abundance	0	23	28.1	104	80
Mite abundance	0	16.5	21.9	102	80
Gamasida abundance	0	3	5.49	38	80
Aboveground herbivore abundance	181	609	665.16	1691	50
Aboveground carnivore abundance	221.5	343.62	338.33	533.5	50
Aboveground omnivore abundance	18.75	49.25	51.17	119.5	50
Aboveground parasitoid abundance	48	140	177.6	468	50
Aboveground hyperparasitoid abundance	0	1	1.46	5	28
Pollinator abundance	6	49	54.98	187	50
Invader abundance	11.14	133.14	179.78	815.67	82
Vole abundance	0	0.5	6.1	67	82

doi:10.1038/nature09492

Supplementary Table 1 (continued)

	Minimum	Median	Mean	Maximum	N
Organism species richness					
Mycorrhizal species richness	3	8	7.4	12	77
Saprophagous macrofauna species richness	0	2	1.94	4	80
Saprophagous mesofauna species richness	0	1	1.39	3	80
Herbivorous macrofauna species richness	0	2	2.58	7	80
Predatory macrofauna species richness	0	4.5	4.59	11	80
Bacterivorous nematode species richness	0	3	2.9	6	72
Fungivorous nematode species richness	0	3	2.42	4	72
Plant-feeding nematode species richness	1	6	5.81	11	72
Predatory nematode species richness	0	0	0.53	3	72
Omnivorous nematode species richness	0	2	1.89	5	72
Collembola species richness	0	6	5.67	11	80
Aboveground herbivore species richness	35	58	62.71	111.5	50
Aboveground carnivore species richness	44	61.5	61.67	75	50
Aboveground omnivore species richness	7	15.25	14.92	24	50
Aboveground parasitoid species richness	9	21.5	22.48	36	50
Pollinator species richness	2	8	8.6	17	50
Invader species richness	2.75	6.62	7.45	16.44	82
Pathogen species richness	0	3	2.65	5	82
Organism interactions					
Community herbivory (percent)	0.02	2.01	2.2	9.48	82
Parasitism (percent)	0	14.43	16.95	57.14	78
Flower visitor frequency (visits/6 Min.)	0	6.83	13.24	108	73
Litter decomposition (percent)	42.33	69.67	69.24	89	44
Seed predation (proportion removed)	0.22	0.78	0.75	1	46
Pathogen severity (percent)	0	1.05	1.35	4.08	82
Invasion (individuals/m^2)	0	1.5	4.19	39	80
Bioturbation (burrows per 400 m^2)	0	14.75	31.45	209	82
Ant activity (colonies per 4 m^2)	0	3	2.98	9	81
Microbial respiration (µL O_2 g soil^{-1} x h^{-1})	1.8	3.05	3.11	7.67	82
Other covariates					
Aboveground plant biomass (g/m^2)	6.71	240.68	277	614.21	82
Aboveground dead plant biomass (g/m^2)	8.84	24.59	26.89	79.34	82
Leaf area index (m^2/m^2)	0.76	2.13	2.42	4.36	82
Root length growth (cm/cm^3 soil)	4.2	20.26	21.37	49.85	81

doi:10.1038/nature09492

Supplementary Table 4 | Parameter estimates of common two-parameter power models. Shown are the estimates of the exponent, z, in models of the form $y=b\times S^z$, where b is an estimated constant and S is the plant species richness of the community. Response, response variable; Compartment, above- or belowground. Measure, abundance or species richness ("diversity"). SE, the standard error of each estimate. Response variables are scaled to [0;1], plant species richness ranges from 1-60 plant species. For example, collembolan abundance

Response	Compartment	Measure	Estimate	SE
Herbivorous invertebrates	aboveground	abundance	0.35	0.05
Carnivorous invertebrates	aboveground	abundance	0.18	0.06
Omnivorous invertebrates	aboveground	abundance	0.12	0.07
Hyperparasitoids	aboveground	abundance	-0.06	0.17
Parasitoids	aboveground	abundance	0.34	0.09
Plant invaders	aboveground	abundance	-0.29	0.09
Pollinators	aboveground	abundance	0.06	0.08
Voles	aboveground	abundance	0.18	0.17
Herbivorous invertebrates	aboveground	diversity	0.39	0.04
Carnivorous invertebrates	aboveground	diversity	0.21	0.04
Omnivorous invertebrates	aboveground	diversity	0.07	0.05
Parasitoids	aboveground	diversity	0.21	0.04
Plant invaders	aboveground	diversity	-0.37	0.07
Pollinators	aboveground	diversity	0.22	0.05
Plant-pathogenic fungi	aboveground	diversity	0.20	0.03
Bacterivorous Nematodes	belowground	abundance	0.08	0.09
Fungivorous Nematodes	belowground	abundance	-0.05	0.10
Omnivorous Nematodes	belowground	abundance	0.02	0.09
Plant-feeding Nematodes	belowground	abundance	0.06	0.07
Predatory Nematodes	belowground	abundance	0.92	0.21
Collembolans	belowground	abundance	0.11	0.06
Earthworms	belowground	abundance	0.07	0.08
Gamasida	belowground	abundance	0.28	0.12
Herbivorous macrofauna	belowground	abundance	0.19	0.08
Predatory macrofauna	belowground	abundance	0.09	0.10
Saprophagous macrofauna	belowground	abundance	0.18	0.08
Mites	belowground	abundance	-0.01	0.09
Bacterivorous Nematodes	belowground	diversity	0.11	0.06
Fungivorous Nematodes	belowground	diversity	0.02	0.05
Omnivorous Nematodes	belowground	diversity	0.03	0.08
Plant-feeding Nematodes	belowground	diversity	0.12	0.05
Predatory Nematodes	belowground	diversity	0.16	0.15
Collembolans	belowground	diversity	0.10	0.04
Earthworms	belowground	diversity	0.01	0.04
Herbivorous macrofauna	belowground	diversity	0.18	0.05
Predatory macrofauna	belowground	diversity	0.04	0.05
Saprophagous macrofauna	belowground	diversity	0.14	0.05
Mycorrhiza	belowground	diversity	0.08	0.04

Supplementary Table 5a | Multivariate comparisons of organism abundances. Columns are (from left to right): ID, variable number; Response variables (herbivore abundance etc.); "1-2" the successive difference contrast between variables 1 and 2 (herbivores vs. carnivores); "2-3" etc. accordingly. Table entries in rows 1-10 are contrast coefficients for successive difference contrasts. The two bottom rows contain the relevant information, namely the F and P values for the hypotheses tested. For example, herbivores and carnivore abundance (1 vs. 2) differ significantly at P<0.01.

ID	**Response variable**	**1-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**7-8**	**8-9**	**9-10**
1	Herbivores	-0.90	-0.80	-0.70	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
2	Carnivores	0.10	-0.80	-0.70	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
3	Omnivores	0.10	0.20	-0.70	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
4	Parasitoids	0.10	0.20	0.30	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
5	Pollinators	0.10	0.20	0.30	0.40	-0.50	-0.40	-0.30	-0.20	-0.10
6	Voles	0.10	0.20	0.30	0.40	0.50	-0.40	-0.30	-0.20	-0.10
7	Plant invaders	0.10	0.20	0.30	0.40	0.50	0.60	-0.30	-0.20	-0.10
8	Herbivorous macrofauna	0.10	0.20	0.30	0.40	0.50	0.60	0.70	-0.20	-0.10
9	Predatory macrofauna	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	-0.10
10	Saprophagous macrofauna	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90
	F-Value	**23.74**	**19.61**	**16.22**	**24.45**	**15.09**	**9.98**	**0.03**	**1.52**	**0.13**
	P-Value	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.85**	**0.22**	**0.73**

Supplementary Table 5b | Multivariate comparisons of organism species richness. Columns are (from left to right): ID, variable number; Response variables (herbivore species richness etc.); "1-2" the successive difference contrast between variables 1 and 2 (herbivores vs. carnivores); "2-3" etc. accordingly. Table entries in rows 1-9 are contrast coefficients for successive difference contrasts. The two bottom rows contain the relevant information, namely the F and P values for the hypotheses tested. For example, herbivores and carnivore diversity (1 vs. 2) differ significantly at P<0.01.

ID	**Response variable**	**1-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**7-8**	**8-9**
1	Herbivores	-0.89	-0.78	-0.67	-0.56	-0.44	-0.33	-0.22	-0.11
2	Carnivores	0.11	-0.78	-0.67	-0.56	-0.44	-0.33	-0.22	-0.11
3	Omnivores	0.11	0.22	-0.67	-0.56	-0.44	-0.33	-0.22	-0.11
4	Parasitoids	0.11	0.22	0.33	-0.56	-0.44	-0.33	-0.22	-0.11
5	Pollinators	0.11	0.22	0.33	0.44	-0.44	-0.33	-0.22	-0.11
6	Invaders	0.11	0.22	0.33	0.44	0.56	-0.33	-0.22	-0.11
7	Herbivorous macrofauna	0.11	0.22	0.33	0.44	0.56	0.67	-0.22	-0.11
8	Predatory macrofauna	0.11	0.22	0.33	0.44	0.56	0.67	0.78	-0.11
9	Saprophagous macrofauna	0.11	0.22	0.33	0.44	0.56	0.67	0.78	0.89
	F-Value	**44.89**	**33.69**	**14.15**	**18.17**	**18.09**	**0.05**	**0.43**	**0.64**
	P-Value	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.83**	**0.52**	**0.43**

Supplementary Table 5c | **Multivariate comparisons of organism interactions.** Columns are (from left to right): ID, variable number; Response variables (herbivory, parasitism, etc.); "1-2" the successive difference contrast between variables 1 and 2 (herbivory vs. parasitism); "2-3" etc. accordingly. Table entries in rows 1-10 are contrast coefficients for successive difference contrasts. The two bottom rows contain the relevant information, namely the F and P values for the hypotheses tested. For example, herbivory and parasitism (1 vs. 2) are not significantly different from one another.

ID	Response variable	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
1	Herbivory	-0.90	-0.80	-0.70	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
2	Parasitism	0.10	-0.80	-0.70	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
3	Flower visitation	0.10	0.20	-0.70	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
4	Decomposition	0.10	0.20	0.30	-0.60	-0.50	-0.40	-0.30	-0.20	-0.10
5	Seed predation	0.10	0.20	0.30	0.40	-0.50	-0.40	-0.30	-0.20	-0.10
6	Microbial respiration	0.10	0.20	0.30	0.40	0.50	-0.40	-0.30	-0.20	-0.10
7	Pathogen damage	0.10	0.20	0.30	0.40	0.50	0.60	-0.30	-0.20	-0.10
8	Invasion	0.10	0.20	0.30	0.40	0.50	0.60	0.70	-0.20	-0.10
9	Bioturbation	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	-0.10
10	Ant activity	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90
	F-Value	**3.69**	**1.27**	**9.13**	**6.22**	**10.48**	**7.57**	**13.94**	**4.73**	**0.39**
	P-Value	**0.06**	**0.27**	**<0.01**	**0.02**	**<0.01**	**0.01**	**<0.01**	**0.04**	**0.54**

doi:10.1038/nature09492

Supplementary Table 6 | Sample covariance matrix used for the structural equation model presented in Fig. 3.

ID	Label	1	2	3	4	5	6	7	8	9	10
1	log (Plant species richness)	2.34									
2	Aboveground plant biomass (g/m²)	0.15	0.03								
3	Aboveground dead plant biomass (g/m²)	0.18	0.02	0.05							
4	Aboveground herbivore abundance	0.21	0.02	0.03	0.05						
5	Saprophagous macrofauna abundance	0.06	0.01	0.01	0.01	0.04					
6	Herbivorous macrofauna abundance	0.15	0.02	0.02	0.02	0.02	0.05				
7	Aboveground carnivore abundance	0.16	0.02	0.02	0.03	0.01	0.02	0.05			
8	Predatory macrofauna abundance	0.05	0.01	0.01	0.02	0.02	0.02	0.01	0.04		
9	Aboveground omnivore abundance	0.08	0.01	0.02	0.01	0.01	0.01	0.02	0.00	0.06	
10	Aboveground parasitoid abundance	0.20	0.02	0.02	0.04	0.01	0.02	0.04	0.01	0.03	0.08

doi:10.1038/nature09492

Supplementary Table 7 | Sample correlation matrix used for the structural equation model presented in Fig. 3.

ID	Label	1	2	3	4	5	6	7	8	9	10
1	log (Plant species richness)	1.00									
2	Aboveground plant biomass (g/m²)	0.57	1.00								
3	Aboveground dead plant biomass (g/m²)	0.56	0.48	1.00							
4	Aboveground herbivore abundance	0.65	0.54	0.60	1.00						
5	Saprophagous macrofauna abundance	0.20	0.26	0.21	0.36	1.00					
6	Herbivorous macrofauna abundance	0.42	0.40	0.37	0.50	0.43	1.00				
7	Aboveground carnivore abundance	0.47	0.39	0.34	0.61	0.30	0.35	1.00			
8	Predatory macrofauna abundance	0.18	0.30	0.13	0.41	0.51	0.53	0.32	1.00		
9	Aboveground omnivore abundance	0.23	0.33	0.29	0.18	0.20	0.13	0.40	0.07	1.00	
10	Aboveground parasitoid abundance	0.46	0.50	0.31	0.59	0.26	0.32	0.59	0.15	0.48	1.00

doi:10.1038/nature09492

Supplementary Table 8 | Unstandardized parameter estimates of the structural equation model presented in Fig. 3. S.E., standard error; C.R. critical ratio (estimate divided by S.E.)

			Estimate	S.E.	C.R.	P
Aboveground plant biomass (g/m²)	<---	log (Plant species richness)	0.06	0.01	4.817	<0.001
Aboveground herbivore abundance	<---	log (Plant species richness)	0.07	0.02	4.178	<0.001
Aboveground herbivore abundance	<---	Aboveground plant biomass (g/m²)	0.27	0.16	1.749	0.08
Aboveground dead plant biomass (g/m²)	<---	Aboveground plant biomass (g/m²)	0.30	0.18	1.696	0.09
Aboveground dead plant biomass (g/m²)	<---	log (Plant species richness)	0.06	0.02	3.055	0.002
Aboveground carnivore abundance	<---	Aboveground herbivore abundance	0.61	0.14	4.257	<0.001
Herbivorous macrofauna abundance	<---	log (Plant species richness)	0.06	0.02	3.172	0.002
Saprophagous macrofauna abundance	<---	Aboveground dead plant biomass (g/m²)	0.15	0.12	1.254	0.21
Aboveground carnivore abundance	<---	Aboveground plant biomass (g/m²)	0.11	0.18	0.64	0.522
Aboveground parasitoid abundance	<---	Aboveground herbivore abundance	0.70	0.17	4.185	<0.001
Aboveground omnivore abundance	<---	Aboveground carnivore abundance	0.42	0.14	3.017	0.003
Predatory macrofauna abundance	<---	Herbivorous macrofauna abundance	0.31	0.10	3.051	0.002
Predatory macrofauna abundance	<---	Saprophagous macrofauna abundance	0.35	0.12	2.92	0.003
Aboveground parasitoid abundance	<---	Aboveground plant biomass (g/m²)	0.27	0.21	1.336	0.182

doi:10.1038/nature09492

Supplementary Table 9 | Standardized parameter estimates of the structural equation model presented in Fig. 3

			Estimate
Aboveground plant biomass (g/m²)	<---	log (Plant species richness)	0.567
Aboveground herbivore abundance	<---	log (Plant species richness)	0.529
Aboveground herbivore abundance	<---	Aboveground plant biomass (g/m²)	0.218
Aboveground dead plant biomass (g/m²)	<---	Aboveground plant biomass (g/m²)	0.237
Aboveground dead plant biomass (g/m²)	<---	log (Plant species richness)	0.426
Aboveground carnivore abundance	<---	Aboveground herbivore abundance	0.563
Herbivorous macrofauna abundance	<---	log (Plant species richness)	0.4
Saprophagous macrofauna abundance	<---	Aboveground dead plant biomass (g/m²)	0.17
Aboveground carnivore abundance	<---	Aboveground plant biomass (g/m²)	0.085
Aboveground parasitoid abundance	<---	Aboveground herbivore abundance	0.521
Aboveground omnivore abundance	<---	Aboveground carnivore abundance	0.396
Predatory macrofauna abundance	<---	Herbivorous macrofauna abundance	0.372
Predatory macrofauna abundance	<---	Saprophagous macrofauna abundance	0.356
Aboveground parasitoid abundance	<---	Aboveground plant biomass (g/m²)	0.164

Supplementary Table 10 | Intercepts for variables in the structural equation model presented in Fig. 3. S.E., standard error; C.R. critical ratio (estimate divided by S.E.)

	Estimate	S.E.	C.R.	P
Aboveground plant biomass (g/m²)	0.62	0.04	15.38	<0.001
Aboveground herbivore abundance	0.13	0.11	1.19	0.233
Aboveground dead plant biomass (g/m²)	0.05	0.12	0.38	0.707
Aboveground carnivore abundance	0.05	0.12	0.38	0.705
Herbivorous macrofauna abundance	0.37	0.06	6.55	<0.001
Saprophagous macrofauna abundance	0.46	0.06	7.95	<0.001
Aboveground omnivore abundance	0.29	0.07	4.08	<0.001
Aboveground parasitoid abundance	-0.11	0.14	-0.74	0.457
Predatory macrofauna abundance	0.20	0.07	2.78	0.005

Supplementary Notes

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Chapter 5

Effects of climate change on herbivore performance

in preparation for publication as:

Scherber C, Gladbach DJ, Andersen KS, Christensen S, Michelsen A, Albert KR, Mikkelsen TN, Beier C (2011) *Effects of warming, drought and elevated* CO_2 *on performance of an insect herbivore in heathland*.

C. Scherber and D. Gladbach are first authors with equal contributions.

An earlier draft of this manuscript has been part of the PhD thesis of D. Gladbach (Chapter 4) with a different author sequence. C. Scherber has meanwhile taken the lead as a corresponding first author.

Full Reference for the earlier version of this chapter:

Gladbach DJ, Andersen KS, Christensen S, Michelsen A, Albert KR, Mikkelsen TN, Beier C & C. Scherber (2010) *Effects of warming, drought and elevated CO2 on performance of an insect herbivore in heathland*. in: Gladbach D, *Plant-insect interactions in changing environments*. Dissertation, Georg August University Göttingen, 2010.

Effects of warming, drought and elevated CO_2 on performance of an insect herbivore in heathland

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Abstract

The impact of climate change on herbivorous insects can have far-reaching consequences for ecosystem functioning. However, experiments investigating the combined effects of multiple climate change drivers on herbivorous insects are scarce. Here we independently manipulated three climate change drivers (CO_2, temperature, drought) in a Danish heathland ecosystem dominated by heather (*Calluna vulgaris*) and grasses. The experiment was a full factorial split-plot with 6 blocks × 2 CO_2 treatments × 4 warming/drought treatments = 48 plots. We exposed a total of 432 larvae (n = 9 per plot) of the heather beetle (Lochmaea suturalis Thomson), an important herbivore on heather, to ambient vs. elevated drought, temperature and CO_2 (plus all combinations) for five weeks. Larval growth and survival were strongly and significantly negatively affected by elevated CO_2 and drought. Warming had negative effects on growth but not on survival. Combined CO_2 and drought significantly reduced growth, while interactions between warming, CO_2 and drought had varying effects. Overall, our study shows that i) drought was the most important factor for this insect herbivore, ii) the effect of climate change drivers on the herbivore was dependent on other co-acting factors, iii) insect herbivore populations can respond negatively to future climate, iv) the complexity of insect herbivore responses increases with the number of combined climate change drivers.

Keywords multiple climate change drivers· FACE experiment· *Lochmaea suturalis*.

Introduction

Herbivorous insects account for about one quarter of all extant organisms (Strong *et al.* 1984; Mayhew 2001) and are essential to ecosystem structure and functioning (Weisser and Siemann 2004). Ecosystem process rates such as herbivory may be altered significantly under climate change (Currano *et al.* 2008). The global mean surface air temperature is expected to increase by 1.8-5.8°C (2090 to 2099 relative to 1980 to 1999), with additional changes in other climate change drivers such as increasing CO_2 levels or extreme weather events (IPCC 2007). In recent studies, effects of global change drivers on herbivorous insects have been studied mostly in single-factor manipulative experiments rather than multi-factorially. For example, studies have shown that increases in CO_2 may alter plant-insect interactions in various ways (Lincoln *et al.* 1986; Lincoln and Couvet 1989; Stiling *et al.* 1999; Stiling and Cornelissen 2007). Elevated temperature (Bale *et al.* 2002) and altered water conditions (Mattson and Haack 1987; Morecroft *et al.* 2002) have also been considered independently. However, although several studies have started to investigate the combined effects of global change drivers on ecosystem processes (Shaw *et al.* 2002; Pritchard *et al.* 2007), studies on the joint consequences of different climate change drivers on herbivorous insects are scarce (but see Dury *et al.* 1998; DeLucia *et al.* 2008). Multifactor studies, however, will be key to a better mechanistic understanding of plant-herbivore interactions and may function as basis for predicting trophic interactions with respect to climate change.

In the present study we independently manipulated atmospheric CO_2 concentration, near-surface air temperature, and summer drought in a replicated field experiment (Mikkelsen et al. 2008). The experiments were conducted in nutrient-poor heather vegetation dominated by Calluna vulgaris (L.) and *Deschampsia flexuosa* (L.) Trin.. We recorded growth and survival of larvae of an important specialist herbivore, the heather beetle *Lochmaea* *suturalis* (Chrysomelidae), which shows outbreaks and is a major threat to heather worldwide. We directly measured the response of insect individuals on heather to multiple climate change effects under field conditions. Elevated CO_2 may alter the chemical composition of plants (Peñuelas and Estiarte 1998; Awmack and Leather 2002) and thus reduce the nutritive value for herbivores (Lincoln et al. 1986). Consequently, we tested the following hypotheses:

(i) Elevated atmospheric CO_2-concentrations negatively affect growth and survival of *L. suturalis* larvae because of nitrogen dilution (Roth and Lindroth 1994; Goverde and Erhardt 2003).
(ii) Prolonged drought negatively affects plant quality (Brenes-Arguedas et al. 2009) and hence negatively affects larval growth and survival (Scriber and Slansky 1981).
(iii) Warming positively affects larval growth and survival due to higher metabolic rates (Netherer and Schopf 2010).
(iv) Interactive effects of global change drivers on herbivores may reinforce each other (e.g. CO_2 and drought) or act antagonistically (e.g. temperature and CO_2, temperature and drought).

Methods

Site description

The experiment was conducted at the CLIMAITE research site at Brandbjerg (55°53′N, 11°58′E), Denmark between 1st June to 10th July, 2008. The site is located on nutrient poor sandy soils with unmanaged dry heath/grassland mosaic consisting of heather shrubs (*Calluna vulgaris*, 30% cover) and grasses (*Deschampsia flexuosa*, 70% cover). The annual mean temperature was 8°C and the precipitation averaged 600 mm (www.DMI.dk).

Experimental design and treatments

The Brandbjerg field site was designed as a full factorial experiment combining the effects warming (T), drought (D) and CO_2 (CO_2) to mimic a possible climate scenario in Denmark in the year 2075. Climate manipulations (T, D, CO_2), an ambient control (A) and all combinations of them (TD, TCO_2, DCO_2 and $TDCO_2$) were established in October 2005.

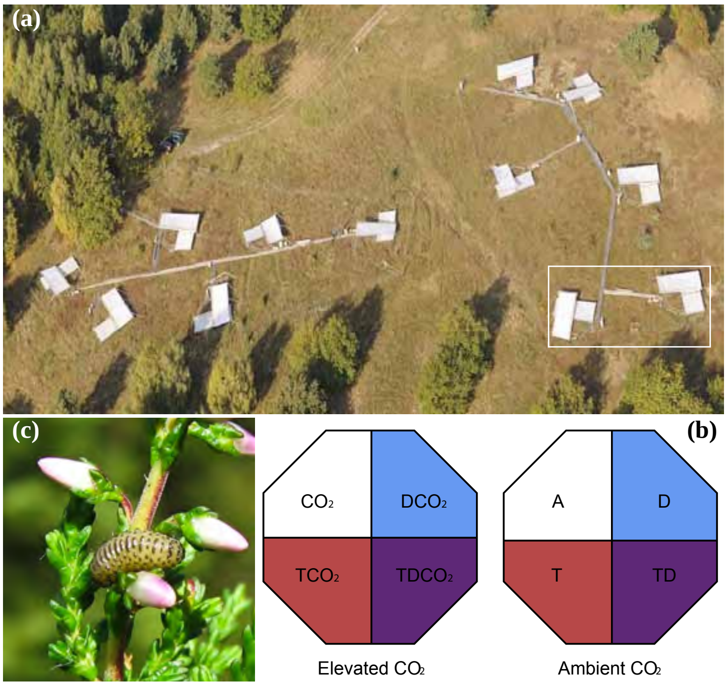

Figure 1. Aerial photograph (a, Copyright by Kim Pilegaard) of the experimental FACE site at Brandbjerg, DK. Curtains were drawn over the plots for illustrative purposes only; (b) split-plot design of the three treatments CO□ (CO□), drought (D) and warming (T) and all combinations, including an ambient control (A), adapted from Mikkelsen *et al.* (2008); (c) 2nd instar larva of *Lochmaea suturalis* feeding on a *Calluna* plant (Copyright by C. Scherber).

The study design contained six blocks (replicates) consisting of two octagons (6.8 m diameter), each divided into four plots (split-plot design), yielding a total of 48 plots (Fig. 1a). CO_2 was manipulated at the octagon level, while drought, elevated temperature, a combination of both treatments and a plot without drought or warming were applied within octagons (Fig. 1b).

CO_2 was elevated to 510 ppm using a free air carbon enrichment (FACE) system (Miglietta et al. 2001). Passive night time warming (Beier et al. 2004) with curtains (height 50 cm) covering the vegetation from sunset to sunrise increased the average temperature (at 20 cm above ground surface) by 1-2°C. The drought treatment was implemented using curtains (controlled by rain sensors) that were activated during May 2008 to simulate a prolonged summer drought. For further detailed information on the facility, treatments and the experimental design see Mikkelsen et al. (2008).

Study organism and measurements

The heather beetle *Lochmaea suturalis* is a strictly monophagous insect herbivore which feeds on *Calluna vulgaris* both as larvae (Fig 1c) and as adults (Mohr 1966). Outbreaks have been reported from northern Europe (Gimingham 1972) in which larvae of *L. suturalis* can reach densities of up to 2000 individuals/m^2 and cause complete defoliation and death of heather (Brunsting 1982).

300 adults of *L. suturalis* were caught near Großalmerode (Germany, 55°15′N, 9°47′E) in a Calluna heathland after they mated in April. The specimens were kept in 6 l plastic boxes (“Faunabox”, 27 × 18 × 18 cm, Savic, Belgium) using standard protocols (Melber 1989) on the 5th of May 2008. Females successively lay up to 300 eggs between end of April and August. Egg batches were transferred to petri dishes where the larvae hatched after 6-11 days and were fed on small pieces of Calluna branches. This was done until we transferred approximately 900 larvae to the field site in Denmark on the 28th of May 2008. Before the start of the experiment on the 1st of June heather beetle larvae were divided into classes according to their weight. Each of the 48 plots received the same amount of larvae from each weight class (9 in total). Gauze mesh bags (length 30 cm, diameter 13 cm) were tied around individual heather twigs to prevent the *L. suturalis* larvae from leaving the plant during the experiment. For comparability between plots we used heather twigs of the same size (estimated with a scale paper). Larvae were collected from four plots within one octagon, weighed and returned to the plants before proceeding to the next octagon. This practice minimized the time during which the larvae were separated from the plants. Individuals lost were counted as alive for the survival analysis. For weighing we used a Mettler AJ100 fine scale accurate to 0.1 mg, placed on a granite block inside the field station. Measures of fresh weight and survival were recorded weekly during larval development. The experiment was terminated when larvae were close to pupation in the litter layer (after 5 weeks). All larvae being alive by the end of the experiment were recollected and kept in a freezer for further analyses.

For additional information of the treatment effects structural equation models (not shown) were calculated with the following measures of June 2007: carbon and nitrogen content of green leaves from plant

Table 1 Performance of *Lochmaea suturalis* larvae. Start and end weights as well as number of remaining larvae are given as means of the six treatment replicates (A = ambient control, T = elevated temperature, D = elevated drought, TD = elevated temperature and drought, CO_2 = elevated CO_2, CO_2T = elevated CO_2 and temperature, CO_2D = elevated CO_2 and drought, CO_2TD = elevated CO_2, temperature and drought). Overall values are grand means of all plots (N = 48).

Treatment	**Mean weight [mg] ± SE at experimental start**		**Mean weight [mg] ± SE after 4 weeks**		**Mean number of larvae ± SE after 5 weeks**	
A	1.96	± 0.05	10.45	± 1.60	6.33	± 0.33
T	2.01	± 0.09	7.57	± 2.10	6.33	± 0.84
D	1.99	± 0.05	4.20	± 1.62	4.33	± 0.92
TD	1.97	± 0.08	9.40	± 0.9	4.33	± 0.61
CO_2	1.92	± 0.09	5.83	± 1.17	2.83	± 0.70
CO_2T	1.98	± 0.06	6.27	± 1.09	5.83	± 0.71
CO_2D	1.94	± 0.06	8.40	± 0.7	2.50	± 0.72
CO_2TD	1.99	± 0.06	4.80	± 1.28	2.33	± 0.84
Overall	1.99	± 0.03	7.16	± 0.77	4.70	± 0.67

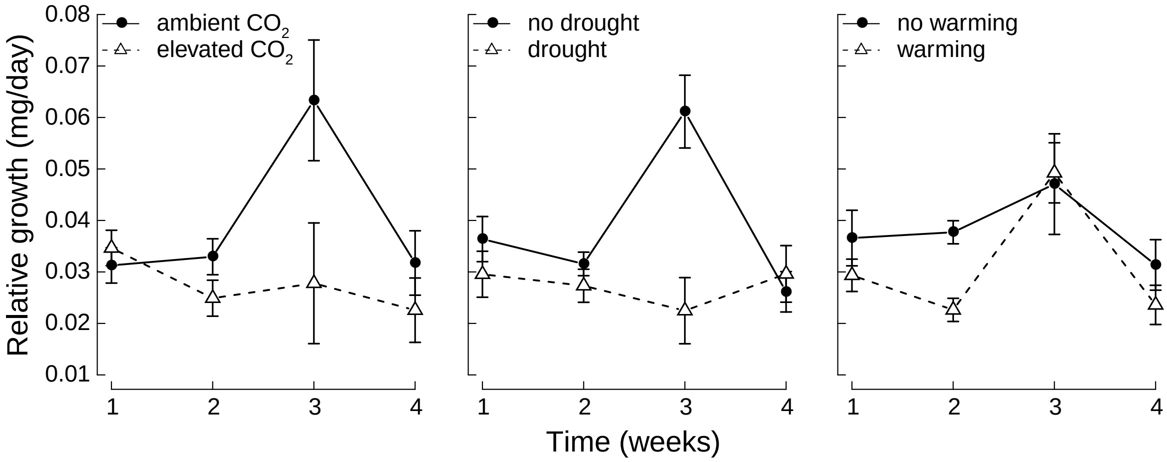

Figure 2. Relative growth rate of *Lochmaea suturalis* larvae over time for all plots with elevated treatments (n=24, broken lines) and controls (n=24, solid lines).

individuals in the same plots were analyzed using an Eurovector CN analyzer coupled to an Isoprime isotope ratio mass spectrometer (ambient CO_2: 26.46 ± 0.74, elevated CO_2: 30.45 ± 0.90, F1, 5 = 13.897, p = 0.01, Supporting information 1). Condensed tannin of green leaves was extracted with methanol and analyzed with a spectrophotometer (ambient CO_2: 39.50 ± 2.27 mg/g, elevated CO_2: 45.74 ± 2.60 mg/g, F1, 5 = 10.23, p = 0.02, Supporting information 2). Soil moisture was continuously measured in each plot using TDR-probes (see Mikkelsen et al. 2008).

Analyses and statistics

Larvae relative growth rates were calculated from larval weights as indicator of larval development (Hoffmann and Poorter 2002; Awmack et al. 2004) using the formula

$$RGR = (\ln W_{t(x)+1} - \ln W_{t(x)}) / (D_{t(x)+1-t(x)}) \qquad [eqn\ 1]$$

where RGR is relative growth rate (Stamp and Yang 1996), Wt(x) and Wt(x)+1 the weights (in mg) for time step x and D the time between two time steps.

Because of high larval mortality, the 5th time step was excluded from the growth rate analyses to keep the design balanced. Larval weights were pooled for each plot and time step. Kaplan-Meier survivorship for each plot and time steps 1-5 was calculated using the survfit function from the survival package (version 2.35-7, 2008) in R 2.10.1 (R Development Core Team 2009). Survival rate and relative growth rate were taken as response variables in linear mixed effects models (lme models, Pinheiro et al. 2009) to account for the split-plot design of the experiment. The order of fixed effects terms was time, CO_2, drought, temperature, plus two- and three-way interactions between all terms. Because plots were visited repeatedly over time, we included random intercepts for plots nested in block and CO_2 treatment, and random slopes for weeks 1-4(5). For 48 plots this yielded 192 (response variable: RGR) and 240 (response variable: survival rate) degrees of freedom for error in the full model.

Variance functions (Pinheiro and Bates 2000; Zuur et al. 2009) were used to account for heteroscedasticity. A modified version of the stepAIC function (Venables & Ripley 2002), corrected for small sample sizes (Burnham and Anderson 2002), was used to find the minimal adequate model for each response variable.

Results

Growth

At the beginning of the experiment, larvae weighed approximately 2.0 mg and reached an average final weight of 7.2 mg (Table 1). Elevated CO_2, prolonged drought, and elevated temperature all significantly decreased larval weight (Table 1).

Relative growth rates increased significantly over time and peaked after three weeks (Table 2, Figure 2). Relative growth in elevated CO_2, drought and warming plots was significantly lower compared to the ambient plots (Tab. 2, Figure 2). In addition, there were significant two-way interactions between time and CO_2, time and drought and time and warming (Tab. 2, Fig. 2). In combined CO_2 and drought conditions larvae grew slowly (Average

RGR in week 1 and 2: D 0.027 ± 0.01; DCO₂ 0.045 ± 0.01) particularly in weeks three and four (D 0.01 ± 0.01; DCO₂ 0.00 ± 0.02, Supporting information 3).

Larvae in plots with combined elevation of drought and warming gained on average 0.03 ± 0.06 mg per day. This is less than in plots with warming, but more than in drought-only plots in the second half of the experiment (Tab.2, Supporting information 3).

Survival

Five weeks after the start of the experiment an average of 4.7 ± 0.67 *Lochmaea suturalis* larvae still remained in the plots (Tab. 1). While both, elevated CO₂ and prolonged drought had negative effects on larval abundance after 5 weeks, abundance was slightly higher under elevated than ambient temperature (but only when warming was combined with elevated CO₂, Tab. 1).

Resembling a type II response (Pearl 1928), Kaplan-Meier survivorship declined significantly with time (Tab. 2, Fig 3). Type III responses of survival were observed in elevated CO₂, and drought (Table 2, Figure 3). Survival rates in drought plots dropped significantly in the second week (time×drought, Table 2, Figure 3). Warming increased survival only slightly (Tab. 2, Figure 3). However, warming increased survival rates to levels of ambient plots in combination with CO₂ (CO₂×warming Table 2, Supporting information 4). Finally the three-way interaction of CO₂, drought and temperature (Table 2, Supporting information 4) yielded the lowest survival rates (0.25 ± 0.059 after 5 weeks, Table 1) in the experiment.

Discussion

We investigated main effects and interactions of the climate change drivers CO₂, warming and drought on growth and survival of larvae of a chrysomelid beetle. All global change drivers adversely affected growth and survival of *Lochmaea suturalis* larvae, with the exception of temperature, which only affected growth. Two- and three-way interactions of global change drivers in most cases amplified the negative impacts of main effects on growth or survival. There are two possible explanations for the observed treatment effects: First, beetles might have been directly affected by increased CO₂, warming or prolonged drought. Second, global change drivers may also have acted indirectly. For example, the application of CO₂, warming and drought treatments since 2005 may have changed the concentrations of certain plant secondary compounds or other physiological parameters of Calluna host plants. As a result, changes in plant physiological status can indirectly affect insect herbivore performance.

The warming treatment, may have had both direct (Netherer and Schopf 2010) and indirect effects (Penuelas and Filella 2001; Cleland et al. 2007) on herbivore performance. The prolonged drought treatment, which was applied in May 2008, i.e. before the described study, may have resulted in drought stress to larval host plants (Gould 2000; Inbar et al. 2001) Jaleel et al. 2009). While some of these plant-mediated responses remain speculative, own investigations show that C/N ratio and tannin concentrations in Calluna plants increased with CO₂ (see Supporting information 1,2) and that larval

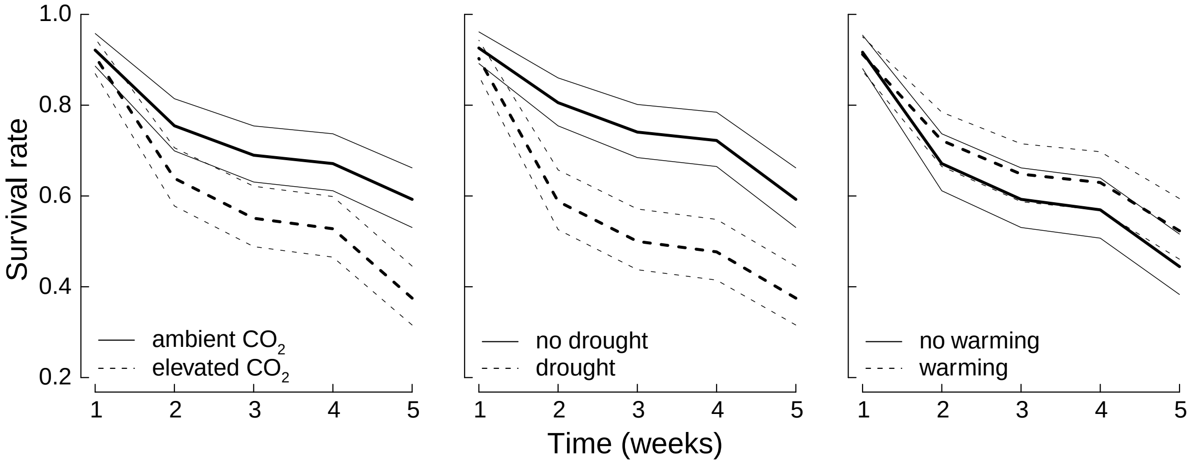

Figure 3. Survival rate of *Lochmaea suturalis* larvae over time for all plots with elevated treatments (n=24, solid lines) and ambient plots (n=24, broken lines). Thin lines show the confidence intervals at 5% and 95%.

Table 2. ANOVA tables of the minimal adequate models for relative growth rate (RGR) and survival rate.

Response variable: RGR	**numDF**	**denDF**	**F-Value**	**P-value**
Time (weeks)	3	107	6.953	<0.0001
CO$_2$	1	5	15.201	0.011
drought	1	107	11.464	0.001
warming	1	107	26.597	<0.0001
time×CO$_2$	3	107	4.978	0.002
time×drought	3	107	5.995	<0.0001
time×warming	3	107	3.001	0.033
CO$_2$×drought	1	107	7.996	0.005
CO$_2$×warming	1	107	2.085	0.151
drought×warming	1	107	5.182	0.024
time×CO$_2$ ×drought	3	107	2.030	0.114
time×drought×warming	3	107	5.887	<0.0001
CO$_2$×drought ×warming	1	107	3.811	0.053
Response variable: Survival rate				
Time (weeks)	4	210	3.8101	<0.0001
CO$_2$	1	5	8.476	0.033
drought	1	210	65.911	<0.0001
warming	1	210	3.161	0.076
time×CO$_2$	4	210	1.325	0.261
time×drought	4	210	5.032	<0.0001
CO$_2$×drought	1	210	0.45	0.498
CO$_2$×warming	1	210	16.186	<0.0001
drought×warming	1	210	0.43	0.508
CO$_2$×drought×warming	1	210	16.555	<0.0001

responses are indeed affected by changes in plant physiological state. Direct negative CO$_2$ effects can be excluded, because concentrations in the octagons were within the range of observed environmental CO$_2$ concentrations for insects (e.g. Nicolas and Sillans 1989). Measured concentrations averaged 2250 ppm at the CO$_2$ tubes -and 500 ppm at the center (Mikkelsen et al. 2008).

In addition to direct and indirect treatment effects, feeding behaviour and survival of larvae could have been influenced by cage effects. However, the space and the amounts of heather resource contained in the 30 cm cages were beyond larval movement (few cm/day) and the material provided by far exceeded larval food consumption (Melber 1989). Gauze cages were light-transmissive, minimizing potential reductions of overall temperature by shading; treatment effects were not affected, because passive night time warming was independent of the light regime.

One possible criticism of our study might be that we only observed larvae and not the full life cycle of the heather beetle. However, insect larval stages are generally considered most sensitive to environmental changes. Hence, if the larval stages are affected by climate change, then overall population growth may also be strongly affected. Larval growth and survival can therefore be seen as indicators of potential fecundity.

CO$_2$ *and drought effects*

In general, growth was particularly strong at intermediate larval stages and reduced when larvae were closer to pupation. This result is consistent with studies on different insect herbivores (e.g. Berger et al. 2006). Confirming our hypotheses (i) and (ii), elevated CO$_2$ and drought reduced growth rates. Analyses of leaf carbon and nitrogen content (Supporting Information 1,2) indicated that CO$_2$ increased the C/N ratios of *C. vulgaris* leaves and thus reduced food plant quality for *L. suturalis* (comp. Scriber and Slansky 1981). It is likely that nitrogen dilution due to enhanced plant growth in elevated CO$_2$ (Lincoln et al. 1986) may have lowered food conversion efficiency of *L. suturalis*, resulting in slower development (Roth and Lindroth 1994; Lawler et al. 1996; Goverde and Erhardt 2003).

There was no effect of drought on leaf C/N, but plants under drought stress (reduced soil water content) often build tougher and therefore harder digestible leaf structures (Lincoln et al. 1993; Awmack and Leather 2002; Rouault et al. 2006), which may be an explanation for reduced larval growth in drought plots. However, consumption of plant material by the larvae was too small to record differences in the field.

Nitrogen dilution effects on growth rates may also be responsible for reduced larval survival (Brunsting and Heil 1985) because of elongated development times (Coviella and Trumble 1999). Analyses of tannins showed that the heather plants growing under elevated CO_2 contained higher concentrations of leaf tannins than those in ambient CO_2. In combination with prolonged small larval stages, which are most sensitive to foliar quality (Rouault et al. 2006), higher tannin concentrations may additionally have increased mortality, particularly among smaller larvae. Reduced soil water content under drought conditions may also have affected leaf water content negatively (Mattson and Haack 1987). In consequence, survival rates in drought plots dropped in week one and two of the experiment, as particularly young developmental stages of *L. suturalis* depend on elevated levels of microclimatic humidity (Melber and Heimbach 1984; Melber 1989).

While main effects of drought and CO_2 reduced survival rates particularly in the first week when larvae were small, the combination of both factors caused strong declines of survival rates also at later larval stages. The negative impact of combined CO_2 and drought was particularly strong from week three onward, where larvae ceased to grow further. This may be explained by tougher leaf structures and low nutritive values of heather plants resulting in lower consumption rates and food conversion efficiency (Lincoln et al. 1986).

Warming effects

Warming effects on *L. suturalis* larvae depended on presence and absence of the other climate change drivers, and effects remained moderate in comparison to CO_2 and drought effects. In contrast to hypothesis (iii), warming adversely affected larval growth. This may be explained by increased consumption and metabolic rates, which can lead to faster tannin accumulation in the larvae (Coviella and Trumble 1999). In the face of unchanged survival rates, increased detoxification of tannins may take place at the cost of growth (Barbehenn *et al.* 2009). This assumption is supported by increased survival in combined CO_2 and warming. We suggest that the detoxification efficiency of defensive metabolites increases with temperature (Mattson and Haack 1987), but becomes significant only when concentrations of carbon-based toxic agents increase (Lawler *et al.* 1996).

However, the negative effects of warming increased in combination with CO_2 and drought, and survival of *L. suturalis* larvae dropped to the lowest levels of the study. Possibly larvae could compensate only certain levels of tannin or nitrogen dilution that were exceeded in the three-way interaction of all climate change drivers. Additionally warming may greatly reduce relative air humidity when combined with drought. We could not exactly determine the mechanism, thus warming may have introduced unexplored side effects of the climate change factors that lead to qualitatively different impacts on herbivore insects.

This is supported by the fact that the combination of drought and warming increased growth relative to the drought-only treatment, while all other combinations or main effects of climate change drivers lead to reduced growth.

Conclusions

We showed that performance of insect herbivores may be strongly affected by drought, CO_2, and by interactions between climate change drivers. Warming effects were generally weak,

The complexity of insect responses increases with the number of combined climate change drivers. In contrast to other studies (e.g. Coley 1998; Himanen et al. 2008; Klapweijk et al. 2010), we found no evidence for an increased insect population growth under experimental warming. Rather, our results indicate that climate change can reduce insect populations. Increasing plant C/N ratios may increase the duration of insect developmental stages, because nitrogen acquisition is more costly to herbivores. Further, “extreme weather” events with prolonged drought periods may negatively affect insect herbivores, which may be aggravated by warming (Rouault et al. 2006).

Our study emphasizes that assessment and generalisations of the overall effects of future climate change based on studies of single climate change drivers should be handled with care, as the effect of one climate change driver demonstrably depends on the concert of co-acting global change drivers.

Acknowledgements

We are grateful to Inger Kappel Schmidt for advice. Anja Gladbach sewed beetle bags and gave useful comments on the manuscript. Lotte Gladbach and Paul Scherber helped catching beetles. DJG acknowledges funding by the Helmholtz Association (VH-NG-247). Travel and overnight costs were funded by CLIMAITE.

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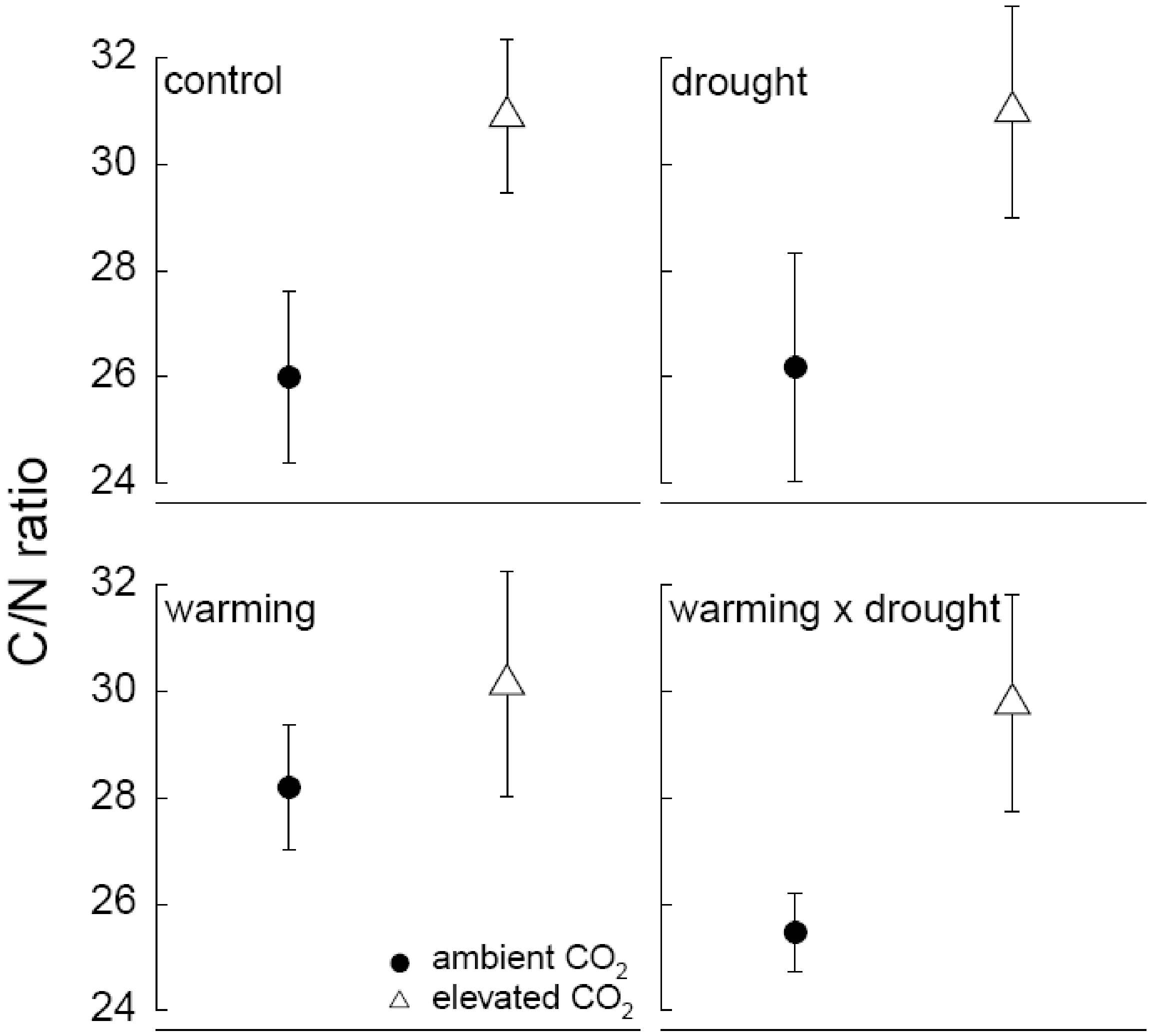
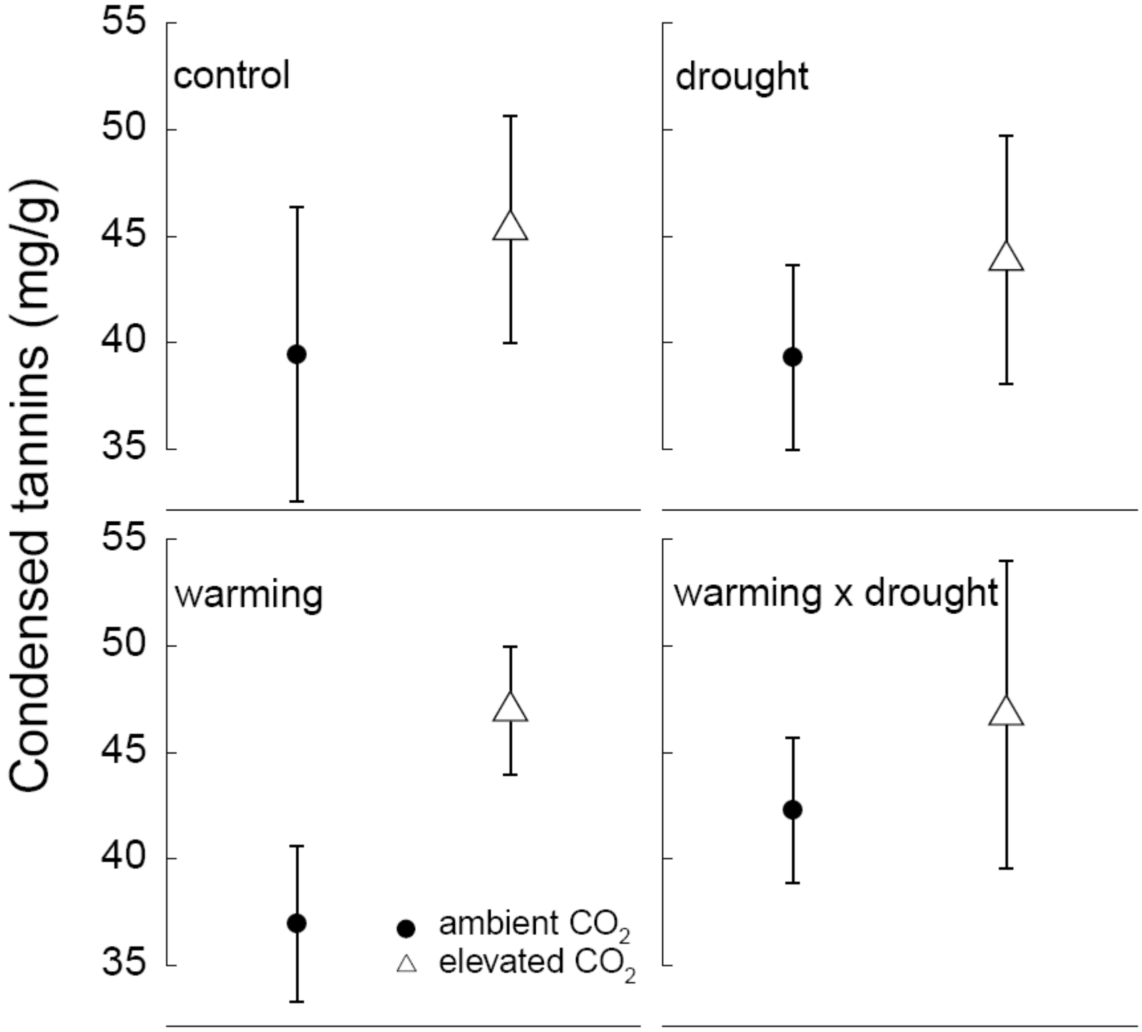
Supporting information

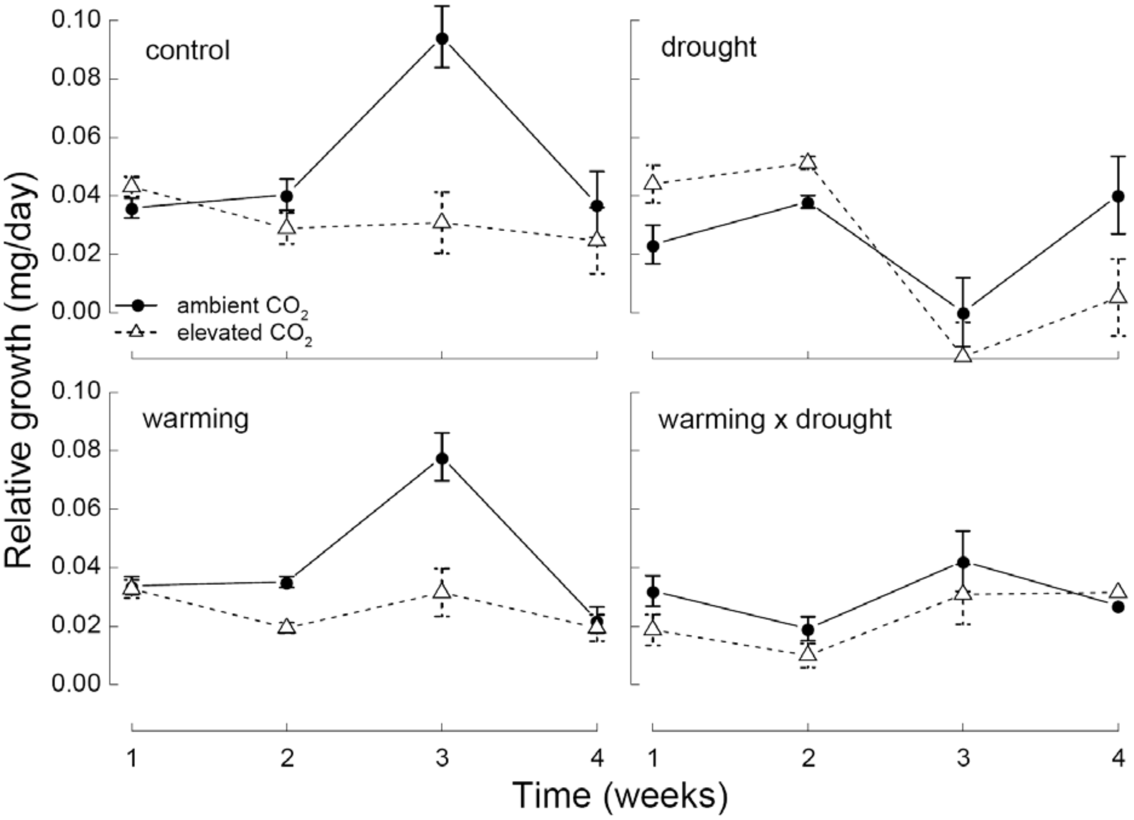
The following supporting information is available for this article online.



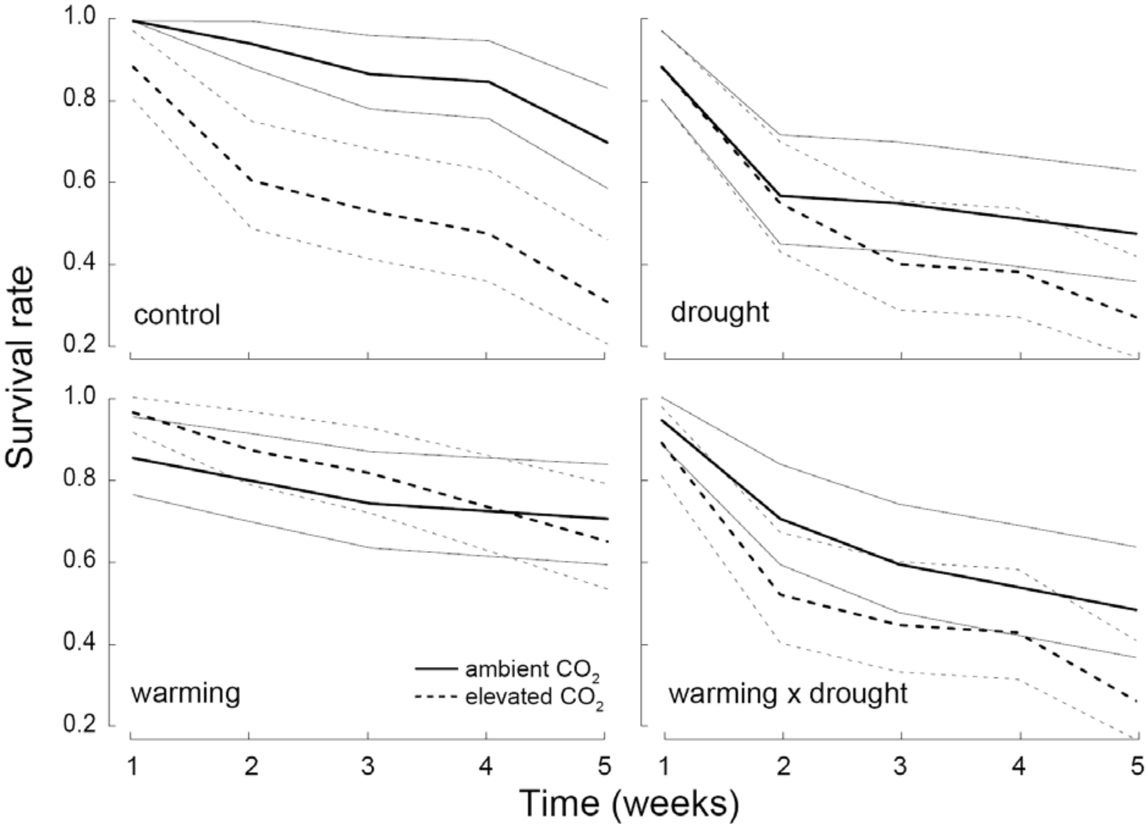
Supporting information 1 Carbon to nitrogen ratio in leaves of heather (*Calluna vulgaris*). The graph panels are ordered according to the split-plot design of the experiment. C/N ratios are given for each treatment in elevated (open triangles) and ambient (solid circles) CO_2 octagons. Thus each graph includes only the subset of plots (n=6) with the respective treatment. The single CO_2 effect is obtained when comparing both symbols in the control panel. Other single effects are obtained when comparing the solid circles of different panels. Two and three way interactions with CO_2 can be taken from the open triangles in all but the upper left panel.



Supporting information 2 Leaf tannin concentration of heather (*Calluna vulgaris*). The graph panels are ordered according to the split-plot design of the experiment. Tannin concentrations are given as mg per g for each treatment in elevated (open triangles) and ambient (solid circles) CO_2 octagons. Thus each graph includes only the subset of plots (n=6) with the respective treatment. The single CO_2 effect is obtained when comparing both symbols in the control panel. Other single effects are obtained when comparing the solid circles of different panels. Two and three way interactions with CO_2 can be taken from the open triangles in all but the upper left panel.



Supporting information 3 Relative growth rate of *Lochmaea suturalis* larvae. The graph panels are ordered according to the split-plot design of the experiment. Relative growth rates are given for each treatment in elevated (broken lines) and ambient (solid lines) CO_2 octagons. Thus each graph includes only the subset of plots (n=6) with the respective treatment. The single CO_2 effect is obtained when comparing both curves in the control panel. Other single effects are obtained when comparing the solid lines of different panels. Interactions with time can be seen along each curve. Two and three way interactions with CO_2 can be taken from the broken curves in all but the upper left panel.



Supporting information 4 Survival rate of *Lochmaea suturalis* larvae. The graph panels are ordered according to the split-plot design of the experiment. Survival rates are given for each treatment in elevated (broken lines) and ambient (solid lines) CO_2 octagons. Thus each graph includes only the subset of plots (n=6) with the respective treatment. The single CO_2 effect is obtained when comparing both curves in the control panel. Other single effects are obtained when comparing the solid lines of different panels. Interactions with time can be seen along each curve. Two and three way interactions with CO_2 can be taken from the broken curves in all but the upper left panel. Thin lines show the confidence intervals at 5% and 95%.

Chapter 6

Effects of climate change on above-belowground interactions

in preparation for publication as:

Stevnbak K, Scherber C, Gladbach D, Beier C, Mikkelsen TN, Christensen S (2011) Climate change disrupts interactions between above- and belowground organisms in a field experiment.

C. Scherber and K. Stevnbak are first authors with equal contributions.

C. Scherber is the corresponding author of this manuscript.

Climate change disrupts interactions between above- and belowground organisms in a field experiment

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Climate change has been shown to affect community composition (Walther et al 2002) and ecosystem process rates (Finzi et al 2011). However, it has remained unclear how climate change affects above-belowground interactions (van der Putten et al. 2009), and how different climate change drivers interactively affect ecosystem components. Here we use a global change experiment that independently manipulated drought, air temperature and atmospheric CO_2 concentration. We show that climate change disrupts the interaction between above- and belowground organisms. We used an insect herbivore that was allowed to feed on experimental grass phytometers under field conditions exposed to all combinations of the climate change factors. Aboveground herbivory increased the abundance of protozoans, microbial growth, and N availability to microbes belowground. Climate change disrupted these linkages through a reduction in herbivory induced by elevated CO_2, and cascading effects through the soil food web under these conditions. Interactions with drought and warming affected the CO_2 response at the next trophic level (protozoa). Our findings imply that

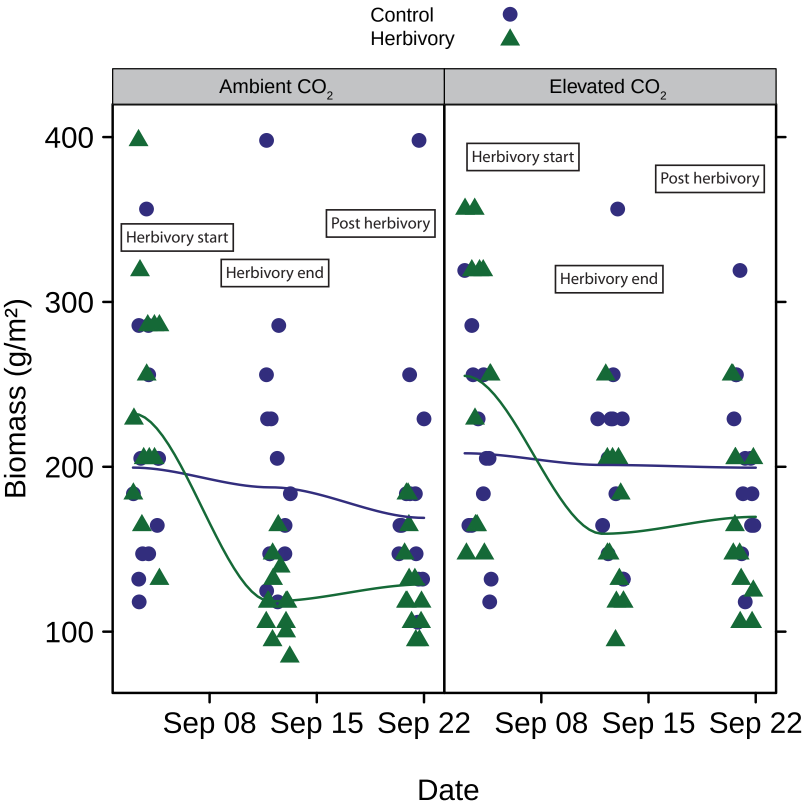

Figure 1 | Effects of elevated CO_2 and herbivory on plant aboveground biomass. The y axis shows the biomass of *Deschampsia flexuosa* (g/m²) in each cage as a function of herbivory (green triangles) or "no herbivory" (blue circles), herbivory time and CO_2 exposure (ambient CO_2: Left panel; elevated CO_2: right panel). Green and blue lines show the averages of grass biomass in cages with and without grasshoppers respectively.

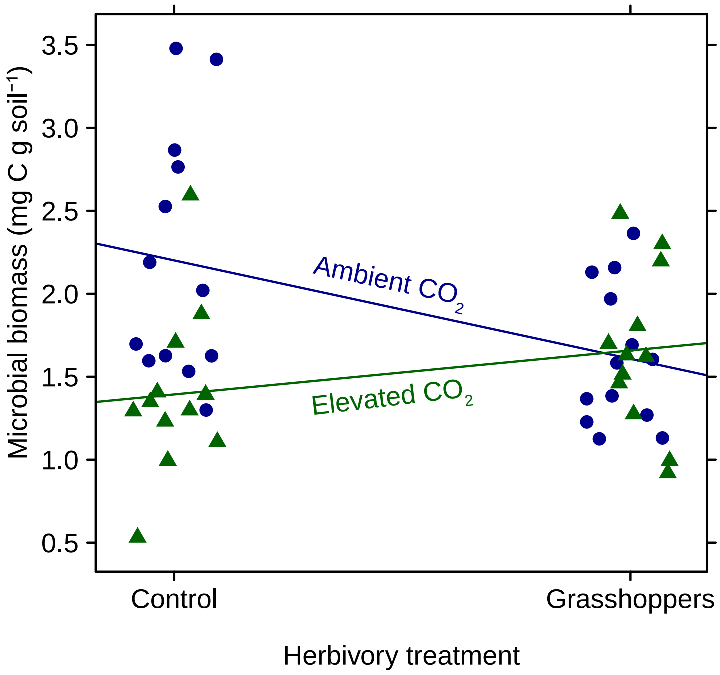

Figure 2 | Effects of aboveground herbivory and global change on belowground microbial biomass. Microbial biomass was reduced by elevated CO$_2$; herbivory increased microbial biomass, but only under elevated CO$_2$.

climate change affects aboveground-belowground interactions via changes in nutrient availability.
Species composition and community structure in terrestrial environments have been predicted to shift in response to climate change (van der Putten et al. 2009). Recent climate change experiments have shown that drought (Stokstad 2005), warming (Arnone et al. 2008), and elevated CO$_2$ (Langley &

Megonigal 2010) can alter ecosystem process rates such as photosynthesis (Albert et al., 2011) and nitrogen turnover (Larsen et al. 2011). However, most studies focused either on single species or combined just a few different climate change drivers. Furthermore, most studies have focussed on either above- or below ground responses and only few experiments have studied climate change effects on above-belowground interactions.

Most terrestrial plant species control or mediate the interaction between above- and belowground subsystems (rhizodeposition) suggesting that changes in the aboveground compartment will cascade to the belowground compartments (van der Putten et al. 2004). For example, herbivores feeding on aboveground plant parts have been shown to induce changes in a wide range of processes in the root zone, affecting rhizodeposition (Erb et al. 2009; Pineda et al 2010) and organisms in the soil food web (Bardgett & Wardle 2003)..

Climate change has been shown to affect aboveground herbivory (Stiling and Cornelissen 2007). The strong link between aboveground herbivory and belowground processes therefore suggests that climate change will lead to herbivory-induced changes in belowground processes such as rhizodeposition (Drigo et al. 2010). However, despite the importance of rhizodeposits for the growth of soil microbes and many other groups of soil organisms feeding on these, it is currently not known how climate change and herbivory interacts and affects rhizodeposition with consequences for a wealth of belowground processes responses. It is therefore crucial to improve our understanding of these interactions, using well-replicated factorial field experiments.

Here, we analyse how climate change affects foliar herbivores and how this effect is transferred to the belowground subsystem. We independently manipulate ambient air temperature by passive night time warming (+1 °C), precipitation by rain out shelters (4 week summer drought) and atmospheric CO$_2$ concentration by a FACE system (Free Air Carbon Enrichment, 510 ppm) in all combinations in fourty-eight 7 m^2 field plots in a shrubland ecosystem in Denmark (Mikkelsen et al., 2008, see **Methods**). We installed 25 herbivory cages (containing locally occurring grasshoppers) and 25 control cages on the plots (Figure S1) for eight days and measured vegetation parameters, abundance of belowground organisms and microbial growth (see **Methods**).

Grasshoppers removed roughly 30 percent of the grass biomass inside the cages under ambient conditions (66±14.7 g/m² from a standing crop of 208±13 g/m²; herbivory effect at harvest: $F_{1,40}$= 27.81, P <0.0001). Under elevated CO_2, herbivory was significantly lower than under ambient conditions (Date:herbivory:CO_2 interaction: $F_{1,68}$=4.55, P=0.036; Figure 1; Table S1a). None of the climate change factors affected leaf structural compounds (Table S2) and elevated CO_2 did not affect silica content (Table S3), indicating that climate change did not influence plant secondary compounds.

Aboveground herbivory had strong and significant effects on all measured components of the belowground subsystem: Microbial biomass, protozoan abundance, as well as microbial growth were highly significantly affected by aboveground herbivory (Table S1b, Figure 2, 3). Herbivory reduced microbial biomass, but greatly increased microbial growth and protozoan abundance (Table S1b), indicating that microbial activity was stimulated by herbivory. In addition, high microbial growth correlated strongly with high protozoan abundances (Figure S2), showing that herbivory effects were passed on in the belowground subsystem. Belowground nematode abundance was not significantly affected by aboveground herbivory. Under experimental climate change, the response of belowground microbial biomass to aboveground herbivory was clearly modified (Table S1b, Fig.2), indicating that global change drivers strongly and interactively affected aboveground-belowground linkages. In a similar study (Tate and Ross, 1997), microbial biomass also increased under elevated CO_2, but only if enough soil nitrogen was available. Notably, belowground grass root biomass and soil organic matter contents were not significantly affected by our climate change treatments, indicating that the observed effects on microbes were not caused by differences in root production or decomposition.

Grasshopper herbivory also had a stimulating effect on bacterivorous protozoa under elevated CO_2 in interaction with drought (Table S1b, Figure S3). This indicates that CO_2 modulated above-belowground effects also on microbivorous soil organisms.

Because our study system was increasingly nitrogen-limited at elevated CO_2 (Larsen et al. 2011), it is likely that soil microbes experienced progressive

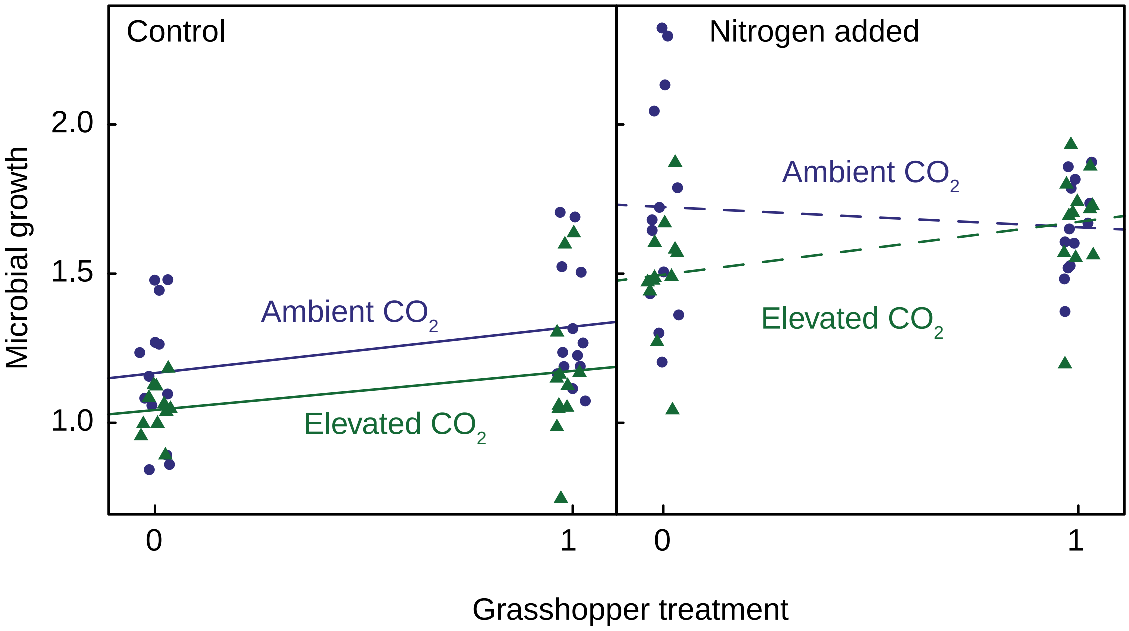

Figure 3 | Limitation of microbial growth. Results from microbial growth assays on soil samples from plants exposed to or excluded from grasshoppers and exposed to ambient CO_2 (blue circles) or elevated CO_2 (Green triangels) and with addition of (a) carbon and (b) carbon + nitrogen sources. Microbes tend to grow less under elevated CO_2 (P=0.077, Table 1); while aboveground herbivory increases belowground microbial growth when additional carbon is added (a) (P=0.020, Table 1) and approaching growth rates observed when N is also added (b). This indicates that herbivory effects are due to relieved N limitation.

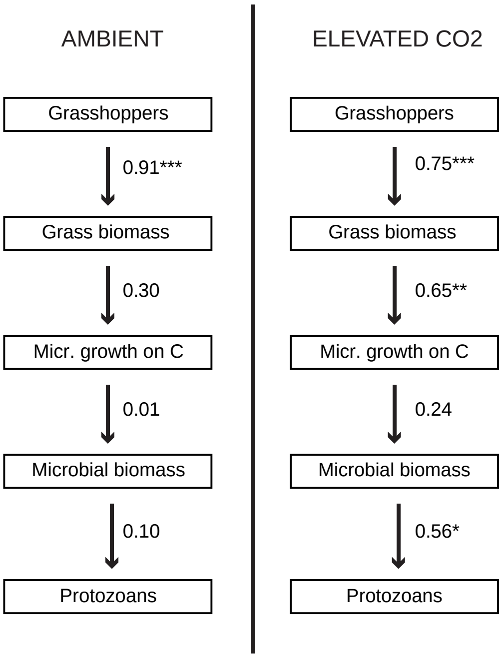

Figure 4 | Effects of elevated CO_2 on above-belowground interactions. The figure shows the pairwise correlations between individual variables with significance indicated by asterisks (*: $P<0.01$; **: $P<0.001$; ***: $P<0.0001$). Corresponding structural equation models produced essentially similar results but are not included here because the number of replicates precludes the use of SEM´s in this case. (a) ambient CO_2, (b) elevated CO_2.

nitrogen limitation (Luo et al. 2004; Reich et al. 2006). Aboveground herbivory may counteract microbial nitrogen limitation by inducing plant nitrogen transfer to the root zone. We tested this hypothesis by providing microbial community assays with extra sources of nitrogen (NH_4NO_3) to test for nitrogen limitation.

These analyses showed that microbial growth was N-limited even under ambient conditions (Fig. 3a). This N limitation was further amplified under elevated CO_2, as predicted by the progressive nutrient limitation hypothesis (Fig. 3a). When we added grasshopper herbivores to the system, microbial growth was consistently stimulated (Figure 3a, 3b). Finally, when we experimentally added nitrogen again, nutrient limitation disappeared (Figure 3b).

Taken together, these findings strongly suggest that plants and microbes competed for nitrogen, and that elevated CO_2 intensified this competition. Aboveground herbivores may reduce this competition by lowering plant growth and hence plants´ demand for nitrogen.

While a transfer of nitrogen from the plant to the soil is a likely explanation for our findings, further studies using labelled compounds in closed-chamber systems will be needed to describe the mechanisms in greater detail.

Recently, long-term experiments (Norby et al. 2010) have shown that terrestrial net primary production under elevated CO_2 may be limited by nitrogen availability. Our study has shown that nitrogen limitation affects not only aboveground plant biomass, but also the belowground subsystem. Meta analyses (Stiling and Cornelissen 2007) have shown that herbivory may decrease under future CO_2 levels. Combined with the findings reported here, this means that terrestrial N limitation may increase severely under elevated CO_2, with no compensatory effects of herbivores on the belowground subsystem. Overall, these processes may alter components of the global N and C cycle and reduce terrestrial carbon sequestration.

Methods summary

Experiments were conducted in a FACE facility in a sand dune area near Brandbjerg (55°53′N, 11°58′E) c.50 km NW of Copenhagen, Denmark where drought, warming and atmospheric CO_2 concentration are experimentally manipulated since 2005 (Mikkelsen et al. 2008). The experimental treatments are (i) elevated temperature (+ 1 °C in the upper 5cm of soil), (ii) elevated CO_2 (ambient 380 ppm, elevated 510 ppm), and (iii) summer drought (soil moisture down to 5% (vol/vol) for about one month). The experiment is fully facto-

rial, giving eight treatments with six replicates, in total 48 plots. In December 2005 two soil cores (10 cm diam., 20 cm deep) were established in all plots and filled with sieved and well-mixed soil from the area. In March 2006, cores were planted with *Deschampsia flexuosa*, the locally dominant grass species. On September 3, 2008, grass height was assessed in the cores and 25 out of the 48 plots had a pair of cores with sufficient grass growth, i.e. plant height 16.0 cm ± 0.5cm (average ±s.e.). The 25 plots were distributed with two replicates in warming*CO_2, four replicates in warming and in CO_2, and three replicates in the remaining five treatments. A nylon net bag was mounted on top of the 50 cores. About 100 females of the dominant grasshopper (*Chorthippus brunneus*) were collected in the area. The following day (September 4) two randomly selected adult female grasshoppers were added to one of the pots in each plot. Effects of drought in this study are legacy effects, because the drought treatment terminated two months earlier and soil water at the time of soil sampling (8.8 weight-%) did not differ between moisture treatments. Weather and soil environment prior to and during the present experiment are presented in Table S3. Dead individuals (four in total) were replaced every 2-3 days during the following eight days. On September 12 grasshoppers were removed and grass height measured in all cores. Ten days later (September 22) grass height was measured again and the 50 soil cores were brought to the laboratory. and rhizosphere soil was analyzed for microbial biomass (substrate induced respiration) during the first four hours of incubation (Anderson and Domsch 1978) but using soil slurries amended with C or C+N (Wamberg et al. 2003); the C amended slurries were used for microbial biomass determination. Microbial growth was assessed as fractional increase in respiration rate (Scheu 1993) in this case between 0-4h and 4-20h incubation of an agitated soil slurry [respiration rate 4-20h / respiration rate 0-4h] in the differently amended soil slurries. Number of bacterivorous protozoa (most probable number method, Rønn et al 1995), and number of nematodes (Whitehead and Hemming 1965) was also assessed. Grass material from cores without grasshoppers was analyzed for Si and crude fiber (Van Soest 1994), and average diameter of grass leaves measured under a dissection microscope.

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Supplementary Material

Table S1a | Parameter estimates from linear mixed-effects models fitted to data on grass height measured on 3rd and 12th September 2008. Note that parameter estimates are tested marginally, i.e. in presence of all other terms in the model. The corresponding sequential F tests are given in the main text. The unit of all parameter estimates is cm grass height. Significant effects are given in bold.

Term	Explanation	Value [cm]	SE	DF	t	P
Overall mean	Mean grass height per cage (tested against 0)	8.94	0.77	68	11.61	0.0000
Date (2008-09-12 minus 2008-09-03)	**Difference in height over time (negative values indicate herbivory)**	**-3.35**	**0.42**	**68**	**-7.97**	**0.0000**
Grasshopper	Marginal main effect of herbivory (Grasshopper minus control cage)	-1.37	0.87	68	-1.57	0.1212
CO_2	Marginal main effect of CO_2 (elevated minus ambient CO_2)	0.87	0.96	4	0.91	0.4156
Drought	Marginal main effect of drought (drought minus no drought)	-1.06	0.93	5	-1.13	0.3079
Date:Grasshopper	**Reduction in height due to herbivory over time**	**-5.76**	**0.58**	**68**	**-9.87**	**0.0000**
Date:CO_2	Interaction between date and CO_2	0.98	0.61	68	1.60	0.1150
Date:Drought	**Interaction between date and drought (grasses are shorter in drought plots)**	**-0.82**	**0.36**	**68**	**-2.28**	**0.0257**
Grasshopper:CO_2	Interaction between herbivory and CO_2 (irrespective of date)	0.89	1.27	68	0.70	0.4875
Date:Grasshopper:CO_2	**Decrease in herbivory in elevated CO_2 over time (grasses are taller)**	**1.82**	**0.85**	**68**	**2.13**	**0.0365**

Table S1b – Parameter estimates from linear mixed-effects models fitted to data on microbial biomass, microbial growth and protozoan abundance. Note that parameter estimates are tested marginally, i.e. in presence of all other terms in the model. The first row in the table gives the overall mean; columns two and three are dimensionless. Rows give (i) main effect parameter estimates, expressed as differences: Grasshopper minus control; elevated CO_2 minus ambient CO_2; Drought minus no drought; (ii) interaction terms (differences between intercepts). For example, a negative CO_2 main effect for microbial biomass means that there were more microbes present under ambient than under elevated CO_2 (compare this with Figure 2).

Variable	**Microbial biomass (mg C g^{-1} soil)**					**Microbial growth* (Control)**					**Microbial growth* (N added)**					**Protozoan abundance (ln g^{-1} soil)**				
	Value	SE	DF	|t|	P	Value	SE	DF	|t|	P	Value	SE	DF	|t|	P	Value	SE	DF	|t|	P
Overall mean	1.92	0.16	36	12.36	**<0.001**	1.24	0.04	37	31.34	**<0.001**	1.69	0.07	36	22.64	**<0.001**	9.99	0.15	28	64.97	**<0.001**
CO_2	-0.28	0.16	4	1.74	0.156	-0.14	0.06	4	2.36	0.077	-0.19	0.10	4	1.87	0.134	-0.13	0.17	4	0.76	0.492
Drought	0.49	0.14	36	3.51	**0.001**	--	--	--	--	--	--	--	--	--	--	-0.2	0.24	28	0.83	0.411
Grasshopper	-0.59	0.18	36	3.34	**0.002**	0.14	0.06	37	2.43	**0.02**	-0.09	0.08	36	1.14	0.262	0.5	0.22	28	2.26	**0.032**
Warming	--	--	--	--	--	--	--	--	--	--	0.09	0.04	36	2.13	**0.040**	0.14	0.23	28	0.62	0.542
Grasshopper:CO_2	0.85	0.25	36	3.33	**0.002**	--	--	--	--	--	0.25	0.11	36	2.16	**0.037**	0.34	0.32	28	1.08	0.289
Warming:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
CO_2:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	-0.26	0.32	28	0.82	0.422
CO_2:Warming	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	-0.15	0.33	28	0.46	0.651
CO_2:Warming:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Grasshopper:CO_2:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.94	0.63	28	3.06	**0.005**
Grasshopper:CO_2:Warming	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.41	0.64	28	2.21	**0.036**
Grasshopper:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	-0.95	0.44	28	2.15	**0.040**
Grasshopper:Warming	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	-0.77	0.45	28	1.72	0.097
Grasshopper:Warming:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Grasshopper:CO_2:Warming:Drought	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

*: (respiration rate 4-20h)/(respiration rate 0-4h)

Table S2 | Effects of global change on chemical composition and morphology of *Deschampsia*. Dry weight (g) of green leaves, senescent leaves, and roots; crude fibre (percent) and leaf diameter (mm) in green *Deschampsia* leaves from soil cores not exposed to herbivory. Treatment levels: A ambient, T warming, D drought, CO2 elevated CO2, plus combinations.

Treatment	Leaf weight				Root weight		Crude fiber		Leaf diameter	
	green (g)		senescent (g)		(g)		(percent)		(mm)	
	avg	s.e.	avg	s.e.	avg	s.e.	avg	s.e.	avg	s.e.
A	0.61	0.14	0.93	0.16	0.50	0.12	26.38	1.33	0.30	0.01
T	0.93	0.22	0.71	0.12	0.75	0.21	33.72	0.93	0.35	0.04
D	0.74	0.25	0.66	0.14	0.77	0.33	29.82	2.01	0.29	0.02
TD	0.43	0.13	0.41	0.04	0.34	0.14	28.71	1.03	0.28	0.03
CO_2	0.62	0.31	0.88	0.42	0.71	0.14	31.68	0.24	0.26	0.01
TCO_2	0.72	0.18	0.83	0.11	0.46	0.04	32.58	2.12	0.29	0.00
DCO_2	1.03	0.49	1.19	0.49	0.38	0.13	32.39	4.14	0.29	0.01
$TDCO_2$	0.38	0.19	0.81	0.42	0.51	0.13	33.41	4.69	0.28	0.01
Significance	n.s.		n.s.		n.s.		n.s.		$P(CO_2) = 0.0750$	

Table S3 Silica concentration (percent of D.W.) in green leaves

	Mean value (%)	s.e.
Ambient CO_2	0.89	0.04
Elevated CO_2	0.89	0.01

Table S4. Weather and soil conditions at the experimental site before, during and after the grasshopper experiment

	Dates in 2008		Air temperature 20 cm		Soil temperature 2 cm		Soil humidity (%). 0-20 cm		CO_2 concentration (µl l^{-1} daytime)	
Event or Time period	**start**	**end**	**Ambient**	**Warming Treatment**	**Ambient**	**Warming Treatment**	**Ambient**	**Drought Treatment**	**Ambient**	**Elevated CO_2**
Drought	05 May	27 May	14.1	14.7	11.2	11.7	13.3 (5 May) 10.4 (27 May)	12.8 (5 May) 5.5 (27 May)	421	498
June	28 May	30. Jun	17.8	18.1	14.7	15.1	6.1	5.5	394	480
July	01. Jul	31. July	19.7	19.8	16.5	16.7	9.8	9.3	382	466
August	01. Aug	03. Sep	17.2	17.1	16.0	16.1	13.9	13.4	365	468
Grasshopper experiment	04. Sep	12. Sep	15.6	15.9	15.1	15.4	14.4	13.9	365	469
Post grasshopper	13. Sep	22. Sep	11.1	11.6	12.2	12.7	12.9	12.3	361	474

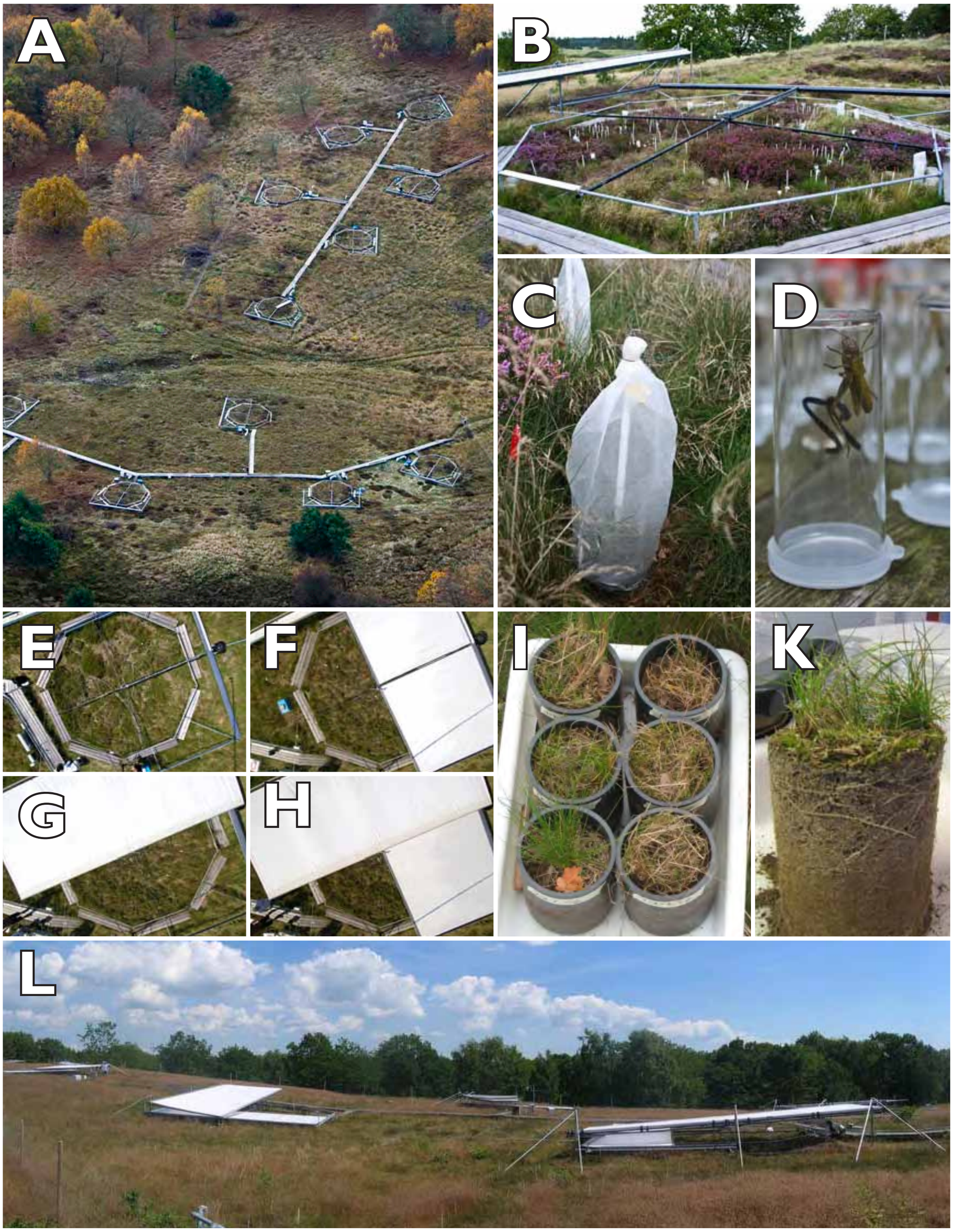

Figure S1. Experimental setup. (A) Aerial view of the CLIMAITE experiment. showing 10 out of 12 octagons (+/- CO_2). (B) A single octagon surrounded by CO_2 pipes and split into four halves for warming and drought treatment combinations. (C) Close-up of a soil core covered with nylon netting; (D) Randomization of grasshopper (Chorthippus brunneus THUNB.) individuals; (E-H) A series showing the positioning of the curtains controlling warming (F). drought (G) and warming plus drought (H); (I) A set of six extracted soil cores (left: control. right: herbivory); (K) close-up of a soil core before post-processing; (L) Ground panorama view of the CLIMAITE experiment. showing curtains in action.

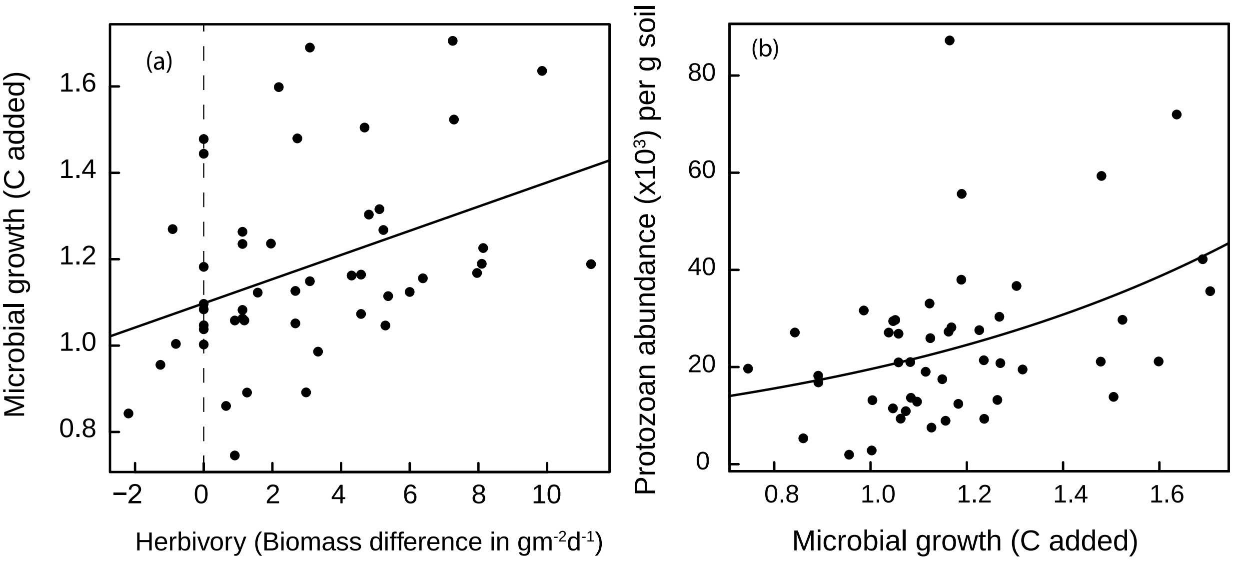

Figure S2| Relationships between herbivory, microbial growth and protozoan abundance. (a) More herbivory translates into higher microbial growth [(respiration rate 4-20h)/(respiration rate 0-4h) during soil incubation] when Carbon is added as the only substrate; solid line is from a linear regression. overall $P<0.0005$; dashed line indicates a biomass difference of 0 between herbivory and control cages; (b) High microbial growth coincides with high protozoan abundance. Note that this relationship does not imply a causal relationship; both abundances could be driven by a third (unmeasured) factor. The non-linear curve was fitted using a generalized linear model with a log-link and microbial growth as the explanatory variable). The slope of the curve was 1.13±0.004. $|z|=291.2$. $P<2x10^{-16.}$

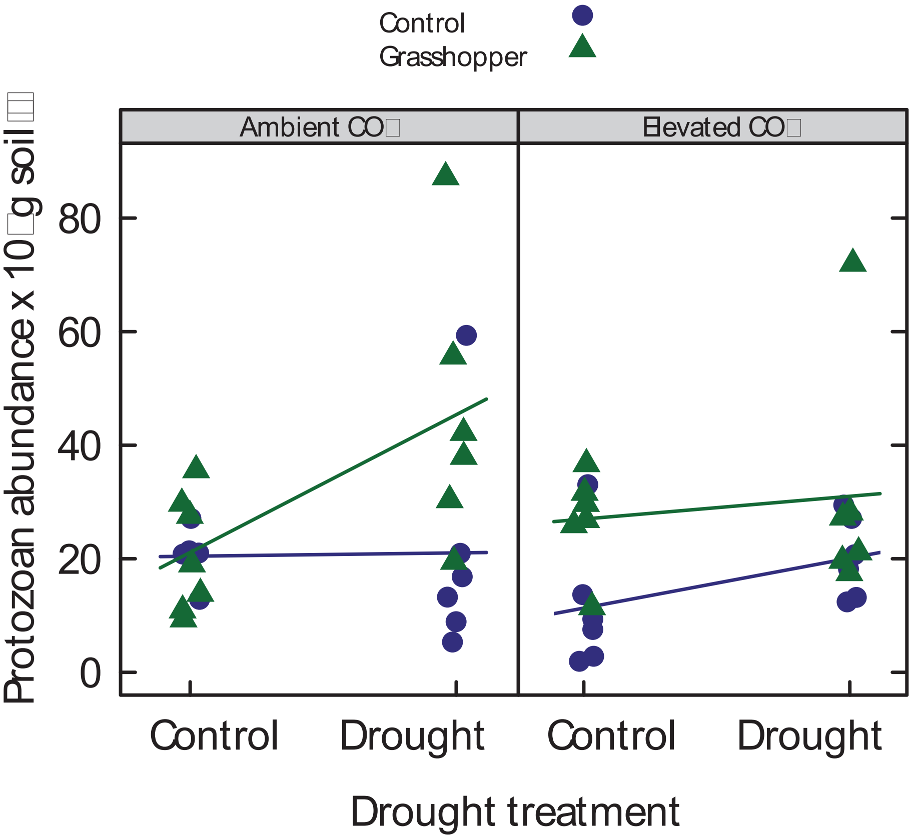

Figure S3| Climate change and herbivory effects on protozoan abundance. Abundance of protozoans as a function of herbivory (Herbivory: green triangles; No herbivory: Blue circles). drought treatment and CO_2 exposure (Ambient: left; elevated: right). Green and blue lines show averages for cages with herbivory and no herbivory respectively. Effects of grasshopper herbivory depended on CO_2 level and drought treatment (P=0.005, see Table S1b).

Chapter 7

Effects of arable fields on multitrophic interactions in wild plants

published as:

Gladbach DJ, Holzschuh A, Scherber C, Thies C, Dormann CF, Tscharntke T (2011) Crop-noncrop spillover: arable fields affect trophic interactions on wild plants in surrounding habitats. Oecologia 166:433-41.

Crop–noncrop spillover: arable fields affect trophic interactions on wild plants in surrounding habitats

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Received: 4 May 2010 / Accepted: 23 November 2010

Abstract Ecosystem processes in agricultural landscapes are often triggered by resource availability in crop and noncrop habitats. We investigated how oilseed rape (OSR; *Brassica napus*, Brassicaceae) affects noncrop plants in managed systems and semi-natural habitat, using trophic interactions among wild mustard (*Sinapis arvensis,* Brassicaceae), rape pollen beetles (*Meligethes aeneus,* Nitidulidae) and their parasitoids (*Tersilochus heterocerus,* Ichneumonidae). We exposed wild mustard as phytometer plants in two cropland habitat types (wheat field, field margin) and three noncrop habitat types (fallow, grassland, wood margin) across eight landscapes along a gradient from simple to complex (quantified as % arable land). Both landscape and local factors affected the abundance of rape pollen beetles and parasitoids. Rape pollen beetle infestation and parasitism rates on these plants were lower in noncrop habitats and higher in wheat fields and field margins, whereas beetles and parasitoids responded differently to landscape scale parameters. We found the hypothesized spillover from OSR crop onto wild plants in surrounding habitats only for parasitoids, but not for pollen beetles. Parasitism rates were not related to landscape simplification, but benefited from increasing proportions of OSR. In contrast, rape pollen beetles benefited from simple landscape structures, presumably due to multi-annual population build-ups resulting from long-term OSR planting (as part of the crop rotation). In conclusion, we showed that spillover from cropland affects parasitism rates on related wild plants outside cropland, which has not been shown so far, but can be expected to be a widespread effect shaping noncrop food webs.

Keywords Habitat identity · Herbivory · Large-scale effects · Local effects

Introduction

Landscape-scale patterns (sensu Turner and Gardner 1991) often affect ecosystem processes locally (Kareiva and Wennergren 1995; Hooper et al. 2005). Spatial configuration and composition of ecosystems and habitat diversity (Turner 1989) have been shown to be interwoven with land-use intensity (e.g., Wrbka et al. 2004), and may influence, as landscape effects, important trophic interactions such as biocontrol and herbivory (Gardiner et al. 2009) or pollination (Ricketts et al. 2008). Hence, both ecosystem services and dis-services (Zhang et al. 2007) in different agro-environments are promoted or constrained to various extents depending on landscape effects. Further, local effects such as habitat type and quality (habitat

Communicated by Jay Rosenheim.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1870-3) contains supplementary material, which is available to authorized users.

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identity) influence diversity and population size of organisms (Matter and Roland 2002; Haynes et al. 2007; Zaller et al. 2008a). Thus, local interactions are triggered by factors such as resource availability at both the landscape and the local habitat scale. However, most studies focus either on just local effects or the distribution of only one habitat type within a landscape (Meyer et al. 2009). Only a few studies have shown the interaction of landscape and local processes and their effect on patterns of insect diversity or trophic interactions (Cushman and McGarigal 2004; Dauber et al. 2005; Schweiger et al. 2005). As a simultaneous investigation of local and landscape patterns is difficult, an experimental approach introducing the same study system in a wide range of habitats and landscapes is a suitable, but little explored technique.

Here, we study the rape pollen beetle *Meligethes aeneus* (Fabricius 1775), which is one of the most important pest organisms in oilseed rape (OSR; *Brassica napus*, L.) (Büchi 2002; Alford et al. 2005). Published studies focused on pollen beetles and their parasitoids on OSR and emphasized that landscape context influences trophic interactions in cropland (e.g., Thies and Tscharntke 1999; Ricketts et al. 2008; Büchi 2002; Bianchi et al. 2006; Thies et al. 2008), whereas wild Brassicaceae have been considered only in their potential role as alternative host plants and not as a substitute resource when OSR fields are not longer available. Thus, examples of crop–noncrop spillover are almost absent (Rand et al. 2006). However, spillover may shape trophic interactions and thus we focus on the effect of cropland such as OSR on wild plants in noncrop habitats as well as in crop systems. Although existing theories predict the spillover of insects from crop to noncrop areas (Tscharntke et al. 2005; Rand et al. 2006; Rand and Louda 2006), we are not aware of studies that actually test how the huge and functionally important crop-related populations distribute across different habitats in the landscape shaping food webs,

In the present study, we investigated how landscape composition affects crop–noncrop spillover and associated trophic interactions. We quantified flower herbivory by rape pollen beetles and its parasitism by an ichneumonid wasp (Nilsson 2003) in different habitat types across a gradient of landscape complexity. Spillover may vary due to the source capacity as well as the attractiveness of the destination.

We hypothesize: (1) that both habitat type and landscape characteristics influence the spillover of pollen beetles (*M. aeneus*) and and parasitism by *Tersilochus heterocerus* (Thomson 1889) across the crop–noncrop interface; and (2) that increasing proportions of OSR as source habitat increases populations of specialized parasitoids more than their generalist hosts (following Thies et al. 2008), thereby affecting parasitism rates.

Methods

Experimental setup

The study was conducted after the flowering period of OSR from 1 June to 15 July 2006 in the vicinity of Göttingen, Lower Saxony, Germany (51°32′N, 9°56′E). The regional landscape pattern varies from intensively managed, simply structured landscapes that undergo a large inter-annual change (arable land up to 90%) to complex, extensively managed landscapes with a high proportion of near-natural, perennial habitats, (i.e., fallow, wood margin; arable land <20%). Eight landscapes, (i.e., landscape sectors) were chosen along this gradient of land-use intensity (Online Resource 1). There was no spatial correlation in the land-use gradient of the landscapes. Within each of the landscapes, we established study plots in five major habitat types (cereal field, field margin, fallow, grassland, wood margin) yielding a total of 40 plots. Field margins were chosen adjacent to cereal fields, wood margins were adjacent to cereal field, maize, or grassland. The locations of the habitats within landscapes were chosen as near to each other as possible (mean 123 ± SE 12 m), in order to achieve maximum similarity with respect to landscape-scale parameters. Distance of habitats to the nearest OSR crops (mean 197 ± SE 22 m) was tested in linear mixed effects models (lme models; Pinheiro et al. 2009) in R 2.9.11 (R Development Core Team 2009) and did not vary significantly ($F_{4,21} = 1.81$, $p = 0.147$). In each habitat we established (1 June) a plot of three wild mustard plants (*S. arvensis*), which are native rural plants found ubiquitously in agricultural and semi-natural habitats flowering from April to October. These sample plants served as phytometers and were grown in pots under standardized conditions in the same soil (standard garden soil, watered every second day), before the start of the experiment. With this phytometer approach, we achieved a maximum of similarity between our sampling units in the different habitats and landscapes. Excluding differences in plant quality was particularly important for this study, because it can change the oviposition rate of rape pollen beetles (Hopkins and Ekbom 1996). As part of the family Brassicaceae, wild mustard is greatly preferred to other yellow flowering plant families by *M. aeneus* (see above). Avoiding competition of the phytometers with other plants within the habitats was important in order to obtain a reliable measure of overspilling target organisms. This competition was minimized by choosing only habitats with low cover of alternative brassicacea plants (highest cover of non phytometer brassicacea was 2% *B. napus* in one plot; Online resource 2). From the time when rape pollen beetles dispersed from the fading OSR fields, the phytometers were freely accessible for rape pollen beetles and their parasitoids, so that differences due to local and landscape effects would be recognizable through population density and parasitism rates.

Study species

All developmental stages of rape pollen beetle *M. aeneus* (Coleoptera: Nitidulidae) feed on pollen. *M. aeneus* is one of the economically most important pest species on OSR, preventing seed development and hence causing loss of yield, but the species also feeds on a range of other plant species (Charpentier 1985), such as wild mustard, our phytometer (Ekbom and Borg 1996; Cook et al. 2006). In late April, adults start moving into (not yet flowering) OSR crops for maturity feeding and subsequent oviposition. In field conditions, the reproductive period usually lasts 2 months, but rape pollen beetles have been shown to exhibit reproductive plasticity depending on environmental or host plant conditions (Ekbom and Borg 1996; Billqvist and Ekbom 2001). In ideal conditions, oviposition may take place until October, and observations of beetles laying eggs in the year of their hatching have also been observed (Bromand 1983). Larvae of rape pollen beetles develop in flowers, drop to the ground on maturity, pupate and emerge after 1–5 weeks. Beetles live on a variety of plants (Hokkanen 2000; Gurr et al. 2003; Lehrman et al. 2008) when OSR crops have faded. Adults of the first generation die after egg laying, second generation beetles move into hibernating sites under herbaceous vegetation or moist woodland debris (Müller 1941; Nilsson 1988; Williams 2004). The larvae of the rape pollen beetle are attacked by the univoltine parasitoids, *T. heterocerus*, *Phradis interstitialis*, and *Phradis morionellus* (Hymenoptera: Ichneumonidae), of which the last is rare. The parasitoids are specialized on rape pollen beetles and attack host larvae in the first (*Phradis* spp.) and second (*T. heterocerus*) instar. After parasitizing the larvae in the flower, both endo-parasitoid species kill their host larvae after they drop to the ground before pupation in the soil (Jourdheuil 1960). Parasitoids peak and start egg deposition in May during OSR flowering (Williams 2006). They overwinter in their hosts in the ground and subsequently emerge from the soil of the last year's OSR crop area.

Data collection

Samples of rape pollen beetles were collected from the phytometers at flowering of wild mustard (27 June 2006) by clipping all flowering stalks and storing them in plastic cups at –22°C. The number of parasitized larvae was determined by dissecting the rape pollen beetle larvae under a binocular (Zeiss, Stemi SV 11). Parasitoid eggs were assigned to the parasitoid species by their typical pigmentation (black:*T. heterocerus*; white: *Phradis* spp.). Because we found only 1–2 individuals of *Phradis* spp. in two different landscapes, only *T. heterocerus* was included for further analyses. After peak ripening, we collected all remaining *Sinapis* plants and stored them at 1°C (15 July 2006). Plant damage to seed set was quantified by counting the number of pods and the podless stalks that remained after rape pollen beetle herbivory.

Landscape parameters were estimated on the basis of the official digital thematic maps (ATKIS – Digitales Landschaftsmodell 25/1; Landesvermessung und Geobasisinformation, Hannover, Germany, 1991–1996) containing areal measures of arable land, grassland, forests, hedgerows, garden land and settlement. In addition, we mapped habitat types in the field during the season, allowing a specific classification of land use in the areas with arable land (Online Resource 4). Data were digitized and analyzed in ArcView 3.2 (ESRI, Redlands, CA, USA) in a radius of 750 m around each experimental patch, since this scale has been shown to be appropriate for the studied host–parasitoid interactions (Thies et al. 2003). Habitats were also characterized by vegetation surveys using the Braun-Blanquet scale (Braun-Blanquet 1964). The surveys were conducted within 2 weeks at the beginning of the study period on five randomly chosen plots per habitat of 2 × 2 m each. Turboveg 2.79 (Hennekens and Schaminée 2001) was used to transform Braun-Blanquet data into plant percentage cover data and to analyze number and abundance of plant species (Online Resource 2).

Data analyses and statistics

Variation of adult rape pollen beetle numbers on the sampled phytometer may, in part, be due to diurnal activity patterns. Therefore, we included only the rape pollen beetle larvae in our analyses. Missing phytometer plants due to mammalian herbivory were treated as NA in the statistical analyses. Although being standardized, the phytometers had different numbers of flowering stalks by the time we collected the samples of rape pollen beetles. This variation, however, was not correlated to habitat type (Online Resource 3) or to any landscape parameters (Online Resource 1). To account for the varying sample size, we analyzed our data with the larval abundance divided by the number of flowers in the respective samples. Larvae per flower and parasitism rates in experimetal patches were arcsine square-root transformed and landscape and habitat type effects were tested in lme models (Pinheiro et al. 2009) in R 2.9.11 (R Development Core Team 2009). Obtaining normally distributed residuals after the transformation, we could use the more established and widely used lme models instead of generalized linear mixed models for analyzing non-normal data, which are more difficult to fit appropriately (Bolker et al. 2009).

Maximal models contained the following landscape-scale predictors: (1) % arable land, selected a priori based on our experimental design; (2) % OSR, as important predictor due to the focus of spillover from OSR into other habitats; (3) a small set of additional landscape-scale predictors shown to be important based on inspection of zero-order correlation matrices (Murray and Conner 2009), namely the mean perimeter to area ratio (MPAR) and the number of arable land patches in the landscape (Online Resource 4). MPAR gives information about the complexity of a landscape (see Bianchi et al. 2006). Low values of MPAR indicate large patches in a landscape whilst landscapes with high MPAR values are characterized by many small patches of fields and habitats, thus the number of different resource types tends to increase with MPAR. Local effects comprised habitat type and the number of larvae per flower. The maximum models were fitted as

$$y = \mathbf{X}\beta + \mathbf{Z}b + \varepsilon \qquad (1)$$

where y is the response variable (larvae per flower, parasitism rate), $\mathbf{X}$ is a fixed-effects regressor matrix, β is the vector of coefficients for local and landscape effects (fixed effects coefficients), b is a vector of random effects for landscapes, $\mathbf{Z}$ is a random-effects regressor matrix, and ε is a vector of independently and normally distributed errors (Pinheiro and Bates 2000). Two-way interactions were included. The random effect *landscape* (with eight levels) was included to represent nesting of habitats in landscapes. Landscape measures and habitat type were ordered according to the spatial scale, (i.e., large-scale effects prior to habitat type).

For each response variable, we used a stepwise AICc function, an information-theoretical approach for small sample sizes (Burnham and Anderson 2002), to find the minimal adequate model. Two maximum models were calculated for the response variable parasitism rate: first, we included conservatively only the design variables, (i.e., landscape effects and habitat type); the second, also included the number of larvae per flower which is a possible predictor for parasitism rates but was not initially included in the experimental design.

Seed number, seed weight, fruit set and destroyed buds were estimated per plant. These plant performance measurements were transformed, if necessary, before we fitted lme-models with landscape effects (see above), habitat type, larval infestation, podless stalks and parasitism as explanatory variables. To examine habitats for differences in species richness and evenness, we applied an ANOVA with Tukey's HSD post-hoc test (Hothorn et al. 2008). Means were calculated as arithmetic means, unless stated otherwise.

Results

Rape pollen beetle larvae

The minimal adequate model (Online Resource 5) for the prediction of rape pollen beetle larvae per flower included MPAR and habitat type as explanatory variables. Rape pollen beetle larvae responded negatively to landscape complexity (MPAR) on the landscape scale ($F_{1,25} = 16.36$, $p < 0.001$; Fig. 1). High larval numbers were observed in simple landscapes (MPAR = 0.05), whilst observations were low in complex landscapes (MPAR = 0.20; Online Resource 1). Other landscape parameters (in particular the proportion of OSR) had no significant effect on larval density. Habitat type significantly affected larvae per flower ($F_{4,25} = 3.13$, $p = 0.032$). Cereal fields (0.34 ± 0.05) and field margins (0.27 ± 0.05) had higher numbers of larvae per flower than fallow (0.21 ± 0.05), grassland (0.16 ± 0.03) and wood margin (0.14 ± 0.04; Online Resource 3). Significant differences of larvae per flower occurred only between cereal fields and field margins on the one hand and fallow, grassland and wood margin on the other hand (Tukey test; Fig. 1).

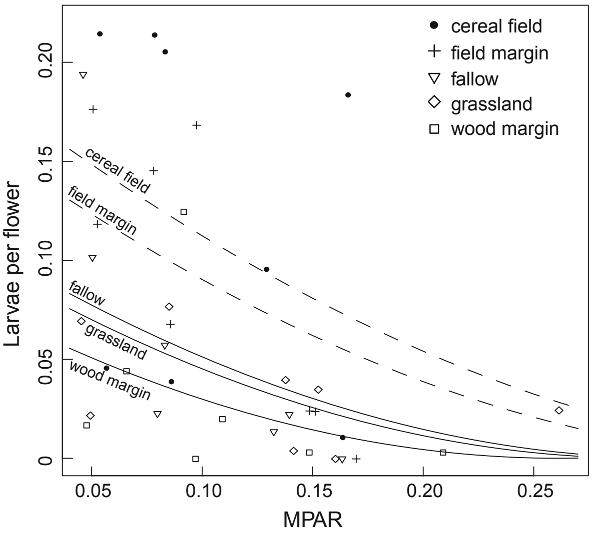

Fig. 1 The back-transformed data of larvae per flower as a function of the significant MPAR (*MPAR*: low values indicate simple, high values complex landscape structure) for each of the five tested habitats. The *lines* represent model predictions of larval infestation for each of the habitats. Wheat and field margin (*dashed lines*) had significantly higher larval infestation than grassland, fallow and wood margin (*solid lines*). *Lines* of the same type do not differ significantly from each other (Tukey's HSD)

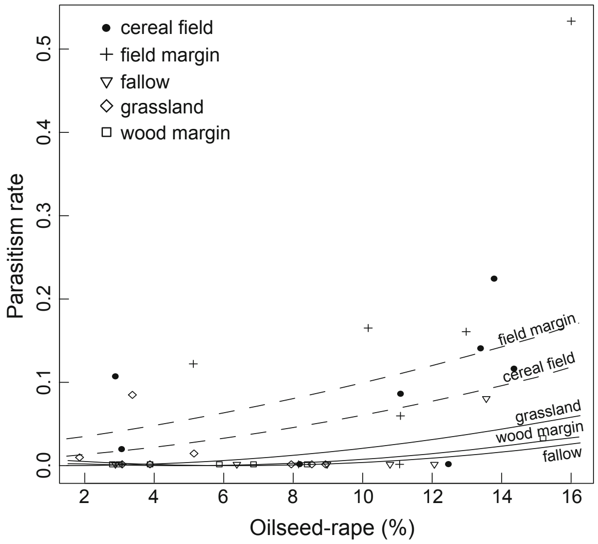

Fig. 2 Back-transformed data of parasitism rates as a function of percentage of oilseed rape crop area for each of the tested habitats. The *lines* represent model predictions of parasitism rates in each of the habitats. Parasitism rates were significantly higher in wheat fields and field margins (*dashed lines*) than in grassland, fallow and wood margins (*solid lines*). *Lines* of the same type do not differ significantly from each other. Also significant was the increase with OSR crop area

Parasitism rates

At the landscape scale, parasitism rates responded only to % OSR crop area ($F_{1,23} = 13.06$, $p = 0.002$; Figs. 2 and 3; Online Resource 5). Locally, host density, (i.e., larvae per flower; $F_{1,23} = 6.84$, $p = 0.015$) and habitat type ($F_{4,21} = 2.88, p = 0.047$) were significant predictors. Since these two factors correlated with each other, we calculated two different models, the design model with % OSR and habitat type (Fig. 2), and the model that included % OSR crop area and larvae per flower (Fig. 3). Parasitism rates increased more strongly with larval density if OSR crop area was high as shown by the interaction between both factors ($F_{1,23} = 6.09, p = 0.022$; Fig. 3). In landscapes with a low OSR crop area of 2%, parasitism was not observed, or only at rates below 10%. Parasitism rates by *T. heterocerus* increased with larvae per flower and increasing proportion of OSR crops (up to a maximum of 50%, Fig. 3).

Plant performance

The seed set of *S. arvensis* plants was not significantly influenced by any of the landscape variables nor by habitat type, the minimal adequate model was the null-model (Online Resource 5). A lme-model including the number of branches as a measure for plant size and podless stalks as a measure for herbivory (and landscape as random effect) explained the weight of all seeds of a plant, (i.e., yield) best. Total seed weight increased significantly with the number of branches ($F_{1,19} = 8.88$, $p = 0.008$) and decreased with the number of podless stalks ($F_{1,19} = 4.77$, $p = 0.042$). Surprisingly, the amount of rape pollen beetle

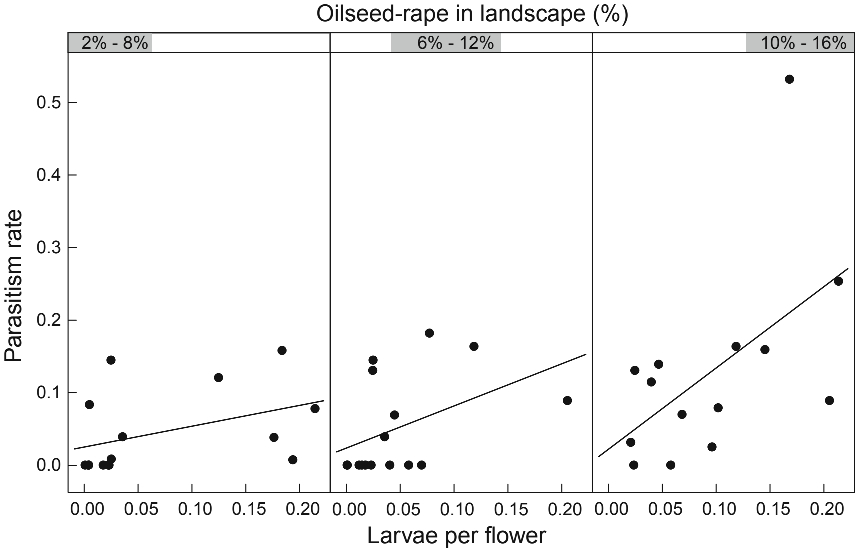

Fig. 3 Back-transformed parasitism rates as a function of the interaction between larval infestation and three categories of oilseed rape crop area (indicated by the *shaded areas* and the percentage values at the *top*). Note that this figure was created using the percentage of OSR as a conditioning variable (see Becker and Cleveland 1996; Sarkar 2008). Graphs are overlapping for OSR crop area to avoid too distinct separations of this continuous variable. Parasitism rates responded positively to larval densities and OSR crop area. The synergistic interaction between larvae per flower and rape crop area is apparent in the increasing slope from *left* to *right*

larvae per flower however could not be linked to the number of podless stalks ($p = 0.633$).

Discussion

We showed that both landscape and local factors affect the abundance of rape pollen beetles (*M. aeneus*) and parasitism by *T. heterocerus*. Whilst the reaction to habitat type was similar, both species responded to different landscape parameters. We found the hypothesized spillover from OSR crop onto wild plants in surrounding habitats only for parasitism, but not for pollen beetles, providing one of the first pieces of evidence for shifts in trophic interactions caused by organisms emigrating from cropland.

Habitat type effects on rape pollen beetle larvae

Twice as many rape pollen beetle larvae per flower were found on phytometer plants in cropland habitats such as wheat fields and adjacent field margins in comparison to numbers in the semi-natural habitats (grassland, fallow, wood margin). The higher colonization of phytometers in cropland habitats may be the result of a multiannual population build-up of this crop inhabiting species (Rand and Tscharntke 2007). Crop rotation with periodic availability of mass-flowering resources has been shown to change landscape-wide densities of associated organisms (Thies et al. 2008). The higher colonization of phytometers support this study and reflect elevated densities of rape pollen beetles in cropland habitats. In contrast, near-natural habitats provide resources constantly, but at a lower level, thus preventing the establishment of high pollen beetle abundances.

Habitat type effects on parasitism

Similar to the results of the larval density of rape pollen beetles, parasitism rates were high in wheat fields and field margins and low in the other three habitat types, i.e., parasitoids were more successfull than their hosts in crop systems.

Parasitism rates increased with larval density (as, for example, in Elzinga et al. 2007), indicating that higher numbers of larvae can be detected more easily. Since *T. heterocerus* is highly specific to the olfactory signals of (infected) Brassicaceae (Lewis and Tumlinson 1988; Vet et al. 1995; Renwick 2002; Wackers 2004; Jönsson et al. 2005; Jönsson and Anderson 2007), parasitoids concentrated on host plants with high rape pollen beetle infestation. Thus, habitat triggered infestation levels of *S. arvensis* with rape pollen beetle larvae and thereby even stronger parasitism rates.

Landscape-scale effects on rape pollen beetle larvae

The numbers of rape pollen beetle larvae on the phytometer plants decreased with an increase of landscape complexity, which is in line with some previous studies (Thies and Tscharntke 1999; Thies et al. 2003; but see Zaller et al. 2008b). Simple landscapes may support a population build-up of rape pollen beetles over many years, because they consist of large arable crop patches (including OSR) with uniform resources (Grilli and Bruno 2007). Complex landscapes, in contrast, have scattered small patches of different resource types and thus are likely not to provide enough supply for local mass-populations.

In contrast to our expectation that OSR fields are the main source for spillover of rape pollen beetles, we found no correlation between OSR area and infestation rates of the rape pollen beetle larvae. This is in line with Thies et al. (2008), but in contrast to other studies suggesting pest pressure to increase with cropping area (Jonsen and Fahrig 1997; den Belder et al. 2002; Klug et al. 2003). The lack of response to OSR crop area may be a result of large-scale dispersal patterns (Thies et al. 2008), intraspecific larval competition on the phytometers (Nilsson 1988; Ekbom 1998; Hokkanen 2000), or due to abscission of heavily infected buds (Williams 2004).

Landscape-scale effects on parasitism

Oilseed rape appeared to be a great source of parasitoids in June. The positive correlation between parasitism rates and OSR crop area indicates that the parasitoids shift from OSR to other (more limited) resources in the landscape after depletion of hosts in OSR fields. This supports similar results of Thies et al. (2008), who showed that reductions of OSR between years enhanced parasitism. Apart from the positive effect on parasitism rates, OSR crop area interacted significantly with the number of rape pollen beetle larvae. The increase of OSR crop area intensified the positive response of parasitism rates on host density, i.e., larvae per flower. This is possibly the consequence of an easier detection at higher host densities combined with a higher availability of parasitoids from larger OSR areas. Despite these spillover and concentration effects on the landscape scale, mean parasitism rates remained at a low level (<20%; Figs. 2 and 3). Two mechanisms may explain this pattern. First, parasitoid populations peak in May (Williams 2006). With a limited lifespan of 1–2 weeks during the summer (Nilsson 2003), the observed parasitism rates may be the result of a declining population. Second, Elzinga et al. (2007) reported that parasitoids occur with lower frequency in small patches compared to larger ones. The three phytometer plants established in the habitats constitute a small patch in contrast to the OSR and this is why the observed parasitism rates ranged below the ones that are usually observed in OSR crops (*T. heterocerus* parasitism rate 0.2–0.3; Thies et al. 2003).

Thies et al. (2008) considered the regional population pool, (i.e., the pool present within OSR areas) more important for biological control than local management (in their case establishing field margins), and stated that parasitoids in agricultural landscapes can be strongly influenced by interannually changing crops. Thus, the lack of response of parasitism to the area of semi-natural habitats in a landscape can be best explained with the specialization of *T. heterocerus* which binds the parasitoid strongly to the area of OSR. Further, the response of parasitoids, but not herbivores, to changes in OSR area with corresponding changes in parasitism rates supports the general idea that parasitoids are more sensitive to disturbances and environmental change than their hosts (Kruess and Tscharntke 1994; Holt et al. 1999; Elzinga et al. 2007).

Seed set of *Sinapis arvensis*

The decrease of total seed weight per phytometer plant with an increase of podless stalks indicated that herbivory negatively affected the yield of *S. arvensis*. Podless stalks are a typical sign of herbivory by rape pollen beetles (Thies and Tscharntke 1999). However, the number of rape pollen beetles or their larvae was not related to the number of podless stalks. This may have been caused by the fact that the observed herbivory is not only due to the rape pollen beetle numbers at the time of collection but also a result of continuous herbivory throughout the experiment. Second, loss of ripe pods due to maturity of the phytometer plants (Bruce et al. 2002) may account for variation that remains unexplained.

Conclusions

Landscape-scale factors explained the observed change of insect trophic interactions more than habitat type due to spillover. Mortality of rape pollen beetles by parasitism was higher in simple landscapes with a high proportion of OSR crops. The response of parasitism to host density profited particularly well from a larger proportion of OSR in the landscape. Positive density dependence in parasitoids is widespread and a basis of successful biological control stabilizing prey populations at low levels (Hassell and May 1974). According to our results, parasitoid spillover from cropland may significantly influence trophic interactions in wild habitats, which is rarely shown, but should be widespread shaping natural food webs.

Acknowledgments We thank K. Eckel, K. Krewenka, G. Hornemann, F. Goedecke and P. Weigelt for their help in the field and the farmers for providing their field-sites. We would also like to thank Jay A. Rosenheim and two anonymous referees for comments on an earlier version of this manuscript. Funding by the BESS (Biotic Ecosystem Services) project of the Helmholtz Association of German Research Centres (VH-NG-247) is acknowledged.

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Electronic Supplemental Material

Online Resource 1 Measures are averaged over all habitat types and given as mean values ± 1SE for each landscape.

	Barterode		Bodensee		Grossenrode		Meensen		Reinshof		Roringen		Settmarshausen		Varlosen	
larvae	97.20	±71.99	117.60	±93.13	65.50	±67.1	92.00	±99.62	32.25	±58.52	64.00	±56.47	53.80	±73.92	120.80	±188.58
flowers	768.60	±374.39	405.80	±86.64	667.75	±675.44	475.60	±207.95	306.50	±222.35	360.40	±190.04	361.00	±264.88	382.00	±298.83
parasitism rate	0.14	±0.23	0.00	±0.01	0.00	±0.01	0.05	±0.04	0.00	±0	0.08	±0.08	0.06	±0.07	0.08	±0.11
number of patches	138.60	±9.63	90.20	±3.83	199.80	±26.34	80.20	±27.49	95.40	±15.76	112.60	±8.26	239.60	±60.58	171.20	±7.56
mean patch size (ha)	1.28	±0.09	1.95	±0.08	0.87	±0.15	2.36	±0.61	1.89	±0.37	1.57	±0.12	0.77	±0.21	1.03	±0.05
habitat diversity (Simpson Index)	0.71	±0.22	1.06	±0.06	1.46	±0.06	1.18	±0.28	0.69	±0.2	1.47	±0.19	1.72	±0.11	1.48	±0.11
number of patches arable land	88.80	±14.36	48.20	±3.7	45.00	±5.48	24.60	±2.07	40.80	±8.9	34.00	±2.92	22.00	±6.78	52.40	±7.47
MPAR	0.11	±0.02	0.05	±0	0.15	±0.01	0.10	±0.03	0.21	±0.04	0.05	±0.01	0.16	±0.01	0.08	±0.01
% arable land	83.50	±6.03	66.70	±4.04	43.71	±5.18	55.82	±20.31	84.69	±4.85	36.81	±4.86	18.34	±1.26	41.21	±6.17
% fallow	1.42	±1.16	3.85	±1.44	2.35	±0.55	2.82	±0.72	1.14	±0.67	6.92	±1.17	8.69	±2.57	14.88	±2.97
% natural near habitats	7.58	±4.27	24.02	±4.82	43.65	±8.68	36.06	±19.73	5.02	±1.86	45.78	±5.99	60.82	±6.34	35.23	±4.23
% cereal crops	64.88	±2.72	46.56	±4.51	26.79	±11.29	36.93	±14.12	63.21	±4.85	25.96	±2.24	14.83	±1.55	28.54	±1.9
% OSR	12.74	±3.48	3.59	±1.29	9.99	±4.08	8.66	±3.46	6.80	±4.45	10.73	±2.68	3.47	±1.05	10.28	±4.1
% grassland	2.99	±2.82	11.64	±1.24	11.97	±6.01	10.62	±5.9	1.75	±0.97	9.26	±13.06	34.09	±3.98	29.81	±1.36
% wood	2.99	±2.38	12.07	±4.56	28.66	±13.52	22.63	±9.35	0.02	±0.01	31.96	±17.65	22.68	±10.37	2.18	±4.3

Online Resource 2 Mean area (or length) plus standard error are calculated over all landscapes for all habitats. Shannon index and species richness are given for all plants that have been recorded in the respective habitats over all landscapes. For each habitat the 10 most abundant plants are listed, with percentaged occurrence of all plots of the respective habitat. Additionally the mean cover for each of the plants is given for all plots that contained the respective plant.

presence in landscape			vegetation				
habitat	mean	standard error	shannon index	species richness	plants	relative presence in plots	mean cover in % (in plots where present)
cereal field (ha)	38.46	2.91	0.23	2.91	*Triticum aestivum*	100.00	86.00
					Viola arvensis	28.33	2.29
					Alopecurus myosuroides	16.67	22.60
					Papaver rhoeas	13.33	2.88
					Fallopia convolvulus	8.33	2.40
					Fumaria officinalis	8.33	1.80
					Aphanes arvensis	6.67	14.00
					Cirsium arvense	6.67	3.50
					Poa pratensis	6.67	2.50
					Brassica napus	6.67	2.00
field margin (m)	26297.32	1733.85	1.67	12.40	*Dactylis glomerata*	91.67	12.00
					Poa trivialis	81.67	24.04
					Poa pratensis	73.33	17.30
					Elymus repens	55.00	10.58
					Alopecurus pratensis	51.67	18.90
					Taraxacum Sec. Ruderalia	51.67	4.39
					Arrhenatherum elatius	45.00	14.41
					Bromus hordeaceus	45.00	9.85
					Festuca pratensis	40.00	6.21
					Galium aparine	33.33	4.80
fallow (ha)	5.26	0.74	2.01	13.55	*Poa trivialis*	65.00	6.33
					Arrhenatherum elatius	63.33	37.53
					Poa pratensis	50.00	8.10
					Dactylis glomerata	46.67	11.36
					Taraxacum Sec. Ruderalia	45.00	4.04

presence in landscape			vegetation				
habitat	mean	standard error	shannon index	species richness	plants	relative presence in plots	mean cover in % (in plots where present)
					Cirsium arvense	40.00	4.13
					Festuca rubra	38.33	20.74
					Elymus repens	38.33	12.26
					Holcus lanatus	36.67	30.77
					Bromus hordeaceus	33.33	2.70
grassland (ha)	14.02	1.95	1.86	14.32	*Poa pratensis*	81.67	10.35
					Poa trivialis	75.00	28.02
					Alopecurus pratensis	73.33	26.25
					Taraxacum Sec. Ruderalia	61.67	7.30
					Dactylis glomerata	60.00	7.08
					Cerastium holosteoides	58.33	2.29
					Lolium perenne	38.33	39.04
					Holcus lanatus	36.67	5.77
					Veronica arvensis	36.67	2.23
					Arrhenatherum elatius	35.00	25.95
wood margin (m)	9311.50	1393.62	1.67	12.08	*Dactylis glomerata*	80.00	10.85
					Galium aparine	73.33	3.84
					Poa pratensis	53.33	6.50
					Arrhenatherum elatius	46.67	22.18
					Geum urbanum	46.67	2.64
					Poa trivialis	43.33	15.92
					Elymus repens	43.33	11.96
					Fraxinus excelsior	43.33	3.08
					Bromus sterilis	41.67	22.52
					Veronica hederifolia	36.67	2.86

Online Resource 3 Measures are averaged over all landscapes and given as mean values ± 1SE for each habitat type.

	cereal field		fallow		field margin		grassland		wood margin	
larvae	163.00	±136.32	38.57	±46.56	100.00	±81.22	68.63	±78.86	27.86	±28.39
flowers	603.00	±343.44	287.00	±137.62	452.88	±234.38	549.25	±532.29	402.00	±174.65
parasitism rate	0.09	±0.08	0.01	±0.03	0.13	±0.18	0.01	±0.03	0.00	±0.01
number of patches	140.63	±56.37	137.63	±65.04	147.25	±83	152.38	±61.84	126.88	±35.49
mean patch size (ha)	1.46	±0.63	1.58	±0.8	1.49	±0.68	1.31	±0.49	1.49	±0.43
habitat diversity (Simpson Index)	1.21	±0.38	1.23	±0.39	1.17	±0.42	1.32	±0.46	1.18	±0.38
number of patches arable land	48.00	±26.27	39.38	±16.45	47.88	±22.48	44.75	±22.26	42.38	±20.47
MPAR	0.10	±0.05	0.12	±0.07	0.11	±0.05	0.13	±0.07	0.12	±0.05
% arable land	55.52	±23.34	56.10	±22.18	56.08	±25.19	49.83	±26.53	51.70	±25.32
% fallow	4.82	±4.28	5.47	±4.47	4.68	±4.04	5.91	±5.37	5.40	±6.22
% natural near habitats	31.02	±20.28	29.87	±17.17	30.02	±19.87	34.33	±22.68	36.12	±23.03
% cereal crops	38.01	±18.81	39.87	±15.01	38.63	±19.89	38.53	±20.91	37.28	±21.66
% OSR	9.92	±4.72	8.79	±4.35	9.74	±4.19	5.35	±2.77	7.61	±4.96
% grassland	12.30	±12.63	14.07	±12.59	12.30	±13.1	19.29	±13.95	12.13	±10.92
% wood	15.95	±15.33	13.47	±11.53	15.12	±17.26	10.68	±12.76	21.76	±17.98

Online Resource 4 The correlation matrix shows r^2-values of dependent variables for the most important landscape-scale parameters. Bold values have been used as predictor variables in the maximal models. Landscape-scale parameters were measured in all landscapes on a radius of 750m.

	larvae/flower	parasitism rate
Landscape structure metrics		
mean edge/patch	–0.044	–0.041
mean edge/patch arable land	–0.033	–0.213
mean patch size	0.037	–0.152
mean patch size arable land	–0.033	–0.208
MPAR	**–0.367**	–0.131
MPAR arable land	–0.006	0.158
number of patches	–0.039	0.115
number of patches arable land	0.040	**0.361**
total edge	–0.091	0.247
total edge arable land	–0.002	0.273
wood edge	–0.075	–0.071
Landscape composition metrics		
% arable land	–0.05	0.092
% beans	–0.3	–0.169
% cereal field	–0.105	0.080
% fallow	0.250	–0.025
% grassland	0.139	–0.071
% maize	0.192	–0.14
% OSR	0.155	**0.482**
% orchard	0.012	0.250
% perennial near–natural habitats	0.033	–0.117
% potatoes	–0.089	–0.038
% sugar beet	–0.198	–0.113
% urban area	–0.192	0.018
% water	–0.22	–0.146
% wood	–0.041	–0.094
% shrubs	–0.194	0.079
crop diversity (Simpson Index)	0.109	–0.028
crop evenness	0.113	0.086
habitat diversity (Simpson Index)	0.064	–0.148
habitat evenness	0.077	–0.114
number of crop types	0.080	0.269
number of habitat types	0.088	0.096

Online Resource 5 The maximal and minimal adequate models from the stepwise AICc analysis were calculated with landscape as random factor and are given for the respective response variable. The maximal models were fitted with the following landscape-scale predictors: % arable land + MPAR + % OSR + number of arable land patches.

dependent	model	model fixed factors	factors	required DF	observations	F-value	p-value	AICc
larvae/flower	maximal model	landscape factors + habitat identity + landscape predictors * habitat identity						69.14
	minimal model	MPAR + habitat identity	MPAR	1	25	16.36	< 0.001	–41.86
			habitat identity	4	25	3.13	0.032	
parasitism	maximal model	landscape factors + habitat identity + landscape predictors * habitat identity						167.75
	minimal model	%OSR + habitat identity	%OSR	1	21	12.03	0.002	–12.75
			habitat identity	4	21	2.88	0.047	
parasitism	maximal model	landscape factors + larvae/flower + landscape factors * larvae/flower						93.48
	minimal model	(%OSR + larvae/flower)^2	% OSR	1	23	13.06	0.002	–18.48
			larvae/flower	1	23	6.84	0.015	
			%OSR:larvae/flower	1	23	6.09	0.022	

Online Resource 5 (continued)

dependent	model	model fixed factors	factors	required DF	observations	F-value	p-value	AICc
seed set	maximal model	landscape factors + habitat identity + larvae/flower + landscape predictors * habitat identity + landscape predictors * larvae/flower						56.14
	minimal model	1 (null model)	intercept	1	25	109.46	< 0.001	45.24

Chapter 8

Scale effects in biodiversity and biological control

accepted for publication as:

Scherber C, Lavandero B, Meyer KM, Perovic D, Visser U, Wiegand K, Tscharntke T (2012) *Scale effects in biodiversity and biological control: methods and statistical analysis*. Book chapter in: Gurr GM, Wratten SD, Snyder WE (eds.) Biodiversity and Insect Pests: key issues for sustainable management. Wiley Blackwell, to appear in print 2012.

1 Definitions of scale, and an outline for this chapter

The structure of agricultural landscapes is likely to influence organisms living in these landscapes, and in particular, insect pests and their natural enemies (Gámez-Virués et al., this volume). Interactions at a local scale (for example an individual field) are likely to be influenced by processes acting at larger scales (for example the surroundings of that field; Plate 9.1). This is often called scale dependence or context dependence (Pearson 2002).

This chapter serves as an introduction to the design and analysis of studies on biocontrol at different spatial scales. Spatial scale can be described by two factors, grain and extent (Wiens 1989; Fortin and Dale 2005). Grain is the size of an individual sampling unit (for example a plot measuring 4 m²); extent is the total size of the study area (for example a landscape measuring 100 ha). The grain size used for individual study units should be carefully chosen to match the spatial structure of the phenomenon being studied. For example, a grain size of 0.5 cm could be necessary in a study of insects inhabiting wheat stems (where the spatial arrangement of damaged vs. intact wheat stems is of interest). In addition, the grain size can also be important when it comes to data analysis - that is, when data are aggregated for statistical analysis. Hence, "spatial scale" can refer to an individual study organism, an individual sampling unit, or an individual unit of statistical analysis (see also Dungan et al. 2002).

Knowing now what we mean by "scale", we may now ask: How can scaling effects be included in studies on pest control? Before addressing scale effects out in the landscape, it is often useful to start with smaller-scale laboratory systems where it is easier to control for confounding variables. We therefore start this chapter with an introduction to the problem of "upscaling", that is, the extrapolation from smaller to larger scales. We then move on to the landscape scale, and provide an overview of field methods used to study the movement of organisms through the landscape. This section is followed by two sections on data analysis and modelling. Finally, we conclude the chapter with some guidelines likely to be useful for practitioners who want to incorporate scale effects in their own biocontrol studies.

2 From the laboratory to the field: upscaling problems

In traditional biocontrol studies, it is often necessary to start with a series of smaller-scale laboratory experiments before moving to the field scale. For example, we need to understand the host specificity of biocontrol agents, or the food plant spectrum of individual insect herbivores, before we can begin to understand what is happening in the field. Often, the underlying interactions between the biological

Plate 9.1: Scale transitions and landscape complexity in agroecosystems. (a) Wheat spikes are attacked by pest insects (e.g. aphids) interacting with biocontrol agents on a local scale; (b) a complex agricultural landscape near Holzminden (Central Germany); (c) a simple agricultural landscape in the cereal plain of Chizé (France). All photographs by C. Scherber.

control agent and the pest organisms occur at the individual level at a scale of centimeters and smaller. To develop efficient biological control measures, we need to understand individual-level ecological processes such as herbivory, parasitism, colonization, and competition and then upscale this knowledge to the level of whole plants or whole stands. However, upscaling is not a straightforward task for ecological and methodological reasons. The ecological processes that drive small-scale and large-scale patterns are usually not the same and do not necessarily overlap (Hartley et al., 2004; Teodoro et al., 2009; see also Gámez-Virués et al., this volume). For instance, the foraging pattern of gall-forming insects differs across scales from the leaf over the branch to the tree level (Lill, 1998). Similarly, parasitism by different parasitoids of the forest pest *Malacosoma disstria* was affected both by spatial scale and by parasitoid body size (Roland & Taylor, 1997). Hence, ecological mechanisms between scales cannot always be easily compared. The main methodological challenge is to maintain the high resolution (grain, see introduction) of small-scale laboratory studies when increasing the extent of a study to the field scale (e.g. Xia et al., 2003). This is often not possible due to logistic constraints such as limited manpower, facilities, or computing power. The methodological alternative is to decrease the resolution of a study when moving from the laboratory to the field scale. Aggregation procedures can be used to achieve this decrease in resolution. However, nonlinearities and thresholds often complicate aggregation procedures, so that aggregation provides no simple upscaling solution, either.

These difficulties of scaling up from small to large scales are reflected in the scarcity of upscaling approaches and of studies that adopt or test these approaches by using scales as explanatory variables. The simplest approach is to take samples at different scales, ideally in a nested manner (hierarchical sampling approach). Due to the logistic constraints mentioned above, the resolution of the samples will in most cases change across scales (for an exception see Roland & Taylor, 1997). If the relationship between the ecological variable of interest and the scales on the x-axis is linear, upscaling of the ecological process can be performed based on this relationship. Unfortunately, most studies adopting this approach have found scale-dependence of the ecological process, preventing straightforward upscaling (e.g. parasitism: Lill, 1998; Matsumoto et al., 2004; mite predation: Zhang Anderson 1993; 1997; foraging in multitrophic systems:Heisswolf et al., 2006; pathogenic nematode attack: Efron et al., 2001). We are aware of one exception, where upscaling of parasitoid foraging from the local to the landscape scale yielded consistent results (Fraser et al., 2008).

Three general approaches can be taken to scale up from small to large scales: Sampling at different scales, interpolating between local estimates to cover larger scales, and extrapolating from local estimates to larger scales (Table 9.1). The first approach of taking (hierarchical) samples at different scales is often analyzed with scale-area plots to determine the scale-dependence of ecological processes (Table 9.1). When sampling is not possible at multiple scales, local estimates have to be used to reach larger spatial or temporal scales, either by interpolating or extrapolating. In the second approach, the space or time between estimates is interpolated to cover larger areas or time frames. Methods of spatial interpolation include Voronoi polygons and thin plate spline interpolation (Table 9.1) and have been applied to species distribution modelling (Jarvis & Collier, 2002). Species distribution modelling is also the major field of application of the third approach in which bioclimatic models extrapolate local estimates to larger scales using regression techniques (Table 9.1). However, non-climatic factors such as biotic interactions, rapid evolutionary change and dispersal may also affect species distributions, but are often not included in bioclimatic models (Pearson & Dawson, 2003).

For a successful extrapolation across scales, critical scale transitions (He and Hubbell 2003) and the extent and direction of change in the interactions between organisms at these transitions have to be identified. Critical scale transitions are characterized by abrupt changes in a landscape parameter (e.g. field perimeter) with changing spatial scale (for details, see He and Hubbell 2003).

A useful starting point to study such scale transitions is the biological control of microbial leaf pathogens. Population sizes of microorganisms on the leaf surface vary unpredictably across scales and are highly aggregated at all scales from leaf segments to tree stands (Kinkel et al., 1995, Kinkel 1997; Hirano & Upper, 2000). Hence, there is no optimal sampling scale from which population sizes at other scales can simply be extrapolated (Kinkel et al., 1995). This is also reflected in the variable efficiencies of biological control measures observed at the seed and at the field scale (Kildea et al., 2008).

Table 9.1: Commonly used methods of upscaling from smaller to larger scales

Purpose	Method	Selected references	Applications
Analysing the impact of scales on an ecological process	Scale-area plots	Kunin, 1998	Hierarchical sampling Assessment of scale-dependence of range sizes of plant species (Hartley et al., 2004)
Interpolating between local estimates to cover larger scales	Voronoi polygon method (=Dirichlet tessellation)	Dale, 1999	Prediction of species distributions Interpolation of local temperature estimates to the landscape level to predict phenological events in the life cycle of three pest species (Jarvis & Collier, 2002)
	Thin plate spline interpolation	Hutchinson, 1991	Thin plate spline interpolation performed better than the Voronoi polygon method (Jarvis & Collier, 2002)
Extrapolating local estimates of ecological and climatic limits of a species to landscape and global scales	Bioclimatic modelling	Pearson & Dawson, 2003	Inferrence of actual or potential species distributions via climate envelopes Inference of the distribution of the biological control agent *Podisus maculiventris* (Legaspi & Legaspi, 2007), cautioning against basing field-level decisions on bioclimatic models due to the lack of sufficient data for their parameterisation and validation

Microbial systems can be a worthwhile starting point to test the performance of current and new upscaling approaches before transferring the results to insect biological control agents.

The lack of overarching upscaling approaches indicates that, probably, each scale requires its own approach, so that we should advance the coupling of existing approaches rather than aiming at developing the universal up-scaling approach (Meyer et al., 2010). One example of a coupled approach is the pattern-oriented modelling strategy (Grimm et al., 2005) where small-scale mechanisms are derived from large-scale patterns. Pattern-oriented modelling can be used to distinguish between alternative hypotheses on the transition from one scale to the other and thus identify the most appropriate upscaling approach for a particular biological control study.

Overall, upscaling studies show that it can be difficult to compare results obtained in laboratory systems to the field or landscape scale. It is therefore inevitable to move one step further and try to follow organisms out in the agricultural landscape. In the next section, we will see how we can track the movement of insects through real landscapes - a prerequisite for many approaches that follow.

3 Field methods for understanding landscape-scale patterns

Moving from smaller laboratory systems to the field and landscape scale, researchers often have to become detectives – simply because there is so much space available for study-organisms to hide and escape. This is not so much of a problem under small-scale laboratory conditions, but is central to the success or failure of large-scale field studies. Up-scaling from the laboratory to the field thus requires a whole new set of approaches to track arthropods at the large scale. During the last few decades, a series of different marking and tracking techniques have been developed to study arthropod movement and dispersal. These techniques can be used to identify the land uses that (1) act as sources of movement into crops, for both pests and natural enemies, and (2) act as alternative resources and resource subsidies for natural enemies. In the following brief overview of marking and tracking techniques we outline how different techniques have been used to investigate the movement and spatial ecology of arthropods and suggest areas for future focus. Due to the limits on space, however, the following section is by no means an in-depth review of this subject (more detailed reviews are highlighted in Table 9.1)

Following animals from one point to another is the basic requirement of any marking and tracking technique. The fact that "old fashioned" techniques such as fluorescent dyes have continued to be used (e.g. Schellhorn et al., 2004; Bianchi et al., 2009) despite the high-tech revolution of recent decades illustrates the power of the basic guidelines (for example outlined by Hagler and Jackson, 2001) that a marking technique should be simple to apply, readily detectable, inexpensive, safe and not affect the biology or ecology of the target species. Fluorescent dyes score well in all of these categories (see Table 9.1). For example, despite the relatively low recapture rates compared with rare-earth labels (Hagler & Jackson, 2001; Prasifka et al., 2001), fluorescent dyes are cheaper to apply and there is no need for specialised laboratory equipment with trained technicians to process the samples. And while rare-earth labelling techniques may offer much greater capture rates, in mark-capture trial (e.g., see Prasifka et al. 2001), rare-earth labelling requires intensive background sampling before the mark–capture is conducted (in order to firstly establish the naturally occurring variation, within the local population, of the elements to be used as a marker (e.g., rubidium). Similarly, the enormous potential, for mass mark–capture, offered by marking with cheap proteins for ELISA analysis (described by Hagler and Jones 2010) may be overshadowed, for many researchers, by the need for specialised equipment for identification. Although fluorescent dyes may offer a good, cheap, all-purpose type of marking solution, they are perhaps best suited to mark-release-recapture type investigations (where a large number of collected or laboratory-reared individuals are marked and release, en masse, from a central point and subsequently recaptured). The emerging potential of marking with cheap proteins (for example, milk and egg protein as described in Hagler and Jones 2010) offers the opportunity to apply the marker to unprecedentedly large areas of vegetation in order to mark wild populations of arthropods in mark-recapture type investigations.

Traditional mark-capture techniques suffer from several disadvantages. In particular, mark-recapture techniques require equal catchability of marked individuals, and often high numbers of individuals need to be marked. Often, a technique described as “self-marking” may be preferable, where arthropods obtain the mark, for example through foraging, rather than being directly and intentionally marked by the observer. The extra ecological information from such studies can be useful in habitat management and conservation biological control. For example, HPLC nectar analysis (Wäckers, 2007), pollen marking (Silberbauer et al., 2004) and the use of stable carbon isotopes (to identify C_3/C_4 feeding, e.g. Prasifka & Heinz, 2004) can identify the resources, resource subsidies and alternative habitats utilised by pests and natural enemies. However, these approaches may not have the critical information about the origin of the ‘mark’ (unless there is a unique source of pollen, nectar or C_3 plants in the area). It is here that rare-earth labels are perhaps most useful (e.g. Lavandero et al., 2005; Scarratt et al., 2008), because plants can be intentionally marked via the vascular system, leaving no doubt about how and where the mark had been obtained (stable isotopes can also be employed in this fashion, e.g. Wanner et al., 2006; see Table 9.1). Rare-earth elements, such as rubidium and strontium, have the advantage of moving through trophic levels (as do stable isotopes), they may, therefore, provide information on the foraging habits of captured insects (Prasifka et al. 2004). The identification of sugars in the gut contents of natural enemies can also help to inform on the use of resource subsidies or the foraging of pest-originated sugars such as melezitose included in lepidopteran frass and homopteran honeydew (Heimpel et al., 2004).

Perhaps the greatest potential for marking and

Table 9.2: An overview of marking and tracking techniques commonly employed in landscape-scale biological control studies.

Characteristics				Recent Examples		Reviews
Technique	**Simplicity**	**Cost**	**Requires specialist equipment**	**Movement studies**	**Resource use (self-marking) studies**	
Dyes	simple	low	no	Bianchi et al., 2009	-	Schellhorn et al., 2004
Rare Earths	moderate	relatively low	yes	Prasifka et al., 2004	Lavandero et al., 2005; Scarratt et al., 2008	Southwest Entomologist Special Issue 14 1991
Sugar analysis	moderate	relatively low	yes	Desouhant et al., 2010	Winkler et al., 2009	Heimpel et al., 2004
Stable Isotopes	moderate	relatively low	yes	Prasifka & Heinz, 2004	Wanner et al., 2006	Hood-Nowotny & Knols, 2007; Prasifka and Heinz,
Protein marking	increasingly simple	relatively low	yes	Jones et al., 2006	See Jones et al., 2006	Hagler & Jones, 2010; Horton et al., 2009

tracking techniques in biological control, especially with a focus on biodiversity, is the use of multiple markers to adapt techniques to more complex field situations; for example, to simultaneously identify multiple resources (i.e. different source habitats or different resource subsidies). The recent advances in identifying common proteins with ELISA (Hagler & Jones 2010) offers great potential in this endeavour; e.g., to use milk proteins to mark one field, or one prey species, and egg proteins to mark another field or prey species.

Great potential is also offered by combining different disciplines, for example in ’landscape genetics’. In recent years, the use of landscape genetics, which is the combination of high resolution genetic markers with spatial data analysis, has been particularly relevant when assessing the influence of landscape characteristics on the genetic variability and the identification of barriers to gene flow (Storfer et al., 2007). Examples of the assessment of suppressive landscapes using landscape genetics are still scarce, although molecular markers are available for many species (Behura, 2006), and area-wide pest management programs provide valuable information about landscape attributes (Calkins & Faust, 2003; Carrière et al., 2004; Beckler et al., 2005; Park et al., 2006). Correctly identifying sinks and sources of pests and natural enemies can inform on refuge placement and determine whether a landscape is pest suppressive or not. As different parasitoid races can be specific to different host species (for parasitoids with a great host range), genetic and allozyme studies have shown that there is gene flow between refuge-alternative hosts and the target pest on the target crop (Blair et al., 2005; Forbes et al., 2009; Stireman et al., 2006). Thus, the ability of a parasitoid to control different hosts on different host plants may not be constant, even among different genotypes of a single species (Henry et al., 2010). In a recent study in Central Chile’s main apple production area, the relationships between aphid (*Eriosoma lanigerum*) and parasitoid (*Aphelinus mali*) population genetics were studied. Samples were taken from commercial apple orchards and from a different *E. lanigerum* host (*Pyracantha coccinea*) in a farm hedge dominated by the plant genus *Pyracantha*. Prior studies had shown geographic barriers interrupting gene flow of the aphid host between neighbouring populations independently from geographical distances (Lavandero et al., 2009). Evidence of extensive gene flow between sites, and no evidence of reproductive barriers for the parasitoid were found, suggesting no host-plant related specialisation and therefore indicating that *Pyracantha* hedges are a source of parasitoids for the crop. Based on this knowledge, future integrated pest management programs could rely on the use of refuges of alternative hosts to increase migration of parasitoids to areas where they are more rare, aiding the augmentation of the parasitoid population after disturbances.

Box 9.1 The spatial population dynamics of insects exploiting a patchy food resource (Dempster et al. 1995)

Movements between plant patches were studied with the use of chemical markers (Rb, Sr, Dy and Cs) which were applied as chloride salts to individual patches, and which were translocated to the flowerheads and so to insects feeding on the seed, and to their parasitoids.

These analyses showed that individual of all species moved considerable distances, with movements of up to 2 km being commonly recorded. Estimates of rates of immigration to patches showed that movement plays an important role in the population dynamics of these insects.There was some evidence that immigration was density-dependent: it was highest when the resident populations (numbers per flowerhead) were low.

Overall, the approaches highlighted in this section show a wide range of methods available to the researcher - from marking and tracking to landscape genetics. We will now move on to another important area, which is experimental design and statistics.

4 Design and statistical analysis of large-scale biological control

Knowing how to mark and track insects in agricultural landscapes, we can now move on to think of how to apply this knowledge to conduct a biocontrol study on a landscape scale. First, we need to consider the spatial arrangement of study sites and treatments (experimental design). Second, we need to come up with sampling schemes that work for our study organisms (sampling design).

4.1 Experimental design

Of the wide variety of available experimental designs (e.g. Fig. 1 in Hurlbert 1984), the completely randomized design will probably be the least useful. It is almost certain that our study sites will need to be arranged in blocks in space and time. Blocks share similar abiotic conditions (e.g. soil parameters) and help reduce the unexplained variation in data. To reduce workload and costs, it is often advisable to apply split-plot designs in which smaller subplots are nested within larger plots. Experimental treatments (for example bagging, caging, pesticide application etc.) are then applied at random at increasingly smaller spatial scales.

4.2 Sampling design

After deciding on the experimental design to be used in our biocontrol study, we need to define an appropriate sampling scheme to estimate organism abundance, species richness, predation rates and so forth. To decide on an appropriate sampling method, we need to know our study organisms: How large are they, how mobile will they be, and how will they respond to landscape features (Wiens, 1989)? Secondly, we need to employ sampling, marking and tracking procedures that are as unbiased as possible (Hagler & Jackson, 2001). This requires setting-up traps and other devices according to systematic or random schemes (Fortin & Dale, 2005; see Table 9.3). At this stage, we will also need to know which types of analyses we want to conduct with the data after they have been collected. For example, grid-based sampling will lead to different types of geostatistical procedures than random sampling (Fortin and Dale 2005).

4.3 Combining observational and experimental approaches

In landscape-wide biocontrol studies, observational data ("mensurative experiments" sensu Hurlbert, 1984) should be combined with experiments to achieve what is called "strong inference" (Platt 1964). For example, if we study multitrophic interactions in oilseed rape, it is a good idea to experimentally establish own oilseed rape plots in addition to fields already existing in the landscape (Thies & Tscharntke, 1999). Additionally, experimental plant individuals ("phytometers") may be used to study local-scale phenomena (Gibson, 2002). Such approaches may help to standardize plant cultivars, soil conditions and other confounding variables. Experimental plots can then be used for specific treatments on a subplot scale (e.g. fertilization, insecticide treatment, or caging experiments). In general, an "ideal" landscape-scale study always involves experimentation ("manipulative experiments" sensu Hurlbert 1984): Experimental establishment of hedges (e.g. Girma et al., 2000), experimental fragmentation of habitats (e.g. Lindenmayer et al., 1999; Debinski& Holt, 2000), experimental application of herbicides, insecticides and biocontrol agents (e.g. Cochran & Cox, 1992). However, in many cases, experimentation will be impossible for logistical reasons. Landscape-scale studies cover large areas, and individual fields often belong to landowners who individually manage their fields. Under these circumstances, we can study gradients in landscape complexity, composition or configuration. Paired designs using "pseudo-treatments" can also yield insights - for example if organic and con-

Table 9.3: Experimental or sampling designs employed in landscape-scale biocontrol studies

	Experimental studies	Observational studies
Most frequent experimental or sampling schemes applied	Completely randomized design	Landscape gradients (e.g. gradients in landscape complexity)
	Randomized blocks designs	Concentric circles design (to study landscape context)
	Paired designs	Grid sampling schemes
		Paired designs (e.g. paired comparisons between organic-conventional farms)
Main advantages	Clear separation of response and explanatory variables	Realism
	Classical hypothesis testing, strong inference	Direct application to real-world scenarios possible
Main disadvantages	Sometimes unrealistic	Causes and effects may be difficult to separate
	Small power if sample sizes is low	Unanticipated block-by-treatment interactions
	Upscaling problems	

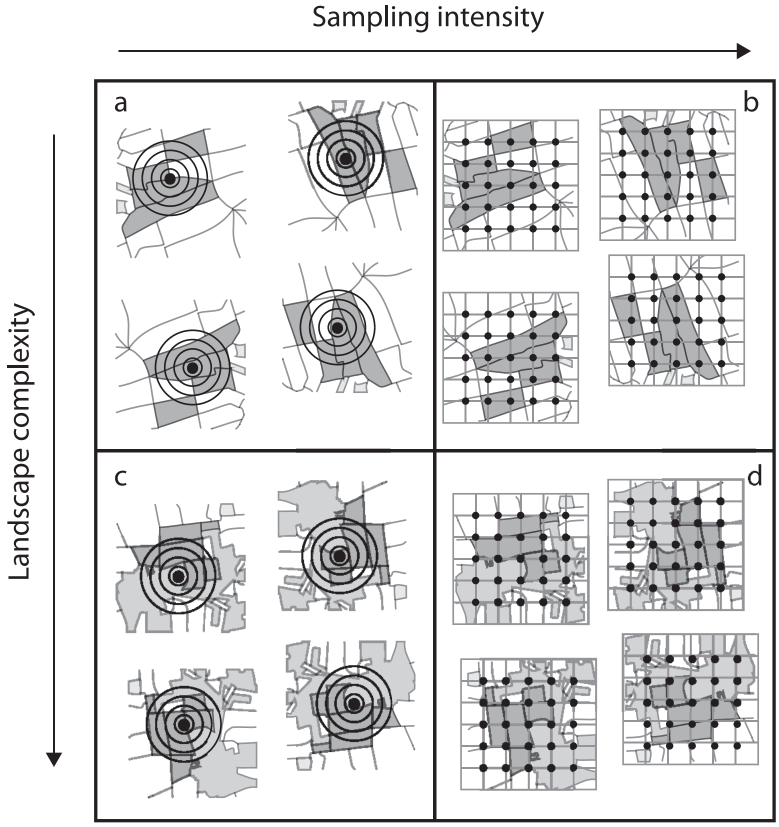

Figure 9.1: Sampling designs in biocontrol studies on a landscape scale. Sampling sites are indicated by filled black dots within landscapes; (a) and (c), low sampling intensity (N=4 datapoints in 4 landscapes), landscape structure around each sampling site is measured in concentric circles with increasing radii. (b) and (d) high sampling intensity (N=25 datapoints in 4 landscapes); landscape structure and spatial information about sampling locations are measured simultaneously. Landscape complexity increases from (a) to (c) and from (b) to (d). Figure created by C. Scherber.

ventional farming systems are studied (e.g. Kleijn et al., 2006). Below, we list some of the most important features to consider for successful experimental design of biocontrol studies.

4.4 Importance of blocking

Blocks are still among the most useful "devices" to control for variations in abiotic conditions in both experimental and observational studies on a landscape scale. For example, individual countries can form blocks in continent-wide studies (Billeter et al.; 2008; Dormann et al., 2007). Likewise, pairs of farms can be considered as blocks (Kleijn et al., 2006). Further, individual observers moving through the landscape can be "applied" to different groups of study plots and "observer effects" can then easily be incorporated into the block effect in statistical models.

4.5 Proper use of random effects

Every study site has its own characteristics, and we will never be sure which of these characteristics will exactly be important for a given study. In the statistical design and analysis of landscape-wide studies, it is therefore important to be very clear about which factors should be treated as 'random'(McCulloch & Searle, 2001; Bolker et al., 2009). Imagine you begin your study with a selection of 30 study sites, scattered through a larger landscape. If someone else would have selected these 30 sites, he or she would probably have chosen different ones. Hence, the population of possible sites may probably have been almost infinitely large. The sites you chose just happened to be that particular 30. Hence, your sites are actually random effects, and this should be clear from the beginning of the study (Zuur et al., 2009). As a final note, random effects should always have at least twolevels, and ideally as many as possible

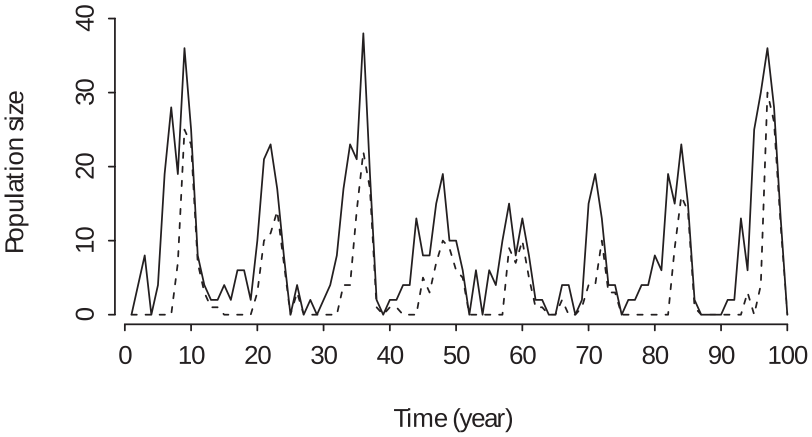

Figure 9.2: Population density of adult hosts (black line) and parasitoid larvae (dotted line) oscillating with time in one exemplary cell; simulation run with landscape parameters as visualised in Figure 9.3. Adapted from Visser et al., 2009.

(Giovagnoli&Sebastiani, 1989; McCulloch & Searle, 2001).

4.6 How to incorporate the landscape context

Observations at a single site may be influenced by the surrounding landscape; these indirect influences are commonly termed "landscape context" (Pearson, 2002). The traditional approach has been to use individual sampling points, scattered through landscapes differing in landscape complexity. These points were then surrounded by concentric circles in which landscape parameters were assessed (Figure 9.1a, c). However, this means that landscape effects can only be guessed from correlations between what we observed at an individual plot, and some features of the landscape surrounding that point. It is more desirable to also collect replicated samples in space, for example using replicated grids of sampling points at every study site (e.g. Billeter et al., 2008; Dormann et al., 2007; see Figure 9.1b, d). Note, however, that the grid cell size needs to match the cell size of the expected spatial pattern (Fortin & Dale, 2005). Alternatively, stratified random sampling may be employed; that is, each habitat forms an own 'stratum' and is sampled separately. The sample size will then be a function of habitat area and costs of sampling (for details, see Krebs, 1999).

4.7 Know your response and explanatory variables

It is always a good idea to set up an artificial dataset before the beginning of a study. You can then already try out different statistical models and do power analyses to estimate the sample sizes needed (e.g. Crawley, 2002). In biocontrol studies, we will often encounter count data (numbers of insects) or proportion data (proportion parasitised hosts). These data types usually require special types of statistical models such as generalised linear (mixed) models (McCulloch & Searle, 2001).

4.8 How to do the statistical analysis of landscape-scale biocontrol studies

After successful data collection, we usually want to draw inferences from these data using statistical techniques. In the past, many datasets have been analysed using standard regression techniques, although datasets actually had a clearly spatial na-

Box 9.2 Persistence of parasitoid populations and parasitism rate

We focus on two measures that are widely used to assess the performance of biocontrol: persistence (a measure of the parasitoid's reliability), and parasitism rate. The first measure is commonly used in theoretical studies and the latter in field studies.

Persistence of parasitoid populations and parasitism rate are measures often applied in theoretical and field studies, respectively. Each of them reveals important properties of biocontrol, namely reliability and effectiveness, respectively.

Visser et al. (2009) found that the amount of habitat in a landscape modulates the effect of fragmentation on parasitoid persistence. Parasitism rate, on the other hand, decreased with fragmentation regardless of the habitat amount in a landscape. Consequently, the effect of fragmentation and isolation on the performance of biocontrol as an ecosystem service hinges on whether the focus is on persistence or parasitism.

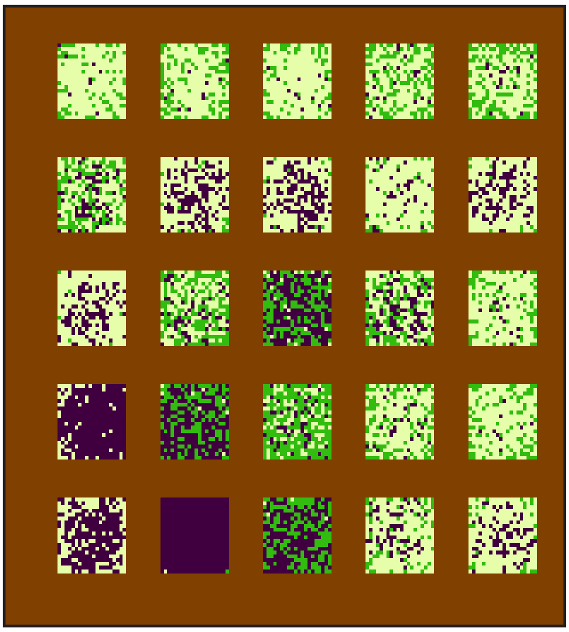

Figure 9.3: Snapshot of a virtual landscape of the scenario with low amount of habitat (habitat amount 2500 cells, number of patches 25, patch distance 10 cells) during a simulation run; white: cells with only host population, dark pink: cells with host and parasitoid population, brown:matrix cells, green: empty habitat cells. Adapted from Visser et al., 2009.

ture (Dormann, 2007). The most important steps in the analysis of datasets on landscape-scale biocontrol are the following:

(1) Decide on how to deal with count and proportion data. Usually, you may wish to analyse them using generalized linear (mixed) models, but current software packages often lack methods to incorporate spatial and/or temporal autocorrelation into these models (for an overview, see Bolker et al., 2009). The best solution often is to transform the response variable, or to use variance functions to account for non-constant variance.

(2) Decide on what to do with space and time. If you are interested in spatial trends, decide if you want to interpolate between sampling locations (kriging), or if you simply want to account for spatial autocorrelation (correlation structures in the residuals); a good introductory reference is Fortin and Dale (2005). If you are interested in temporal trends, make sure that your observations are regularly spaced in time and that there is sufficient temporal replication (Zuur et al., 2009). Treat temporal pseudoreplication using time series analysis or by incorporating time as a random slope. Avoid incorporating time as a pseudo-“subplot” because this may violate the sphericity assumption (sphericity is a measure of variance homogeneity in repeated measures analyses; for details, see von Ende, 2001).

(3) Plot the data, together with the model predictions, instead of plotting linear regressions provided by graphics software. Remember that model predictions from generalised linear models look nonlinear on the untransformed scale.

5 Modelling scale effects in biological control

Even the most sophisticated statistical analysis often opens up new questions. For example, we may find that landscape context influences the distribution of a specialist parasitoid, but we may be unclear about the mechanisms. Modelling can be a useful tool to understand the spatiotemporal dynamics of pests and their biocontrol agents in the field. Modelling is also needed as a final step in designing pest-suppressive landscapes. In order to be able to give management recommendations towards promotion of biodiversity and biocontrol via design of pest-suppressive landscapes, a good understanding of the ecological processes acting at different scales (e.g. Levin, 2000, Turner 2005) is important. Key questions are: Which species are promoted/threatened in a given landscape structure and what are the species and landscape characteristics making these species abundant/prone to extinction in such a landscape? How can a landscape be altered to promote beneficial species and suppress pest species?

The basic idea of ecological modelling is to reconstruct the basic features of ecological systems in simulation models. In other words, these models are a representation of all essential factors of the real system that are relevant with respect to the scientific question being addressed (Wissel, 1989). In case of rule-based simulation models, these essential factors and their interactions are being described using ‘if-then-rules’ (Starfield et al., 1994). For example, one rule in the model might be: ***if*** a parasitoid finds a host individual at a specific location, then the parasitoid lays an egg into the larva and at this location no host but a new parasitoid will develop. Experts that know from field experience which factors shape the system are a great help to model development.

Typically, several model variants are developed that can be used to test specific hypotheses on the functioning of the system. Factors can be added or removed, parameter values are being increased or decreased and thereby our understanding of the system can be greatly improved. Models can also be used to help the planning of new field experiments. Using virtual experiments, different landscapes can be created and the (insect) species are being placed into these landscapes and their populations develop according to the model rules. In such experiments, long time series can be investigated, which would not be possible in the field.

There are two main classes of models that are most frequently used to model large-scale spatiotemporal dynamics of organisms: Individual-based models (IBM) and grid-based models. In IBM, each individual is tracked explicitly, along with its properties (e.g. size, sex, developmental stage). Population processes emerge from the combined behaviour of many individuals (e.g. Bianchi et al. 2009).

In grid-based models (e.g. Bianchi & van der Werf 2003), space is represented as a grid of cells. This means each of these cells represents a small subunit of space in a certain position and contains specific information for example about its suitability for the regarded species (e.g. "habitat") or the presence of the organisms to be studied (e.g. "occupied by host population") (see also the grid-based sampling approach shown in Figure 9.1b,d). Within a cell, non-spatial processes such as reproduction can take place. Cells are interlinked via dispersal and this way the reproduction and spread of a local insect population can be depicted. Inspecting the landscape-level patterns emerging from such a model can help to scale up local insect dynamics to the landscape.

Visser et al. (2009) developed a grid-based host-parasitoid model based on the ecology of the rape pollen beetle *Meligethes aeneus* (Fabricius) and its specific parasitoids in semi-natural habitats. In fragmented landscapes, parasitoids have been found to go extinct before their hosts do, which suggests that species at different trophic levels experience a landscape differently (Kruess & Tscharntke, 1994; Tscharntke et al., 2002). Parasitoids are often antagonists of important pest insects and therefore a good understanding of host-parasitoid systems in agricultural landscapes is of great interest to biocontrol.

One grid cell in the model represents a 100 m × 100 m area of an agricultural landscape which can be either suitable "habitat" for the host (e.g. set asides) or unsuitable 'matrix' (e.g. other crops, but not rape). Each cell can contain a subpopulation of host and parasitoid and is the place for the local processes reproduction, parasitism, and mortality. Local subpopulations are linked by dispersing host and parasitoid individuals. For model details see Visser et al. (2009).

Habitat fragmentation was studied by varying the number, size of, and mutual distance between habitat patches in the virtual landscapes of the host-parasitoid model (Visser et al., 2009). A habitat patch is defined as a continuous area of adjacent habitat cells. Across all scenarios, host parasitoid dynamics in a given cell is oscillating in time (Fig. 9.2). Generally, these local oscillations of host and parasitoid densities lead to a wave-like or chaotic spatial pattern (Fig. 9.3) with increasing local host populations at the wave front, followed by increasing parasitoid populations (see also Hirzel et al., 2007). These waves of hosts and parasitoids move across the landscape with time. As the parasitoid populations cause the local extinction of the host, they leave a zone of empty cells behind. Analyses across fragmentation scenarios show the following trends: (1) Parasitation rates decrease with the number of patches and decrease with patch distance, and (2) host outbreak duration increases with the number of patches, and (3) parasitoid persistence is additionally modulated by habitat amount: if habitat is abundant persistence decreases with the number of patches and with patch distance, if habitat is scarce persistence is highest at intermediate levels of fragmentation (Visser et al., 2009)..

In summary, the amount of habitat in a landscape modulates the effect of fragmentation on parasitoid persistence. Parasitation rates, on the other hand, decreased with fragmentation regardless of the habitat amount in a landscape. Consequently, the effect of fragmentation and isolation on the performance of biocontrol as an ecosystem service hinges on whether the focus is on persistence or parasitation rates.

Although the dispersal of both hosts and parasitoids is hindered by increasing fragmentation and isolation, this effect is much stronger for the parasitoid. This is due to the fact that the parasitoid depends on a more ephemeral resource (host) than the host (habitat).With increasing fragmentation, the disadvantage of the parasitoid increasingly leads to the decoupling of the host population from the control of the parasitoid, which results in prolonged host outbreak duration and decreased average parasitation rates. Thus, the modelling study by Visser et al. (2009) confirms the findings of several field studies that increasing fragmentation and isolation can decrease parasitation rates (Kruess& Tscharntke, 1994), increase prey outbreak duration (Kareiva, 1987) and reduce prey tracking at a certain scale (With, et al. 2002). It also reveals that the basic mechanism underlying their observations may be neither the difference in dispersal abilities of host and parasitoid (which were kept identical in the model) nor the predator searching behaviour interacting with landscape features (which was not incorporated in the model), but the decoupling of the population dynamics of pest and antagonist due to habitat structure.

The example of the host-parasitoid model illustrates that modelling can improve our understanding of complex systems beyond the possibilities of field studies. The model shows that landscape effects on biological control agents can be found without any significant differences in local dispersal abilities and even without any specific active response of the organisms to the landscape features. This was greatly facilitated by the fact that, within a model, properties such as dispersal ability and degree of interaction with landscape features can be changed while keeping all other properties constant.

6 Summary and conclusions

Data collection, sampling design, tracking and marking techniques, statistics as well as modelling of data on a landscape scale can be challenging for the individual researcher. In this chapter, we have tried to cover the areas that we believe are most relevant for landscape-scale studies. As everywhere in science, innovation is often based on methodological or technological advancements. For example, landscape genetics would be unthinkable without the rapid developments in molecular biology. Likewise, analyses of landscape structure are greatly aided by advances in multiband satellite imagery and image processing and classification software. Finally, new types of sampling design, such as grid-based landscape-wide sampling, may provide new insights and opportunities for modelling. All in all, we think that there are several key steps that can be followed to make the most of an individual study:

(1) Start off with a small-scale study (for example with your favourite biocontrol agent and insect pest), and try to predict what might happen on larger spatial scales.

(2) Choose from selected marking and tracking techniques, and do preliminary studies in your type of landscape. Find out which spatial and temporal scales you can reasonably cover.

(3) Know your study organisms, their biology, life cycle and dispersal behaviour.

(3) Invest time into finding an appropriate sampling or experimental design. If your design is solid, your study will also be (provided you know your organisms). If you have too low replication, or block-by-treatment interactions, you can often not cure this at the statistics stage.

(4) Use established, robust and well-documented statistical procedures for data analysis. This doesn´t mean you should use “canned” solutions, but don´t become too excited about approaches that are still under development (such as generalized linear mixed models). Always graph your data before you start any analyses.

(5) Use the advantages of modelling and simulation techniques to derive predictions that extend across the scales of your study.

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Chapter 9

Effects of tree diversity on beetle communities

published as:

Sobek S, Steffan-Dewenter I, Scherber C, Tscharntke T (2009) Spatiotemporal changes of beetle communities across a tree diversity gradient. Diversity and Distributions 15: 660–670

BIODIVERSITY RESEARCH

Spatiotemporal changes of beetle communities across a tree diversity gradient

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ABSTRACT

Aim Plant and arthropod diversity are often related, but data on the role of mature tree diversity on canopy insect communities are fragmentary. We compare species richness of canopy beetles across a tree diversity gradient ranging from mono-dominant beech to mixed stands within a deciduous forest, and analyse community composition changes across space and time.

Location Germany's largest exclusively deciduous forest, the Hainich National Park (Thuringia).

Methods We used flight interception traps to assess the beetle fauna of various tree species, and applied additive partitioning to examine spatiotemporal patterns of diversity.

Results Species richness of beetle communities increased across the tree diversity gradient from 99 to 181 species per forest stand. Intra- and interspecific spatial turnover among trees contributed more than temporal turnover among months to the total γ-beetle diversity of the sampled stands. However, due to parallel increases in the number of habitat generalists and the number of species in each feeding guild (herbivores, predators and fungivores), no proportional changes in community composition could be observed. If only beech trees were analysed across the gradient, patterns were similar but temporal (monthly) species turnover was higher compared to spatial turnover among trees and not related to tree diversity.

Main conclusions The changes in species richness and community composition across the gradient can be explained by habitat heterogeneity, which increased with the mix of tree species. We conclude that understanding temporal and spatial species turnover is the key to understanding biodiversity patterns. Mono-dominant beech stands are insufficient to conserve fully the regional species richness of the remaining semi-natural deciduous forest habitats in Central Europe, and analysing beech alone would have resulted in the misleading conclusion that temporal (monthly) turnover contributes more to beetle diversity than spatial turnover among different tree species or tree individuals.

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Keywords

Beta diversity, biodiversity conservation, canopy arthropods, *Fagus sylvatica* L., functional groups, habitat heterogeneity.

INTRODUCTION

Being the most species-rich and prevalent insect taxon worldwide (Grove & Stork, 2000), beetles (Coleoptera) contribute greatly to biodiversity in forest habitats and play various roles in ecosystem dynamics and functioning (Erwin, 1997; Lassau *et al.*, 2005). Among them are numerous forest pests (e.g. Scolytidae, Curculionidae), as well as effective predators (e.g. Carabidae, Cleridae, Coccinellidae) capable of top-down biocontrol (Reeve, 1997). Only few current studies exist that directly compare beetle communities of different tree species (i.e. Wagner, 2000; Hulcr *et al.*, 2007), and due to limited availability of comparable forest stands of different diversity within the same forest neighbourhood, so far these examinations mostly focused on local single-stand observations (but see Gering & Crist, 2000). Sometimes accessibility of habitats can be a problem as well, especially if sampling is not constrained to the understorey, but also includes the forest canopy.

The forest canopy is known as a major pool of global insect diversity (Erwin, 1988; Stork, 1988; Novotny & Basset, 2005), and especially in the tropics beetles are one of the best-studied taxonomic groups in this habitat. In contrast to the vast number of studies conducted in tropical forest canopies, canopy research in temperate deciduous forests is still fragmentary. Especially, turnover in space and time has largely been neglected (Ulyshen & Hanula, 2007), although it might be of importance for determining forest insect diversity (Hirao *et al.*, 2007). For temperate deciduous forests, Gering & Crist (2000) have demonstrated the importance of tree species, season, and spatial variability for structuring species richness and abundance patterns of beetles, and have also shown that particularly in late summer tree species identity plays a major role in determining beetle species richness. They also emphasized that with regard to spatial dependency of tree-dwelling arthropod communities, temperate forests remain vastly unexplored.

Due to host specificity (Erwin, 1982; Stork, 1988) and habitat preferences, species-rich forests can be expected to exhibit a greater diversity of beetle species, and in experimental forest habitats, tree diversity has been shown to affect positively arthropod species richness (Vehviläinen *et al.*, 2008). As a measure of host specificity in insects, May (1990) introduced the term ‘effective specialization’. Effective specialization *sensu* May (1990) is defined as the weighted quantity of an insect assemblage specialized to a certain host tree species. However, effective specialization of beetles has been demonstrated to depend strongly on the spatial scales considered (Gering *et al.*, 2007). Moreover, community analysis across various spatiotemporal scales also increases the chance that ecologically relevant scales are included, which might otherwise be overlooked (Huston, 1999). In particular for canopy beetles, community interaction takes place in individual tree crowns (Gering & Crist, 2002), and sample-based α-diversity can be utilized as a snapshot of this community at a given time. Even trees in close proximity to each other (< 1 km) might vary significantly in their species composition (Gering *et al.*, 2003). Identifying community composition at various spatiotemporal scales can thus be of value for biodiversity conservation and forest management, by pinpointing species unique to certain scales and by preserving them accordingly (Summerville *et al.*, 2003a). Hence, the interrelationship of tree species, space and time needs to be disentangled, which can be accomplished by comparing beetle community patterns in highly diverse forest stands with patterns in species-poor stands within one and the same forest ecoregion.

Here we examine species richness and composition of canopy beetle communities across a tree diversity gradient ranging from mono-dominant beech to mixed stands in Germany’s largest remaining deciduous forest habitat, the Hainich National Park. No studies have focussed on *Fagus sylvatica* in forest stands of different diversity, we compare beetle communities of various tree species with beetle communities of single beech trees across the gradient. Being the most important tree species in Central Europe (Gessler *et al.*, 1998), it is of special interest to what extent beech contributes to hosting local and regional arthropod diversity. Due to more acidic soils, thicker leaf layer and often lesser light permeability, beech dominated stands are usually characterized by low plant diversity (Ellenberg, 1996; Mölder *et al.*, 2008). They also appear generally homogeneous (Kenderes *et al.*, 2008) and less structurally complex compared to diverse forests.

Whereas up to now a plethora of studies conducted on forest beetle communities in Europe has focused on saproxylic species only [many of them reviewed in Grove (2002), Davies *et al.* (2008)], but to a lesser extent included other functional groups, we carry out a complete survey of all captured species and analyse community composition of the different stands. We use additive partitioning (Lande, 1996; Veech *et al.*, 2002; Crist *et al.*, 2003) to not only account for overall species richness per forest stand, but to also include spatial and temporal differences in the observed patterns.

Specifically, we test the following hypotheses: (1) Due to increased habitat heterogeneity, species-rich forest stands house a greater number of beetle species (γ-diversity) compared to mono-dominant beech stands. The presence of a wide variety of different tree species enhances habitat complexity and thus niche availability, which should support a greater array of beetle species. The same accounts for (2) species turnover (β-diversity), which we expect to be higher in species-rich forest stands. The various tree species and other plants in diverse forests might attract a greater variety of feeding specialists, which in turn could increase predator diversity. Several beetle species show a high degree of host specialization and are closely associated with certain tree species, for example oak (Müller & Goßner, 2007), with a decreased chance of encounter on non-host trees. Hence, we assume that in the most diverse forest stands (3) spatial turnover (β_{space}) between trees contributes more to overall γ-diversity than temporal (monthly) turnover $\beta_{\text{time.}}$ (4) In contrast, spatiotemporal patterns of beetle diversity on beech alone should remain constant across the tree diversity gradient with a greater contribution of monthly turnover to the total diversity, unless beetle species richness on single beech trees in mixed forest stands increases due to spill-over effects. Due to differences in life cycle and voltinism, beetles show a strong seasonality and several species are only actively dispersing as adults for a short period of time (Gaylord *et al.*, 2006), thereby increasing temporal turnover. The latter is likely to be more prominent in mono-dominant beech forests, where spatial turnover between conspecific trees is expected to contribute less to overall diversity.

METHODS

Study area and field sites

Trees were sampled in Germany's largest connected semi-natural broadleaved forest, the Hainich National Park, Thuringia. Established in 1997, 7600 ha of forest (of a total area of 16,000 ha) are currently under protection (Nationalpark Hainich; http://www.nationalpark-hainich.de), while the surrounding area is dominated by arable land. Sampled forest stands are located in the north-eastern part of the protected zone south of the village Weberstedt. The region has a temperate climate, with an average temperature of 7.5 °C and a mean precipitation of 590 mm (1973–2004, Deutscher Wetterdienst). The average annual temperature of the area in 2005 was 9 °C, annual precipitation in 2005 was 601 mm (2005, Meteomedia, Bochum). The predominant soil type is stagnic luvisol on loess–limestone as parent material.

Various deciduous tree species grow in the mild climate of the research area. In the examined forest stands, dominant tree species are beech (*Fagus sylvatica* L.), lime (*Tilia platyphyllos* Scop., *Tilia cordata* L.) and ash (*Fraxinus excelsior* L.). Conifers occur only exceptionally, and removal is part of the management concept of the national park to allow for a late successional stage of purely deciduous forest.

Sampling was carried out in 12 forest stands of different tree diversity and designed *a priori* to test effects of the tree diversity gradient on beetle diversity. All forest stands shared main characteristics like stagnic luvisol soil on loess–limestone as parent material, flat elevation, absence of canopy gaps and had remained undisturbed for more than 40 years since the last logging event. To determine tree diversity of each stand, 50 × 50 m plots were established representing a gradient from mono-dominant beech to mixed forests with up to 11 deciduous tree species. [i.e. *Acer platanoides* L., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Prunus avium* (L.), *Quercus robur* L., *Sorbus torminalis* L., *Tilia cordata* L., *Tilia platyphyllos* Scop., *Ulmus glabra* Huds.]. We reported tree diversity of the sampled plots as Shannon indices based on stem counts (diameter breast height > 7 cm), which accounts for the relative abundance of individual tree species as well as for richness (Magurran, 2004) (Appendix S1).

Sampling of beetles and sample processing

Beetles were sampled using cross-window flight interception traps. The traps consisted of two translucent polycarbonate panes measuring 60 × 40 cm, which were attached to funnels of lorry tarp guiding to an upper and lower collecting jar filled with ethylene-glycol (1 : 1 diluted with water) as a preserving liquid. Flight-interception traps of this type are non-attractive, and insects are caught by chance when hitting the crossed panes in flight. Across all forest stands, 72 traps (six traps per stand) were installed in the centre of individual tree crowns using a crossbow and following a sampling scheme based on the relative abundance of beech. In highly beech dominated stands with up to four tree species (83–100% beech), only beech (*Fagus sylvatica*) was sampled, in stands with up to seven tree species and at least 48% beech, the three most dominant species were sampled [beech, lime (*Tilia* sp.), ash (*Fraxinus excelsior*)], and in stands with up to 11 tree species and the proportion of beech decreasing below 42%, six tree species were sampled [beech, lime, ash, sycamore maple (*Acer pseudoplatanus*), hornbeam (*Carpinus betulus*) and either oak (*Quercus robur*) or service tree (*Sorbus torminalis*)]. Sampled trees were randomly selected on the 50 × 50 m plots or in a 10-m-wide corridor in the directly adjacent forest. Clearance of traps was accomplished every 4 weeks over a period of 6 months from May to October 2005. To allow for a comparison of single beech trees across the gradient, four additional traps were installed in beech trees on the four most diverse plots. Analyses for beech alone were then based on two randomly drawn or sampled trees per plot.

Beetles were separated from plant material and other debris and stored in 70% ethyl alcohol. All individuals were identified to species level. When condition of the material did not allow for species-level determination, specimens were assigned to other taxonomic levels (at least to family). Alcohol-preserved voucher specimens were deposited in an in-house collection (Agroecology, Georg-August-University Göttingen). For each species, information on ecology (rarity, habitat specialization, feeding guild) was annotated based on details outlined in Böhme (2004) (Appendix S2), resulting in the following groupings: common (common or only regionally rare)/rare (rare or very rare), forest species/habitat generalists and predators/herbivores/fungivores.

Data analyses

All analyses were performed based on six sampled trees per stand (beech or a mix of species), and for two beech individuals per stand separately. Observed species richness (γ-diversity) was calculated as accumulated number of species per plot (pooled over space and time). A nonparametric species estimator, the first order Jackknife, was used to estimate sampling success. The more species appear in a single sampling unit (here tree), the higher the estimated number of species for each plot (Heltshe & Forrester, 1983; Magurran, 2004). All plots turned out to be equally sampled (68–75% of estimated species, Appendix S1), hence all subsequent analyses were performed on observed species richness.

Additive partitioning of γ-diversity was performed for each plot based on Lande (1996), wherein γ (overall regional diversity) = α (mean species richness within sample) + β (species turnover). Here, we partitioned γ_{stand} in $\alpha + \beta_{\text{time}} + \beta_{\text{space}}$, with α defined as mean species richness per tree per month, seasonal turnover β_{time} as mean β_{timeTree} (=observed number of species per tree minus α), and spatial turnover β_{space} specified as observed species richness per plot minus mean number of species per tree (pooled over the sampling season).

Spearman rank correlations were calculated to evaluate the potential of various stand characteristics as explanatory variables for multiple regression analyses and to examine multicollinearity of variables. Tree diversity of the sampled forest stands was highly correlated with several other stand characteristics (Appendix S3). To test for linear relationships between tree diversity and the response variables (γ-diversity, α, β_{time}, β_{space}, factor levels of rarity, habitat specialization and feeding guild), we used multiple regressions with type I sum of squares with beetle log-abundance and tree diversity (Shannon Index) as explanatory variables. Count data were $\log_{10}$-transformed. Beetle log-abundance was included in the model to eliminate differences in species richness simply due to differences in individual abundance (Magurran, 2004). Beetle species richness regressed on beetle log-abundance accounts for the sampling effect and for the variance in the data explained by abundance (e.g. Knops *et al.*, 1999). This approach is an alternative to rarefaction, and directly relates individual log-abundance to the actually observed number of species. Rarefaction has recently been criticized as being biased under certain circumstances, thereby leading to questionable results for a correct estimation of species richness (Collins & Simberloff, in press). Other explanatory variables were not included in the models for reasons of multicollinearity and because only marginally increased explanatory power was expected based on the multiple r^2-values yielded in the simple models including beetle log-abundance and tree diversity only. Beetle log-abundance was strongly positively correlated with tree diversity (Pearson's $\rho = 0.7$, $P = 0.012$), hence we tested different sequences of the variables entered to the model. The latter was not necessary for the communities on beech alone (Pearson's $\rho = 0.39$, $P = 0.208$). Models were fitted separately for each response variable, and analysis of covariance (ANCOVA) was used to test for differences in regression slopes of α, β_{time} and β_{space}-diversity. Model residuals were examined for meeting assumptions of normality and homoscedasticity.

First order Jackknife estimates were computed with EstimateS 8.0 (Colwell, 2006). Other statistical analyses were carried out using R, Version 2.6.2 (R Development Core Team 2007; http://www.R-project.org).

RESULTS

Species richness of beetles (γ-diversity)

A total of 10,360 individuals belonging to 60 families and 422 species were captured (Appendix S2). Observed beetle species richness (γ-diversity) showed a highly significant response to the tree diversity gradient after controlling for variance explained by differences in beetle log-abundance ($F_{1,9} = 46.44$, $P < 0.001$, Fig. 1). The number of observed beetle species per stand increased from 99 to 181 species with increasing tree diversity. For beech alone, the number of observed beetle species also increased across the tree diversity gradient ($F_{1,9} = 6.53$, $P = 0.031$), but only from 58 to 88 species.

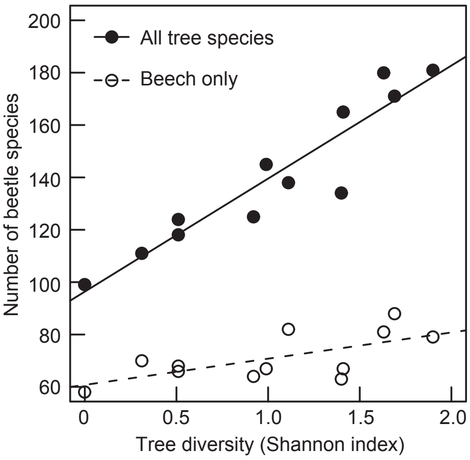

Figure 1 Observed species richness (γ-diversity) of beetles across a tree diversity gradient in a Central European forest.

Additive partitioning of γ-diversity

Beetle α-diversity responded to the tree diversity gradient only if the Shannon Index was introduced to the model first (Shannon: $F_{1,9} = 61.32$, $P < 0.001$, Log-Abundance: $F_{1,9} = 90.32$, $P < 0.001$, Fig. 2a). Temporal turnover β_{time} also increased with increasing tree diversity ($F_{1,9} = 32.76$, $P < 0.001$, Table 1). Spatial turnover β_{space} was higher compared to temporal turnover β_{time} with a steeper slope in the fitted regression (ANCOVA, $F_{2,30} = 33.71$, $P < 0.001$), and also showed a highly significant response to increased tree diversity ($F_{1,9} = 79.33$, $P < 0.001$, Table 1). In contrast, temporal turnover β_{time} was higher if beech alone was analysed (Fig. 2b), but in this case did not respond to the tree diversity gradient ($F_{1,9} = 1.19$, $P = 0.3$), unlike spatial turnover β_{space} ($F_{1,9} = 10.75$, $P = 0.008$, Table 2).

There was no proportional change in the contribution of α-diversity and temporal or spatial species turnover to overall γ-diversity within each forest stand across the tree diversity gradient (Appendix S4), only relative spatial turnover on beech alone showed a slightly increasing linear relationship ($F_{1,9} = 5.17$, $P = 0.049$).

Beetle community composition and functional groups

Most species were classified as habitat generalists (228 species, 54%), whereas strictly forest bound species constituted roughly another quarter of the total (115 species, 27.3%, Appendix S2). Both groups also constituted the majority of individuals (7106 generalist individuals, 68.6%; 2405 forest individuals, 23.3%). Less than 1% of the species were identified as tourists specialized to habitat types other than forest, 67 species (15.8%) lacked information on habitat preference. Habitat generalists and forest species both increased in numbers on the most diverse plots (Fig. 3a), the linear relationship of forest species to tree diversity was highly significant ($F_{1,9} = 41.67$, $P < 0.001$, Table 3). The number of forest species also increased linearly if beech alone was compared ($F_{1,9} = 7.84$,

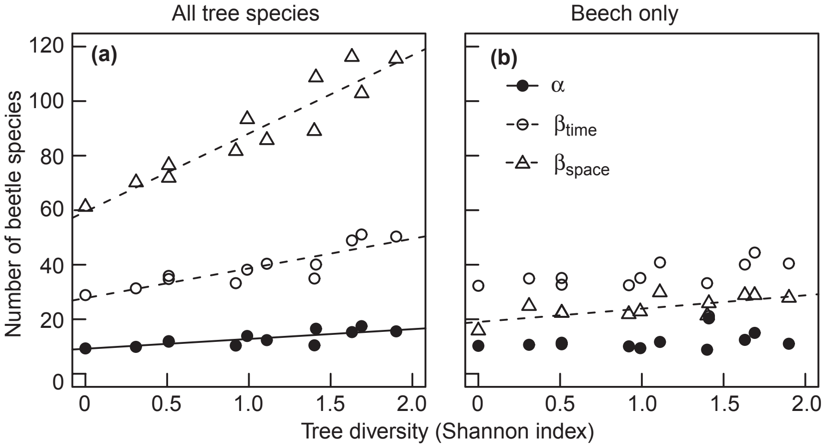

Figure 2 α-, β_{time}- and β_{space}-diversity of beetle communities across a tree diversity gradient based on observed species richness per plot. (a) All tree species sampled, regression slopes differ significantly (ANCOVA, $F_{2,30} = 33.71$, $P < 0.001$), (b) beech only.

Table 1 Multiple regression analyses of species richness parameters for canopy beetles of various tree species across a tree diversity gradient in the Hainich National Park. Log-Abundance = beetle log-abundance, Shannon Index = tree diversity of the sampled forest stands. Significant *P*-values in bold.

		Model A: Log-Abundance + Shannon Index			Model B: Shannon Index + Log-Abundance		
Response variable	Effect	Multiple r^2	*F*	*P*-value	Multiple r^2	*F*	*P*-value
Observed species richness	Log-Abundance		171.24	< **0.001**		18.05	**0.002**
	Shannon Index	0.96	46.44	< **0.001**	0.96	199.64	< **0.001**
α-Diversity	Log-Abundance		90.32	< **0.001**		30.13	< **0.001**
	Shannon Index	0.91	1.04	0.336	0.91	61.23	< **0.001**
β_{time}-Diversity	Log-Abundance*						
	Shannon Index	0.77	32.76	< **0.001**			
β_{space}-Diversity	Log-Abundance*						
	Shannon Index	0.89	79.33	< **0.001**			

*Temporal and spatial species turnover were not linked to turnover in beetle log-abundance, hence this variable was omitted from the model.

Table 2 Multiple regression analyses of species richness parameters for canopy beetles of beech trees across a tree diversity gradient in the Hainich National Park. Log-Abundance = beetle log-abundance, Shannon Index = tree diversity of the sampled forest stands. Significant *P*-values in bold.

		Log-Abundance + Shannon Index		
Response variable	Effect	Multiple r^2	*F*	*P*-value
Observed species richness	Log-Abundance		21.04	**0.001**
	Shannon Index	0.75	6.53	**0.031**
α-Diversity	Log-Abundance*		16.66	**0.003**
	Shannon Index	0.65	0.02	0.9
β_{time}-Diversity	Log-Abundance*			
	Shannon Index	0.11	1.19	0.3
β_{space}-Diversity	Log-Abundance			
	Shannon Index	0.52	10.75	**0.008**

*Temporal and spatial species turnover was not linked to turnover in beetle log-abundance, hence this variable was omitted from the model.

$P = 0.021$, Fig. 3b) while habitat generalists showed no significant response ($F_{1,9} = 4.77$, $P = 0.057$, Table 4).

Based on the classification in Böhme (2004), the majority of species and individuals was denoted as common or only regionally rare (9093 individuals, 87.8%; 310 species, 73.5%, Appendix S2), 76 species (18%) as rare or very rare (1043 individuals, 10%), whereas for the remaining 36 species (8.5%) information on rarity was lacking (224 individuals, 2.2%). The number of common as well as rare species increased across the tree diversity gradient (Fig. 3c), and the response of rare

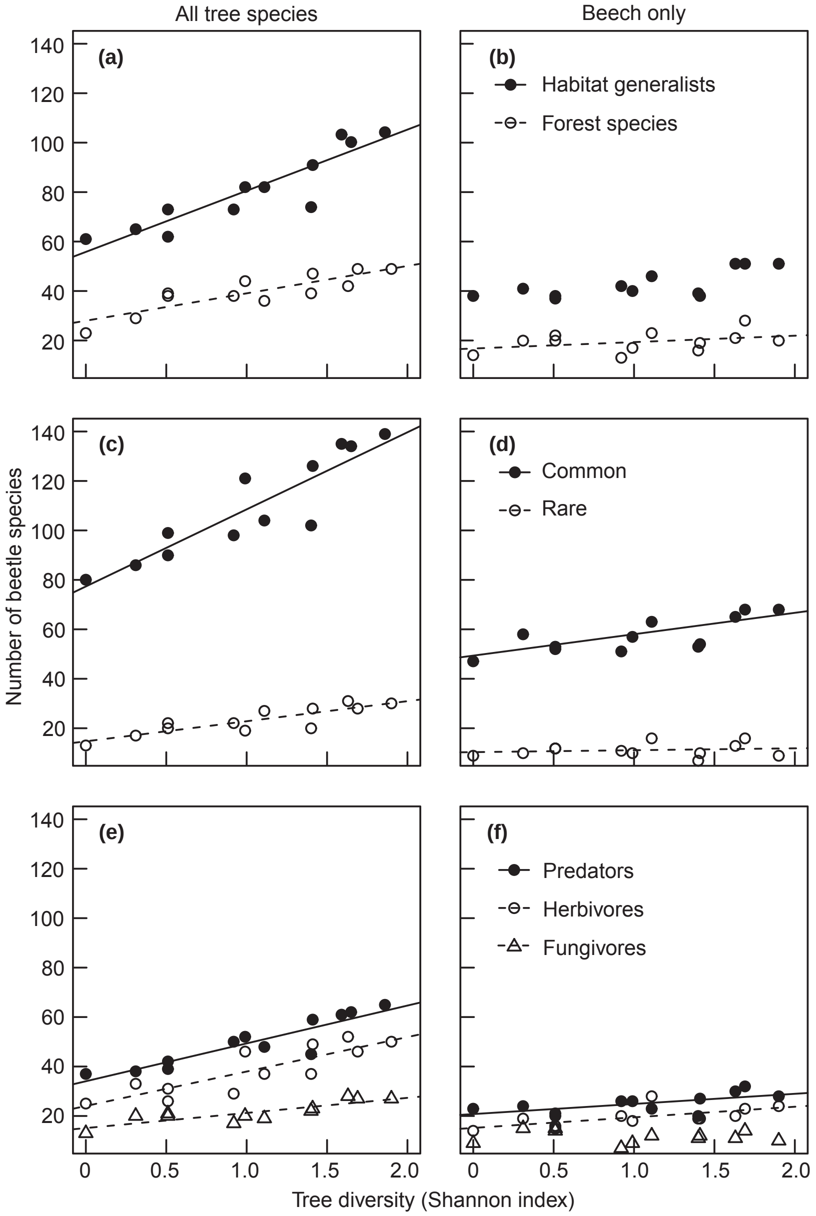

Figure 3 Species richness of functional groups of beetles across a tree diversity gradient on various tree species. (a,b) Habitat specialization, (c,d) rarity, (e,f) feeding guilds (a,c,e: all tree species sampled; b,d,f: beech only).

species was highly significant ($F_{1,9} = 61.62$, $P < 0.001$, Table 3). A similar pattern was found for species on beech alone (Fig. 3d, common: $F_{1,9} = 7.66$, $P = 0.022$; rare: $F_{1,9} = 9.65$, $P = 0.013$).

Grouped into feeding guilds, more than one-third of the species were denoted as predators (36.7%), followed by 119 herbivore (28.2%) and 54 fungivore species (12.8%, Appendix S2). Other feeding guilds each did not include more than 5% of the observed species. In terms of abundance, herbivorous species were most common (3194 individuals, 30.8%), whereas one quarter of all individuals was fungivorous (2782 individuals, 26.9%) and one quarter predatory (2588 individuals, 25%). Among the herbivorous beetles, 48 species (40.3%) were identified as wood feeders (1066 individuals, 38.3%). All three guilds showed a positive linear relationship to increased tree diversity (Fig. 3e), with a highly significant response for herbivore species richness ($F_{1,9} = 58.35$, $P < 0.001$, Table 3), which was not influenced by differences in herbivore log-abundance across the plots. The number of predatory and herbivorous species also increased across the gradient if beech alone was considered (Fig. 3f, $F_{1,9} = 9.78$, $P = 0.012$ and $F_{1,9} = 8.52$, $P = 0.017$), but no effect was found for fungivores ($F_{1,9} = 2.99$, $P = 0.117$). No changes in the relative abundance of species in any of the analysed groupings and guilds could be observed within each forest stand across the tree diversity gradient (Appendix S5), neither for all tree species nor beech alone.

DISCUSSION

In agreement with our *a priori* hypothesis that species-rich forest stands house a greater number of beetle species, overall

Table 3 Multiple regression analyses of functional guild parameters for canopy beetles captured on various tree species across a tree diversity gradient in the Hainich National Park. Log-Abundance = beetle log-abundance, Shannon Index = tree diversity of the sampled forest stands. Significant *P*-values in bold.

		Model A: Log-Abundance + Shannon Index			Model B: Shannon Index + Log-Abundance		
Response variable	Effect	Multiple r^2	*F*	*P*-value	Multiple r^2	*F*	*P*-value
Habitat generalists	Log-Abundance		141.05	< **0.001**		18.39	**0.002**
	Shannon Index	0.94	9.09	**0.015**	0.94	131.75	< **0.001**
Forest species	Log-Abundance		2.5	0.148		5.09	**0.05**
	Shannon Index	0.83	41.67	< **0.001**	0.83	39.08	< **0.001**
Common species	Log-Abundance		76.03	< **0.001**		7.96	**0.02**
	Shannon Index	0.91	14.45	**0.004**	0.91	82.51	< **0.001**
Rare species	Log-Abundance		24.37	< **0.001**		15.07	**0.004**
	Shannon Index	0.91	61.62	< **0.001**	0.91	70.93	< **0.001**
Predators	Log-Abundance		81.77	< **0.001**		6.1	**0.036**
	Shannon Index	0.91	6.51	**0.031**	0.91	82.18	< **0.001**
Herbivores	Log-Abundance		0.62	0.452		1.27	0.288
	Shannon Index	0.76	28.47	< **0.001**	0.76	27.81	< **0.001**
Fungivores	Log-Abundance		58.35	< **0.001**		13.12	**0.006**
	Shannon Index	0.88	7.55	**0.023**	0.88	52.77	< **0.001**

Table 4 Multiple regression analyses of functional guild parameters for canopy beetles captured on beech trees across a tree diversity gradient in the Hainich National Park. Log-Abundance = beetle log-abundance, Shannon Index = tree diversity of the sampled forest stands. Significant *P*-values in bold.

		Log-Abundance + Shannon Index		
Response variable	Effect	Multiple r^2	*F*	*P*-value
Habitat generalists	Log-Abundance	0.77	25.96	< **0.001**
	Shannon Index		4.77	0.057
Forest species	Log-Abundance	0.61	6.33	**0.033**
	Shannon Index		7.84	**0.021**
Common species	Log-Abundance	0.71	14.5	**0.004**
	Shannon Index		7.66	**0.022**
Rare species	Log-Abundance	0.77	19.89	**0.002**
	Shannon Index		9.65	**0.013**
Predators	Log-Abundance	0.72	12.96	**0.006**
	Shannon Index		9.78	**0.012**
Herbivores	Log-Abundance	0.5	0.35	0.57
	Shannon Index		8.52	**0.017**
Fungivores	Log-Abundance	0.45	4.41	0.065
	Shannon Index		2.99	0.117

γ-diversity of beetles increased across the tree diversity gradient. α-diversity was mainly influenced by differences in log-abundance rather than tree diversity, showing that the mean number of species per tree and month did barely change across plots. In contrast, temporal β-diversity was higher in the mixed stands, and especially spatial β-diversity responded strongly to tree diversity indicating a high turnover of beetle species between the tree individuals on the plots. These results show the importance of extensive seasonal and spatial sampling effort for a reliable determination of insect diversity across habitat gradients (Tylianakis *et al.*, 2005). Effective spatial sampling not only demands a sufficient number of sampling replicates (here trees), but also a variety of tree species when forest plots of different diversity are considered. Simply analysing beech alone would have led to the false conclusion that temporal turnover contributes more to beetle diversity than spatial turnover, which is clearly not the case when various tree species or simply more tree individuals are sampled. With an increased number of sampled trees, spatial turnover contributed most to overall beetle diversity. Beech monocultures appear on first sight highly homogeneous, but besides tree species identity as a driver of beetle species richness, individual differences of conspecific trees also seem to play a role for increasing spatial turnover. Summerville *et al.* (2003b) have shown similar effects for lepidopteran caterpillars, but in contrast to our study, turnover between conspecific trees was generally greater compared to turnover between different tree species. Different insect orders and ontogenetic stages thus show different patterns of diversity partitioning, and further research is needed to reveal the mechanisms (e.g. mobility, host preference) behind these patterns.

The observed differences in beetle richness across the *a priori* defined tree diversity gradient can be explained by changes in habitat heterogeneity, which has been proposed to be the driving force of animal species richness across various ecosystems and taxonomic groups (Tews *et al.*, 2004). Structural parameters like tree species identity, tree dimensions, vertical layering, leaf area index, stand openness, amount of coarse woody debris and deadwood availability have been shown to affect community composition of beetles (Larsson & Danell, 2001; Jukes *et al.*, 2002; Fayt *et al.*, 2006; McGeoch *et al.*, 2007;

Müller *et al.*, 2008), and are controlled by canopy tree diversity. In our study, stand structure and complexity changed with the mix and altered biotic and abiotic conditions; the highly diverse plots sampled in this study showed a higher abundance and species richness of herbaceous plant species in the understorey (Mölder *et al.*, 2006). Furthermore, different architecture of various tree species itself is an important factor determining niche-availability and the diversity of associated arthropod communities by controlling micro-climate, shelter-availability and accessibility (Southwood *et al.*, 1982; Lawton, 1983; Halaj *et al.*, 1998, 2000; Goßner & Ammer, 2006). Compared to mono-dominant beech stands, diverse forest stands thus offer a greater array of niches and resources, which enhances beetle diversity.

Alternative hypotheses to explain differences in forest beetle diversity are previous or current human disturbance (Nilsson & Baranowski, 1997; Goßner *et al.*, 2006) and stand age (Hammond *et al.*, 2004; Grimbacher & Catterall, 2007) or stand productivity, which are negligible in our case. None of the investigated stands was pristine, and stand age (Schmidt, *et. al.*, 2008) as well as productivity (Jacob *et al.*, unpublished data) decreased with increased tree diversity, with the youngest stands exhibiting the highest tree and beetle diversity. The latter is particularly striking, because old-age of forest stands is commonly used to explain high beetle diversity. Our results illustrate that apparently even old-age in mono-dominant beech stands does not increase beetle species richness compared to considerably younger forest stands with a diverse mix of tree species. Nevertheless, it should be acknowledged that human impact might be a reason for the overall lack of old-growth relict beetle species *sensu* Müller *et al.* (2005) (Grossmann, 2006).

In total, one-third of the sampled beetle species was classified as habitat specialists, a proportion strikingly consistent with results from other studies in European forest and grassland habitats (Magura *et al.*, 2001; Batary *et al.*, 2007). As expected, more rare species and forest specialists were captured in the most diverse forest stands, but common and generalist species also preferred the more heterogeneous mixed forests. This is probably due to a general lack of available resources in simpler habitats (Gotelli & Colwell, 2001), which was also reflected by lower individual abundance in the less diverse beech stands. Increased species richness within a sampled stand furthermore resulted in increased richness within functional groups. Here, predators outnumbered phytophageous and mycetophageous species across all forest types, and all guilds increased in species richness across the tree diversity gradient, so that the relative proportions within each plot remained constant. This outcome appears to be typical for forest habitats, and different tree species have shown to be consistent by means of relative abundance of feeding guilds (Moran & Southwood, 1982; Southwood *et al.*, 1982; Jukes *et al.*, 2002). Predators tended to be the most speciose guild in various studies, a pattern that seems to be uniform throughout different climate zones and vastly independent of stand structure and vegetation diversity (Southwood *et al.*, 1982; Jukes *et al.*, 2002).

We conclude that for a sufficient judgement of arthropod biodiversity patterns in forest ecosystems, it is crucial to include a variety of spatiotemporal scales in the analyses (Gering & Crist, 2000). It was clearly demonstrated by our comparison of beech alone in contrast to various tree species that otherwise observations can easily result in misleading conclusions, if for example only certain plant species, time points or not enough individuals are considered. Especially, the inclusion of temporal and spatial turnover (β-diversity) adds value to the analyses (Gering *et al.*, 2007), and allows for a fine-grained evaluation of how diversity patterns evolve and what contributes most to the total diversity observed in a region, which in our case was turnover (β_{space}) of beetles among trees.

Furthermore, it was evident that mono-dominant beech stands alone are unsatisfactory in conserving the full set of regional beetle species richness, as opposed to findings by Gering *et al.* (2003), who recommend that rather than maintaining high local tree diversity, establishment of multiple forest sites within ecoregions is of importance. We suggest that sustainable forest management should also aim for maintaining a diverse mix of structurally different tree species, thus enhancing spatial heterogeneity, habitat complexity, and providing resources for a diverse beetle community within sites. Intensive forestry leads to habitat loss, fragmentation and reduced complexity (Kouki *et al.*, 2001; Larsson & Danell, 2001; Hirao *et al.*, 2007), which will eventually result in a scattered, over-simplified forest landscape not suitable to preserve high beetle diversity. Hence, we recommend an integrative approach of forest management by increasing tree diversity locally and site diversity regionally. Species rich forests not only play an important role in conserving rare and strictly forest-dependent species, but also house the majority of generalist species present in a certain area. Failing to include these species in future conservation planning might result in the decline of local populations, and finally lead to a depletion of regional species richness. Due to their abundance, these species might also be functionally dominant (Summerville *et al.*, 2003a), and thus of relevance for maintaining community interactions and forest ecosystem functions (Gering *et al.*, 2003). To reveal hidden differences and driving forces of diversity and community patterns, we moreover recommend that examinations of insect communities should use habitat gradients at different spatiotemporal scales instead of pair-wise comparisons of i.e. managed/unmanaged stands, which currently dominate the available literature.

ACKNOWLEDGEMENTS

This study obtained financial support by the DFG (German Research Foundation) within the Research Training Group 'Graduiertenkolleg 1086: The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests'. We highly acknowledge *C. Leuschner*, *F. Thomas*, *H. Jungkunst* and *S. Fleck* for coordination of the group and also thank *M. Jacob*, *K.M. Daenner*, *M. Gollnow*, *I. Krämer* and *I. Schmidt* for providing data on stand characteristics, furthermore *B. Büche* for his support with beetle identification. Our special thanks go to *M. Erren*, *T. Gebauer*, *M. Goßner*, *S. Schiele* and *U. Simon* for assistance with field work. We also thank *T. Crist* and two anonymous referees for helpful comments to improve the manuscript and *R. Letkeman* for proofreading.

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Editor: Nathan Sanders

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Tree diversity and sampling success.

Appendix S2 List of beetle species.

Appendix S3 Spearman rank correlations of untransformed data.

Appendix S4 Proportional diversity data additive partitioning.

Appendix S5 Proportional data species richness of functional groups/guilds.

Supporting Information

Appendix S1

Tree diversity, relative abundance of the two most dominant tree species, and sampling success of beetle communities in 12 deciduous forest stands in the Hainich National Park. Stands were ranked based on increasing Shannon Indices (tree diversity), rank 3 was assigned twice due to concordant Shannon indices. Sampling Success = % of sampled species referring to number of species estimated with 1st order Jackknife.

Shannon Index	Stand Ranking	Tree Species Richness	% Beech	% Lime	% Sampling Success
0	1	1	100	0	72.1
0.31	2	4	93.5	2.8	70.4
0.51	3a	3	83.3	0	71.3
0.51	3b	4	87.5	3.6	70.6
0.92	4	6	73.7	10.8	69
0.99	5	7	59.4	2.3	71.2
1.11	6	7	60.6	12.1	74.7
1.4	7	6	47.7	33	69.7
1.41	8	7	41.9	34.2	67.8
1.63	9	9	2.4	63.9	70.1
1.69	10	10	3.1	67.4	72
1.9	11	11	13.2	37.9	70

Appendix S2
List of beetle species collected in the canopy of forest stands across a tree diversity gradient in the Hainich National Park. Annotations to habitat, feeding guild, food preference and rarity after Böhme (2004). n^v = number of beetles caught on various tree species, n^b = number of beetles captured on beech alone.

Family	Species	Habitat	Feeding Guild	Rarity	n^v	n^b
Aderidae	*Euglenes oculatus*	forest	other	rare	3	0
Alleculidae	*Allecula morio*	forest	other	common	11	2
	Mycetochara flavipes	forest	other	rare	2	1
	Mycetochara linearis	forest	other	common	24	2
	Prionychus ater	forest	other	common	1	0
Anobiidae	*Dorcatoma chrysomelina*	forest	fungivore	rare	2	0
	Dryophilus pusillus	other	herbivore	common	2	1
	Ernobius mollis	forest	herbivore	common	1	0
	Hemicoelus costatus	no preference	herbivore	common	79	31
	Hemicoelus fulvicornis	no preference	herbivore	common	2	0
	Hemicoelus nitidum	no preference	herbivore	common	8	0
	Ptilinus pectinicornis	forest	herbivore	common	1	0
	Ptinomorphus imperalis	other	herbivore	common	116	37
	Xestobium plumbeum	forest	herbivore	common	39	8
Anthribidae	*Brachytarsus nebulosus*	no preference	predator	common	4	1
	Choragus sheppardi	forest	fungivore	rare	1	1
	Enedreutes sepicola	unknown	fungivore	rare	1	0
	Tropideres albirostris	forest	fungivore	common	1	0
Apionidae	*Holotrichapion pisi*	other	herbivore	common	1	0
	Ischnopterapion virens	no preference	herbivore	common	2	1
	Protapion fulvipes	no preference	herbivore	common	1	0
Bruchidae	*Bruchidius varius*	other	herbivore	rare	1	0
	Bruchus rufimanus	no preference	herbivore	rare	5	1
Byturidae	*Byturus tomentosus*	no preference	herbivore	common	5	1
Cantharidae	*Absindia rufotestacea*	no preference	predator	common	3	0
	Cantharis decipiens	no preference	predator	common	59	5
	Cantharis nigricans	no preference	predator	common	11	2
	Cantharis pellucida	no preference	predator	common	8	3
	Cantharis rufa	no preference	predator	common	1	0
	Lagria hirta	no preference	herbivore	common	2	0
	Malthinus sp.	unknown	predator	unknown	1	0
	Malthodes guttifer	no preference	predator	common	1	0
	Malthodes marginatus	no preference	predator	rare	1	0
	Malthodes minimus	no preference	predator	common	6	1
	Malthodes minutus	unknown	unknown	unknown	2	1
	Malthodes pumilus	unknown	predator	rare	2	0
	Malthodes sp.	unknown	predator	unknown	7	0
	Malthodes spathifer	no preference	predator	common	84	9
	Podabrus alpinus	no preference	predator	common	1	0
	Rhagonycha fulva	no preference	predator	common	8	2
	Rhagonycha lignosa	no preference	predator	common	79	14
	Rhagonycha lutea	no preference	predator	common	5	0
	Rhagonycha translucida	no preference	predator	rare	9	3
Carabidae	*Agonum muelleri*	no preference	predator	common	2	1
	Amara communis	other	other	common	1	1
	Amara familiaris	no preference	other	common	3	2

	Amara lunicollis	no preference	other	common	1	0
	Amara montivaga	unknown	other	common	2	2
	Amara plebeja	unknown	other	common	1	0
	Amara similata	unknown	herbivore	common	5	2
	Bembidion quadrimaculatum	unknown	predator	common	1	1
	Bradycellus verbasci	unknown	other	common	1	0
	Calodromius spilotus	forest	predator	common	1	0
	Calosoma inquisitor	forest	predator	common	1	1
	Dromius agilis	forest	predator	common	8	1
	Dromius fenestratus	forest	predator	common	1	0
	Dromius quadrimaculatus	forest	predator	common	168	46
	Dromius sp.	unknown	predator	unknown	1	1
	Harpalus affinis	no preference	other	common	1	1
	Limodromus assimilis	no preference	predator	common	1	0
	Loricera pilicornis	no preference	predator	common	8	3
	Microlestes minutulus	unknown	predator	common	1	0
	Notiophilus biguttatus	no preference	predator	common	3	0
	Platynus dorsalis	unknown	unknown	unknown	1	0
	Pterostichus oblongopunctatus	forest	predator	common	1	1
	Trechus quadristriatus	no preference	predator	common	53	17
Cerambycidae	*Alosterna tabacicolor*	forest	herbivore	common	11	2
	Anaglyptus mysticus	forest	herbivore	rare	0	1
	Grammoptera abdominalis	forest	herbivore	rare	1	0
	Grammoptera ruficornis	forest	herbivore	common	5	1
	Leiopus nebulosus	no preference	herbivore	common	17	1
	Mesosa nebulosa	no preference	herbivore	common	1	0
	Oberea linearis	no preference	herbivore	rare	0	1
	Phymatodes testaceus	no preference	herbivore	common	1	0
	Pogonocherus hispidus	no preference	herbivore	common	2	0
	Rhagium mordax	forest	herbivore	common	7	3
	Saperda scalaris	no preference	herbivore	common	1	0
	Stenocorus meridianus	no preference	herbivore	common	1	0
	Stenostola dubia	no preference	herbivore	common	15	2
	Tetropium castaneum	forest	herbivore	common	1	0
	Tetrops starkii	forest	herbivore	rare	9	0
Cerylonidae	*Cerylon ferrugineum*	forest	other	common	28	8
	Cerylon histeroides	no preference	other	common	1	1
Cholevidae	*Nargus velox*	forest	other	common	1	1
	Sciodrepoides watsoni	no preference	other	common	4	0
Chrysomelidae	*Aphthona euphorbiae*	unknown	herbivore	rare	54	9
	Aphthona venustula	no preference	herbivore	common	1	0
	Chaetocnema concinna	no preference	herbivore	common	0	1
	Cryptocephalus frontalis	unknown	herbivore	rare	2	0
	Galeruca pomonae	no preference	herbivore	common	1	0
	Galeruca tanaceti	no preference	herbivore	common	2	1
	Longitarsus kutscherae	no preference	herbivore	rare	2	1
	Longitarsus luridus	no preference	herbivore	common	8	2
	Longitarsus parvulus	no preference	herbivore	common	17	4
	Orsodacne cerasi	no preference	herbivore	common	46	4
	Oulema gallaeciana	other	herbivore	common	254	85
	Oulema melanopus	no preference	herbivore	common	14	7
	Phyllotreta atra	no preference	herbivore	common	6	1
	Phyllotreta nigripes	no preference	herbivore	common	5	1
	Phyllotreta vittula	no preference	herbivore	common	6	6
Cisidae	*Cis bidentatus*	forest	fungivore	rare	1	0
	Cis boleti	no preference	fungivore	common	1	0

	Ennearthron cornutum	no preference	fungivore	common	3	0
	Orthocis alni	no preference	fungivore	common	6	1
Clambidae	*Clambus sp.*	unknown	fungivore	unknown	2	0
Cleridae	*Opilo mollis*	forest	predator	common	25	8
	Tillus elongatus	no preference	predator	common	1	0
Coccinellidae	*Adalia decempunctata*	no preference	predator	common	17	2
	Calvia decemguttata	no preference	predator	rare	1	1
	Chilocorus renipustulatus	no preference	predator	common	5	0
	Coccinella septempunctata	no preference	predator	common	5	1
	Exochomus quadripustulatus	no preference	predator	common	17	2
	Halyzia sedecimguttata	forest	fungivore	common	9	2
	Propylea quatuordecimpunctata	no preference	predator	common	11	1
	Scymnus abietis	no preference	predator	common	3	1
Colydiidae	*Synchita humeralis*	forest	fungivore	common	2	0
Corylophidae	*Orthoperus* sp.	forest	predator	unknown	3	0
	Sacium pusillum	no preference	predator	rare	13	2
	Sericoderus lateralis	other	predator	common	1	0
Cryptophagidae	*Atomaria analis*	no preference	other	common	43	7
	Atomaria atricapilla	no preference	other	common	267	82
	Atomaria fuscata	no preference	other	common	6	4
	Atomaria lewisi	no preference	other	common	2	0
	Atomaria linearis	no preference	other	common	124	43
	Atomaria nigrirostris	no preference	other	common	2	1
	Atomaria puncticollis	no preference	other	rare	1	1
	Atomaria punctithorax	no preference	other	rare	7	2
	Atomaria pusilla	no preference	other	common	1	0
	Atomaria sp.	unknown	other	unknown	9	4
	Atomaria testacea	no preference	other	common	13	6
	Cryptophagus acutangulus	no preference	other	common	1	0
	Cryptophagus dentatus	no preference	other	common	37	6
	Cryptophagus intermedius	unknown	other	rare	2	1
	Cryptophagus pilosus	no preference	other	common	23	6
	Cryptophagus pubescens	no preference	other	common	3	2
	Cryptophagus scanicus	no preference	other	common	8	1
	Cryptophagus sp.	unknown	other	unknown	1	0
	Micrambe abietis	forest	fungivore	common	2	0
Cucujidae	*Phloeostichus denticollis*	unknown	unknown	rare	8	0
Curculionidae	*Ceutorhynchus floralis*	no preference	herbivore	common	1	0
	Ceutorhynchus pallidactylus	no preference	herbivore	common	8	6
	Curculio glandium	no preference	herbivore	common	11	1
	Curculio pellitus	other	herbivore	rare	1	0
	Curculio pyrrhoceras	other	herbivore	common	2	0
	Curculio villosus	other	herbivore	common	1	0
	Furcipus rectirostris	no preference	herbivore	common	2	3
	Hypera venusta	other	herbivore	common	2	0
	Larinus planus	unknown	unknown	unknown	1	1
	Magdalis armigera	forest	herbivore	common	1	0
	Magdalis flavicornis	no preference	herbivore	common	1	0
	Phyllobius argentatus	no preference	herbivore	common	31	14
	Phyllobius calcaratus	no preference	herbivore	common	1	0
	Phyllobius maculicornis	no preference	herbivore	common	1	0
	Polydrusus mollis	no preference	herbivore	common	4	2
	Polydrusus pterygomalis	no preference	herbivore	common	34	10
	Polydrusus sericeus	no preference	herbivore	common	17	2
	Polydrusus undatus	no preference	herbivore	common	28	9
	Rhynchaenus fagi	forest	herbivore	common	198	72

	Sitona hispidulus	no preference	herbivore	common	2	1
	Sitona humeralis	no preference	herbivore	common	1	1
	Sitona lineatus	no preference	herbivore	common	14	5
	Sitona macularius	no preference	herbivore	common	1	0
	Sitona sp.	unknown	herbivore	unknown	1	0
	Stereonychus fraxini	forest	herbivore	common	5	1
	Strophosoma capitatum	no preference	herbivore	common	1	0
	Strophosoma melanogrammum	no preference	herbivore	common	1	0
	Tychius picirostris	no preference	herbivore	common	0	1
Cybocephalidae	*Cybocephalus politus*	no preference	predator	rare	1	0
Dasytidae	*Aplocnemus nigricornis*	forest	predator	common	1	1
	Dasytes aeratus	no preference	predator	common	9	3
	Dasytes cyaneus	forest	predator	common	6	2
	Dasytes niger	no preference	predator	common	1	0
	Dasytes plumbeus	no preference	predator	common	69	17
	Trichoceble memnonia	forest	predator	rare	1	0
Dermestidae	*Attagenus pellio*	no preference	omni	common	1	0
	Ctesias serra	no preference	other	rare	3	1
	Megatoma undata	no preference	other	rare	15	4
Dytiscidae	*Agabus* sp.	unknown	predator	unknown	1	0
	Graptodytes granularis	no preference	other	common	1	0
	Rhantus bistriatus	no preference	predator	rare	1	0
Elateridae	*Agriotes acuminatus*	no preference	herbivore	common	30	2
	Agriotes gallicus	unknown	herbivore	rare	1	1
	Agriotes pallidulus	no preference	herbivore	common	7	0
	Agrypnus murina	no preference	predator	common	2	0
	Ampedus pomorum	forest	herbivore	common	10	1
	Athous bicolor	no preference	herbivore	rare	2	1
	Athous haemorrhoidalis	no preference	herbivore	common	40	8
	Athous subfuscus	no preference	herbivore	rare	133	30
	Athous vittatus	no preference	herbivore	common	539	118
	Calambus bipustulatus	no preference	other	rare	8	1
	Dalopius marginatus	forest	other	common	44	11
	Denticollis linearis	no preference	other	common	10	3
	Denticollis rubens	forest	other	rare	6	2
	Hemicrepidius hirtus	no preference	herbivore	common	2	1
	Hemicrepidius niger	no preference	herbivore	common	1	0
	Hypoganus inunctus	forest	herbivore	rare	7	4
	Kibunea minutus	no preference	herbivore	common	1	0
	Melanotus rufipes	no preference	other	common	4	3
Erotylidae	*Dacne bipustulata*	no preference	fungivore	common	55	15
	Triplax russica	no preference	fungivore	common	2	0
	Tritoma bipustulata	unknown	fungivore	common	3	1
Eucnemidae	*Dirhagus lepidus*	forest	other	rare	2	0
	Eucnemis capucina	forest	other	rare	4	0
	Hylis foveicollis	forest	other	rare	2	0
	Melasis buprestoides	no preference	other	common	1	0
Helodidae	*Cyphon* sp.	unknown	herbivore	unknown	6	2
	Cyphon variabilis	unknown	herbivore	common	4	1
	Prionocyphon serricornis	no preference	other	common	10	2
Histeridae	*Carcinops pumilio*	no preference	other	common	1	0
	Gnathoncus buyssoni	no preference	other	rare	1	0
	Plegaderus caesus	forest	predator	common	1	0
Hydrophilidae	*Helophorus nubilus*	no preference	herbivore	common	1	0
Latridiidae	*Cartodere constricta*	no preference	fungivore	common	2	0
	Cartodere nodifer	no preference	fungivore	common	5	0

	Corticaria abietorum	forest	fungivore	rare	10	3
	Corticaria elongata	no preference	fungivore	common	4	0
	Corticaria polypori	forest	fungivore	rare	4	0
	Corticaria umbilicata	no preference	fungivore	common	2	2
	Corticarina fuscula	no preference	fungivore	common	6	2
	Corticarina similata	no preference	fungivore	common	99	37
	Cortinicara gibbosa	no preference	fungivore	common	2030	611
	Enicmus atriceps	forest	fungivore	rare	68	27
	Enicmus fungicola	forest	fungivore	common	1	0
	Enicmus geminatus	unknown	fungivore	rare	2	0
	Enicmus histrio	unknown	fungivore	common	5	2
	Enicmus rugosus	forest	fungivore	common	167	37
	Enicmus transversus	no preference	fungivore	common	35	13
	Latridius hirtus	unknown	fungivore	rare	63	23
	Latridius minutus	no preference	fungivore	common	2	0
	Stephostethus alternans	forest	fungivore	rare	4	1
Leiodidae	*Agathidium nigripenne*	forest	fungivore	common	57	10
	Agathidium varians	no preference	fungivore	common	59	6
	Anisotoma humeralis	forest	fungivore	common	3	0
Lucanidae	*Platycerus caraboides*	forest	herbivore	common	12	4
Malachiidae	*Charopus flavipes*	no preference	predator	common	1	0
	Malachius bipustulatus	no preference	predator	common	4	0
Melandryidae	*Anisoxya fuscula*	forest	other	rare	10	7
	Orchesia fasciata	no preference	fungivore	rare	1	0
	Orchesia micans	forest	fungivore	common	1	1
	Orchesia minor	forest	fungivore	common	19	4
	Orchesia undulata	forest	fungivore	common	5	1
	Phloiotrya rufipes	forest	other	rare	2	1
Monotomidae	*Monotoma longicollis*	no preference	unknown	common	1	1
	Rhizophagus bipustulatus	no preference	predator	common	85	23
	Rhizophagus parvulus	forest	predator	common	1	1
Mordellidae	*Mordellistena humeralis*	unknown	other	common	2	1
	Mordellistena neuwaldeggiana	no preference	other	common	40	12
	Mordellistena variegata	unknown	other	common	21	4
	Mordellochroa abdominalis	no preference	other	common	28	2
Mycetophagidae	*Litargus connexus*	no preference	fungivore	common	80	21
	Mycetophagus atomarius	no preference	fungivore	common	1	0
	Mycetophagus populi	unknown	fungivore	common	8	6
	Mycetophagus quadripustulatus	unknown	fungivore	common	1	0
Nitidulidae	*Cryptarcha strigata*	forest	other	common	13	1
	Cryptarcha undata	forest	other	common	120	37
	Epuraea marseuli	forest	other	common	4	0
	Epuraea melanocephala	no preference	other	common	426	79
	Epuraea unicolor	no preference	other	common	2	0
	Glischrochilus hortensis	no preference	other	common	2	0
	Meligethes aeneus	no preference	herbivore	common	9	6
	Meligethes nigrescens	no preference	herbivore	common	1	0
	Nitidulidae sp.1	unknown	unknown	unknown	1	0
	Soronia grisea	no preference	other	common	127	32
Oedemeridae	*Ischnomera coerulea*	forest	herbivore	rare	3	2
	Ischnomera cyanea	forest	herbivore	common	1	0
	Ischnomera sanguinicollis	forest	herbivore	rare	1	0
Phalacridae	*Stilbus testaceus*	other	herbivore	common	0	1
Phloiophilidae	*Phloiophilus edwardsii*	forest	predator	rare	1	0
Pselaphidae	*Bibloporus bicolor*	forest	predator	rare	26	6
	Bibloporus minutus	forest	predator	rare	49	11

	Bibloporus sp.	forest	predator	rare	2	0
	Trimium brevicorne	forest	predator	common	8	2
	Tychus niger	unknown	predator	common	1	0
Ptiliidae	*Acrotrichis* sp.	unknown	fungivore	unknown	6	1
Ptinidae	*Ptinus rufipes*	forest	other	common	1	1
Pyrochroidae	*Pyrochroa coccinea*	forest	other	common	1	1
	Schizotus pectinicornis	forest	other	common	9	2
Rhynchitidae	*Byctisus betulae*	no preference	herbivore	common	0	1
	Caenorhinus pauxillus	no preference	herbivore	common	1	0
	Deporaus betulae	no preference	herbivore	common	3	0
	Deporaus tristis	forest	herbivore	rare	2	0
	Lasiorhynchites olivaceus	no preference	herbivore	common	2	0
Salpingidae	*Lissodema cursor*	forest	predator	rare	12	2
	Rabocerus gabrieli	unknown	predator	rare	14	5
	Salpingus planirostris	no preference	predator	common	49	14
	Salpingus ruficollis	forest	predator	common	43	16
Scarabaeidae	*Aphodius fimetarius*	no preference	other	common	1	1
	Aphodius granarius	no preference	other	common	2	0
	Aphodius prodromus	no preference	other	common	2	0
	Gnorimus nobilis	no preference	herbivore	common	3	1
Scolytidae	*Cryphalus abietis*	forest	herbivore	common	1	0
	Cryphalus sp.	forest	herbivore	unknown	1	0
	Crypturgus cinereus	forest	herbivore	common	3	0
	Dryocoetes autographus	forest	herbivore	common	5	1
	Ernoporicus caucasicus	forest	herbivore	rare	2	1
	Ernoporicus fagi	forest	herbivore	common	330	131
	Ernoporus tiliae	forest	herbivore	common	2	1
	Hylastes cunicularius	forest	herbivore	common	1	0
	Hylesinus crenatus	forest	herbivore	common	4	1
	Hylesinus oleiperda	forest	herbivore	rare	2	0
	Hylurgops palliatus	forest	herbivore	common	1	0
	Ips cembrae	forest	herbivore	common	1	0
	Ips typographus	forest	herbivore	common	2	0
	Leperisinus fraxini	forest	herbivore	common	30	2
	Pityogenes chalcographus	forest	herbivore	common	57	12
	Polygraphus grandiclava	no preference	herbivore	common	0	1
	Polygraphus poligraphus	forest	herbivore	common	34	26
	Scolytus carpini	forest	herbivore	common	30	7
	Scolytus intricatus	forest	herbivore	common	7	8
	Taphrorychus bicolor	forest	herbivore	common	201	66
	Xyleborus peregrinus	forest	fungivore	rare	270	78
	Xyleborus saxeseni	no preference	fungivore	common	25	6
	Xyleborus sp.	unknown	fungivore	unknown	7	0
Scraptiidae	*Anaspis flava*	no preference	other	common	14	3
	Anaspis frontalis	no preference	other	common	16	1
	Anaspis melanostoma	no preference	other	rare	10	4
	Anaspis rufilabris	no preference	other	common	64	17
	Anaspis thoracica	no preference	other	common	63	13
Scydmaenidae	*Neuraphes elongatulus*	no preference	predator	common	3	1
	Stenichnus bicolor	forest	predator	rare	1	0
	Stenichnus scutellaris	forest	predator	common	1	1
Silvanidae	*Silvanus unidentatus*	forest	predator	common	1	0
	Uleiota planata	no preference	predator	common	3	1
Sphindidae	*Arpidiphorus orbiculatus*	no preference	fungivore	common	1	0
Staphylinidae	*Acrotona* sp.	unknown	predator	unknown	4	1
	Aleochara bipustulata	no preference	predator	common	4	1

Aleochara sparsa	no preference	predator	common	28	5
Aleochara laevigata	no preference	predator	rare	1	0
Aleochara sanguinea	no preference	predator	common	1	0
Aleochara sp.	unknown	predator	unknown	3	1
Aloconota gregaria	no preference	predator	common	10	2
Amarochara bonnairei	no preference	predator	rare	3	0
Amischa analis	no preference	predator	common	3	0
Amischa decipiens	no preference	predator	common	3	0
Amischa sp.	no preference	predator	unknown	53	13
Anomognathus cuspidatus	forest	predator	common	3	1
Anotylus inustus	no preference	other	common	5	1
Anotylus rugosus	no preference	other	common	1	0
Anotylus sculpturatus	no preference	other	common	4	3
Anotylus tetracarinatus	no preference	other	common	19	6
Anthobium atrocephalum	no preference	other	common	3	0
Anthophagus angusticollis	unknown	predator	common	5	2
Atheta amplicollis	unknown	predator	common	2	2
Atheta fungi	no preference	predator	common	381	116
Atheta inquinula	no preference	predator	common	4	2
Atheta nigra	no preference	predator	common	0	1
Atheta palustris	unknown	predator	common	1	1
Atheta sp.	unknown	predator	unknown	74	28
Atheta sp.1	unknown	predator	unknown	1	1
Atheta sp.2	unknown	predator	unknown	1	1
Atheta triangulum	no preference	predator	common	1	1
Bolitobius castaneus	no preference	predator	rare	1	0
Bolitobius sp.	no preference	predator	rare	1	0
Bythinus burrelli	no preference	predator	common	2	0
Callicerus obscurus	no preference	predator	common	1	1
Carpelimus corticinus	unknown	other	common	1	0
Cypha longicornis	no preference	predator	common	3	1
Cyphea curtula	forest	predator	rare	19	1
Euplectus karsteni	no preference	predator	common	4	0
Euplectus punctatus	forest	predator	rare	3	1
Euryusa optabilis	forest	predator	common	2	1
Eusphalerum luteum	no preference	herbivore	common	65	14
Eusphalerum minutum	unknown	herbivore	common	6	4
Eusphalerum pseudaucupariae	unknown	herbivore	rare	40	10
Eusphalerum sp.	unknown	herbivore	unknown	1	0
Geostiba circellaris	no preference	predator	common	3	0
Haploglossa picipennis	forest	predator	rare	1	0
Haploglossa villosula	no preference	predator	common	50	15
Heterothops niger	no preference	predator	common	1	0
Holobus flavicornis	no preference	predator	common	26	6
Hypnogyra glabra	no preference	predator	common	1	0
Ischnoglossa sp.	unknown	predator	rare	4	2
Ischnosoma splendidum	no preference	predator	common	4	1
Lathrobium elongatum	no preference	predator	common	3	0
Leptacinus sp.	unknown	predator	unknown	1	0
Leptusa fumida	forest	predator	common	10	2
Leptusa ruficollis	forest	predator	common	7	6
Lesteva longoelytrata	unknown	predator	common	4	2
Liogluta nitidula	no preference	predator	common	1	0
Liogluta sp.	unknown	predator	unknown	8	2
Meotica sp.	unknown	predator	rare	1	1
Metopsia clypeata	no preference	fungivore	rare	6	2

	Mycetoporus solidicornis	no preference	predator	rare	1	0
	Ocalea sp.	unknown	predator	unknown	1	0
	Oligota pusilima	no preference	predator	unknown	0	1
	Oligota sp.	unknown	predator	unknown	10	5
	Omalium caesum	no preference	other	common	3	0
	Omalium rivulare	no preference	other	common	1	0
	Oxypoda brevicornis	no preference	predator	common	1	0
	Oxypoda sp.	unknown	predator	unknown	2	1
	Philonthus carbonarius	no preference	predator	common	16	7
	Philonthus cognatus	no preference	predator	common	23	10
	Philonthus coracinus	unknown	unknown	unknown	4	1
	Philonthus decorus	forest	predator	common	1	0
	Philonthus rotundicollis	no preference	predator	common	8	6
	Philonthus sp.	unknown	predator	unknown	1	0
	Phloeopora corticalis	no preference	predator	common	496	135
	Phloeopora testacea	forest	predator	common	8	1
	Phyllodrepa floralis	no preference	predator	common	1	1
	Phyllodrepa ioptera	no preference	predator	common	15	5
	Placusa atrata	forest	predator	common	1	1
	Placusa depressa	forest	predator	common	2	0
	Plataraea brunnea	no preference	predator	common	7	2
	Platystethus nitens	no preference	other	common	7	1
	Quedius brevicornis	no preference	predator	rare	3	0
	Quedius fuliginosus	no preference	predator	common	1	1
	Quedius invrae	no preference	predator	common	1	0
	Quedius maurus	forest	predator	rare	24	7
	Quedius ochripennis	no preference	predator	common	2	0
	Rugilus erichsoni	no preference	predator	rare	0	1
	Rugilus rufipes	no preference	predator	common	1	0
	Scaphisoma agaricinum	other	fungivore	common	2	0
	Silusa rubiginosa	forest	predator	common	1	0
	Stenus clavicornis	no preference	predator	common	1	0
	Stenus similis	no preference	predator	common	1	1
	Stichoglossa semirufa	no preference	predator	rare	61	12
	Tachinus sp.	unknown	predator	unknown	2	0
	Tachyporus atriceps	no preference	predator	common	2	1
	Tachyporus hypnorum	no preference	predator	common	46	12
	Tachyporus nitidulus	no preference	predator	common	21	6
	Tachyporus obtusus	unknown	predator	common	3	0
	Tachyporus solutus	no preference	predator	common	8	4
	Xantholinus linearis	no preference	predator	common	19	7
Tenebrionidae	*Diaperis boleti*	forest	fungivore	common	13	3
	Latheticus oryzae	unknown	fungivore	rare	1	0
	Palorus depressus	no preference	other	rare	1	0
	Platydema violaceum	unknown	other	rare	1	0
Tetratomidae	*Tetratoma ancora*	unknown	fungivore	common	28	8
Throscidae	*Aulonothroscus brevicollis*	forest	herbivore	common	4	0
	Trixagus dermestoides	no preference	unknown	common	1	0
	Trixagus sp.	unknown	unknown	unknown	3	0
Trogossitidae	*Nemosoma elongatum*	no preference	predator	common	10	3

Appendix S3

Spearman rank correlations of untransformed response (beetle richness) and explanatory variables.

	Beetle Richness	Beetle Log-Abundance	Tree Diversity (Shannon)	Stand Age	Stem Density	Tree Height	Crown Area	Plant Area Index	Dead Wood Volume
Beetle Richness	1								
Beetle Log-Abundance	0.85	1							
Tree Diversity (Shannon)	0.94	0.7	1						
Stand Age	-0.7	-0.35	-0.81	1					
Stem Density	0.18	-0.18	0.34	-0.72	1				
Tree Height	-0.68	-0.36	-0.78	0.95	-0.63	1			
Crown Area	-0.32	0.01	-0.49	0.84	-0.92	0.69	1		
Plant Area Index	0.57	0.3	0.65	-0.75	0.46	-0.69	-0.6	1	
Dead Wood Volume	-0.3	-0.05	-0.36	0.66	-0.54	0.77	0.51	-0.21	1

Appendix S4

Relative contributions of α- and β-diversity to beetle species richness of communities sampled on various tree species in 12 forest plots across a tree diversity gradient. Values for beech alone are set in parentheses. Stands were ranked based on increasing Shannon Indices (tree diversity), rank 3 was assigned twice due to concordant Shannon indices.

Forest Stand	% α	%β_{time}	%β_{space}
1	9.4 (17.7)	29.2 (55.6)	61.4 (26.7)
2	8.9 (15.1)	28.2 (49.9)	62.9 (35)
3a	10 (15.9)	29.4 (51.7)	60.6 (32.4)
3b	9.7 (17.1)	28.9 (49.5)	61.4 (33.3)
4	8.3 (15.6)	26.6 (50.8)	65.1 (33.6)
5	9.6 (14.1)	26.3 (52.4)	64.1 (33.6)
6	8.9 (14.2)	29.2 (49.8)	61.8 (36)
7	7.8 (14)	26 (52.6)	66.2 (33.3)
8	10 (30.3)	24.3 (31.6)	65.7 (38.1)
9	8.5 (15.3)	27.2 (49.5)	64.4 (35.2)
10	10.2 (17)	29.9 (50.6)	59.9 (32.4)
11	8.6 (13.9)	27.8 (51.3)	63.6 (34.8)

Appendix S5

Relative contributions of species abundance to functional guilds for canopy beetles captured on various tree species across a tree diversity gradient in the Hainich National Park. Values for beech alone are set in parentheses. Stands were ranked based on increasing Shannon Indices (tree diversity), rank 3 was assigned twice due to concordant Shannon indices.

Forest Stand	% Habitat Generalists	% Forest Species	% Common Species	% Rare Species	% Predators	% Herbivores	% Fungivores
1	61.6 (65.5)	23.2 (24.1)	80.8 (81)	13.1 (13.8)	37.4 (39.7)	25.3 (24.1)	13.1 (15.5)
2	58.6 (58.6)	26.1 (28.6)	77.5 (82.9)	15.3 (12.9)	34.2 (34.3)	29.7 (27.1)	18 (21.4)
3a	52.5 (55.9)	33.1 (29.4)	76.3 (77.9)	18.6 (16.2)	33.1 (30.9)	22 (22.1)	17.8 (22.1)
3b	58.9 (56.1)	30.6 (33.3)	79.8 (78.8)	16.1 (16.7)	33.9 (30.3)	25 (24.2)	16.1 (21.2)
4	58.4 (65.6)	30.4 (20.3)	78.4 (79.7)	17.6 (15.6)	40 (40.6)	23.2 (31.3)	13.6 (10.9)
5	56.6 (59.7)	30.3 (25.4)	83.4 (85.1)	13.1 (13.4)	35.9 (38.8)	31.7 (26.9)	13.8 (13.4)
6	59.4 (56.1)	26.1 (28)	75.4 (76.8)	19.6 (18.3)	34.8 (28)	26.8 (34.1)	13.8 (14.6)
7	55.2 (61.9)	29.1 (25.4)	76.1 (84.1)	14.9 (9.5)	33.6 (31.7)	27.6 (30.2)	16.4 (17.5)
8	55.2 (56.7)	28.5 (28.4)	76.4 (80.6)	17 (13.4)	35.8 (40.3)	29.7 (28.4)	13.9 (17.9)
9	58.3 (63)	23.3 (25.9)	75 (80.2)	17.2 (14.8)	33.9 (37)	28.9 (24.7)	15.6 (13.6)
10	59.6 (58)	28.7 (31.8)	78.4 (77.3)	16.4 (17)	36.3 (36.4)	26.9 (26.1)	15.8 (15.9)
11	58.6 (64.6)	27.1 (25.3)	76.8 (86.1)	16.6 (10.1)	35.9 (35.4)	27.6 (30.4)	14.9 (12.7)

Chapter 10

Effects of tree diversity on herbivory, herbivores and predators

published as:

Sobek S, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. Oecologia 160:279–288.

Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest

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Received: 13 June 2008 / Accepted: 27 January 2009 / Published online: 24 February 2009

Abstract Tree species-rich forests are hypothesised to be less susceptible to insect herbivores, but so far herbivory–diversity relationships have rarely been tested for tree saplings, and no such study has been published for deciduous forests in Central Europe. We expected that diverse tree communities reduce the probability of detection of host plants and increase abundance of predators, thereby reducing herbivory. We examined levels of herbivory suffered by beech (*Fagus sylvatica* L.) and maple saplings (*Acer pseudoplatanus* L. and *Acer platanoides* L.) across a tree species diversity gradient within Germany's largest remaining deciduous forest area, and investigated whether simple beech or mixed stands were less prone to damage caused by herbivorous insects. Leaf area loss and the frequency of galls and mines were recorded for 1,040 saplings (>13,000 leaves) in June and August 2006. In addition, relative abundance of predators was assessed to test for potential top-down control. Leaf area loss was generally higher in the two species of maple compared to beech saplings, while only beech showed a decline in damage caused by leaf-chewing herbivores across the tree diversity gradient. No significant patterns were found for galls and mines. Relative abundance of predators on beech showed a seasonal response and increased on species-rich plots in June, suggesting higher biological control. We conclude that, in temperate deciduous forests, herbivory–tree diversity relationships are significant, but are tree species-dependent with bottom-up and top-down control as possible mechanisms. In contrast to maple, beech profits from growing in a neighbourhood of higher tree richness, which implies that species identity effects may be of greater importance than tree diversity effects per se. Hence, herbivory on beech appeared to be mediated bottom-up by resource concentration in the sampled forest stands, as well as regulated top-down through biocontrol by natural enemies.

Keywords Diversity-functioning relationships · Leaf damage · Mines · Multitrophic interactions · Plant–animal interactions

Introduction

The relationship between plant biodiversity and ecosystem functioning is a central question in ecology (Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006), but so far the majority of studies have focused on plant productivity in experimental grasslands. Research on the effects of plant diversity on other trophic levels, for example insect

Communicated by Diethart Matthies.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1304-2) contains supplementary material, which is available to authorised users.

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herbivores as primary consumers, has a long tradition in agricultural habitats (reviewed in Andow 1991), while natural habitat types have only recently begun to be considered. In most of these studies, reduced insect herbivory was observed with increased plant diversity, both in agricultural (Risch et al. 1983) and grassland (Unsicker et al. 2006) or forest habitats (Jactel et al. 2006; Jactel and Brockerhoff 2007; Kaitaniemi et al. 2007). However, some authors found the opposite (Vehviläinen et al. 2006) or no effect at all (Scherber et al. 2006), and the outcome often appears to be species dependent (Jactel and Brockerhoff 2007; Vehviläinen et al. 2007). Identity of the observed plant species and of species in the surrounding community, as well as host specificity of herbivores, have been shown to affect the herbivory–plant diversity relationship (Koricheva et al. 2006; Unsicker et al. 2006; Jactel and Brockerhoff 2007). According to data from other invertebrate herbivores (e.g. molluscs), diversity–herbivory relationships are not controlled by plant diversity in the local neighboorhood, but by plant diversity observed on community level (Hanley 2004).

Lower susceptibility of species-rich plant communities to insect herbivores, also described as associational resistance (Tahvanainen and Root 1972; Karban 2007; Sholes 2008), can be explained with two well-established concepts: the resource concentration hypothesis (Tahvanainen and Root 1972; Root 1973) and the enemies hypothesis (Root 1973; Russell 1989). The resource concentration hypothesis is based on the assumption that specialist herbivores accumulate in dense patches of their host plants and reside there if the conditions are favourable (Root 1973). In diverse plant communities, individual plant species are often less prone to herbivore infestation, because host-finding is hindered due to lower host plant densities. Plants growing in small patches of low abundance appear to be structurally or chemically masked by their surrounding neighbours (Mauchline et al. 2005; Karban 2007). According to the enemies hypothesis, a diverse matrix of flowering plants in species-rich assemblages offers alternative prey, accessory food (e.g. pollen, nectar) and various shelter options for predators and parasitoids (Root 1973; Russell 1989, Jactel et al. 2005). This increased structural diversity enhances natural enemy abundance and functional diversity, finally resulting in effective biological control of specialist herbivores.

More recently, a mechanism called associational susceptibility (White and Whitham 2000) has been suggested to explain why in some studies no reduction, or even an increase, in herbivory with increased plant diversity was found. According to this idea, generalist herbivores are thought to spill over from preferred plant species to less favoured hosts in the adjacent neighbourhood (Jactel et al. 2005; Carnus et al. 2006).

In diversity gradients across forest ecosystems, most studies carried out so far primarily focused either on specific forest pests (e.g. Su et al. 1996; Jactel et al. 2002) or generalist insect herbivores (Vehviläinen et al. 2006). Predator abundance was not included in these investigations, although it is sometimes referred to as a possible explanation for observed differences in herbivore damage (Su et al. 1996), and has only recently gained more interest in studies of forest herbivory (Jactel et al. 2006; Vehviläinen et al. 2008).

The impact of herbivore damage on plant survival is strongest in early developmental stages (Maron 1997; Hanley and Fegan 2007), and during ontogeny defensive plant traits are subject to change (Boege and Marquis 2005). In forest ecosystems, most studies have focused on herbivore damage in the canopy tree layer, but naturally grown saplings have rarely been used as target organisms for observation. Although early-stage tree damage caused by large herbivores (i.e. deer browsing) has been intensively investigated (Hester et al. 2000), data are scarce for insect herbivory. Studies usually only include low hanging branches of trees and larger saplings (e.g. Le Corff and Marquis 1999; Forkner et al. 2006), rather than surveys of whole saplings in an early stage of regeneration. For juvenile trees at this stage, only data for experiments with planted trees exist (Ladd and Facelli 2005; Löf et al. 2005; Massey et al. 2006; Norghauer et al. 2008), while in situ observations of individuals already established in the natural forest environment are so far missing. Although experiments with planted trees can be of great value for manipulating diversity per se, they are insufficient in imitating the age structure and spatial heterogeneity of the natural forest canopy and understory (Leuschner et al. 2009).

If trees are damaged by herbivores, growth and productivity of infested individuals is either reduced, eventually leading to a disadvantage in competition, or reinforced by overcompensation (Ayres et al. 2004; Zeide and Thompson 2005; Huttunen et al. 2007). Damage may also enhance vulnerability to fungal or bacterial pathogens (Kluth et al. 2001). Insect herbivory on saplings might, thus, affect forest regeneration and play an important role in the establishment of future forest communities. No studies have been published so far on sapling herbivory and tree diversity in exclusively deciduous forests of the temperate climate zone. In particular, it is remarkable that no studies have investigated this relationship using *Fagus sylvatica* L., which has been declared to be “the most successful Central European plant species” in its manner of expansion across the continent (Leuschner et al. 2006).

In this study, we addressed this research gap by examining tree diversity effects on herbivory of young instead of mature trees and also included a survey of invertebrate herbivores predators. We used a gradient ranging from simple beech to diverse forest stands within a temperate, deciduous, semi-natural forest in Central Europe, and studied leaf damage in beech and maple saplings across this gradient. We hypothesised that herbivory rates decrease with increased tree diversity due to host-finding limitations, and that relative abundance of predators increases, thereby enhancing top-down control of herbivorous insects. We also tested for host plant specific differences in herbivore and predator responses. Specifically, we addressed the following questions: (1) Which sapling species is affected most by leaf-chewing insects, and how severe is the extent of leaf area loss? (2) Are diverse forest stands less susceptible to insect herbivores than simple stands? (3) How is the frequency and distribution of galls and mines across the gradient? (4) How is the relative abundance of predators and parasitoids related to tree diversity and the herbivore damage patterns?

Materials and methods

Study area

The study was carried out in Germany's largest remaining connected semi-natural deciduous forest, the Hainich National Park, Thuringia. The Hainich forest covers a total area of 16,000 ha. Approximately half of it was designated national park in 1997 (Nationalpark Hainich; http://www.nationalpark-hainich.de).

All research plots were located in the north-eastern part of the protected area close to Weberstedt (approximately 51°1′N, 10°5′E) and the average distance between plots was 4.9 km. The study site had an elevation of 350 m asl and a temperate climate, with an average temperature of +7.5°C (1973–2004, Deutscher Wetterdienst). Average annual temperature in 2006 was 9.4°C (Meteomedia 2006). Mean annual precipitation is 590 mm (1973–2004, Deutscher Wetterdienst), and was 518 mm in 2006 (Meteomedia 2006). The predominant soil type was stagnic luvisol on loess-limestone as parent material.

Plots were established across an existing gradient of canopy tree diversity ranging from simple beech to mixed forest stands with a varying number of deciduous tree species [Electronic supplementary material (ESM) S1]. The mild climate in the area favours a wide variety of deciduous trees. The dominant tree species in the Hainich forest are *Fagus sylvatica* L. (Fagaceae), *Tilia platyphyllos* Scop., *T. cordata* Mill. (both Tiliaceae) and *Fraxinus excelsior* L. (Oleaceae). The species *Carpinus betulus* L. (Betulaceae), *Acer campestre* L., *A. platanoides* L., *A. pseudoplatanus* L. (all Aceraceae), *Prunus avium* (L.), *Sorbus torminalis* L. (both Rosaceae), *Quercus robur* L. (Fagaceae), and *Ulmus glabra* Huds. (Ulmaceae) occur less frequently. Coniferous trees such as *Abies alba* Mill., *Picea abies* (L.) H. Karst., *Pinus sylvestris* L. and *Larix decidua* Mill. (all Pinaceae) are scarce. All conifers are logged to regain a late successional stage of deciduous forest throughout the protected area.

Site selection, assessment of herbivore damage and insect communities

Nine observation sites were established in spring 2005. To ensure comparability, all plots were selected to share equal major stand characteristics, such as stagnic luvisol on loess soils, flat elevation, absence of canopy gaps, and not having been logged for at least 40 years. On each site, an observation plot measuring 50 × 50 m was fenced with a 2-m-tall fence constructed of narrow mesh wire and wooden and steel pickets. The fence was build to exclude browsing and trampling by ungulates (e.g. wild boars, fallow deer, roe deer and red deer). To exclude small mammals like rabbits and hares from accessing the observation sites, the lower part of the mesh-wire was burrowed into the soil. To ensure that observed leaf damage was caused by invertebrates only, the exclosures where installed in 2005, one year prior to estimation of herbivory. The exclosures were effective in excluding large and small herbivorous mammals (ungulates, rabbits and hares) and vertebrate predators (i.e. foxes) from the plots (no signs of browsing, no scat found in 2006).

All herbivory related parameters were assessed in late June and late August 2006. This timing was chosen to allow for a sufficient time span since leave flush in early May, in which measurable herbivore damage levels could develop. Prior to June, herbivore damage was observed only exceptionally and hence not estimated. Species identity and relative abundance of tree saplings were recorded in six random 5 × 5 m subplots inside each 50 × 50 m main plot (Mölder et al. 2009), while herbaceous plant species were identified in the 5 × 5 m subplots and additionally in a larger 20 × 20 m subplot per 50 × 50 m plot (Mölder et al. 2006, 2008).

Saplings (young trees <75 cm tall) of common beech (*Fagus sylvatica*), Norway maple (*Acer platanoides*) and sycamore maple (*A. pseudoplatanus*) were examined for signs of invertebrate herbivory (leaf area loss caused by leaf-chewing insects, presence of galls and mines). The three species were abundant on all plots, but the proportion of beech saplings declined with increased canopy tree diversity, while the abundance of Norway maple increased and the abundance of sycamore maple remained constant (ESM S1 and S2). Diversity of tree saplings was marginally correlated with canopy tree diversity (Pearson's $\rho = 0.66$, $P = 0.055$). To meet the prerequisites of stratified random sampling, each 50 × 50 m plot was equally divided in four quarters, and ten individuals of each sapling species were randomly drawn from these subplots. Hence, on each plot, 120 saplings (= 40 per species) were inspected for leaf area loss and presence of galls and mines. An exception was made for Norway maple, which was absent on one plot and, hence, not sampled on this plot.

In total, 1,040 saplings (13,728 leaves) were examined. Leaf area loss caused by leaf-chewing invertebrates was estimated in situ by visual inspection of each single leaf using percentage score classes modified after Wint (1983); 0 = no damage, 1 = 1–5%, 2 = 6–30%, 3 = 31–50%, 4 = 51–70%, 5 = 71–90%, 6 = 90–100%. Damage rates were calculated per sapling by summing up the score class means for each leaf. The sum was then divided by the number of leaves per sapling. We furthermore punched eight leaves of every tree species per plot with a hole puncher in June 2006. The length of the leaves, and of two undamaged control leaves, and the diameter of the holes were measured. Measurements were repeated in August 2006. The results showed that leaf growth did not affect the extent of leaf area loss (data available upon request).

Furthermore, the presence or absence of galls and mines was noted for each leaf and damage was expressed as proportion of infested leaves per plant. Additionally the number of leaves, sapling complexity (= number of primary branches), sapling height and percentage vegetation cover in a 1 × 1 m sampling quadrat surrounding the sapling were recorded. On each plot, abundance and species identity was assessed for all canopy trees with a diameter breast height (dbh) >7 cm.

Each sapling used for the estimation of herbivory was also carefully inspected for the presence of invertebrates, which were identified in situ to at least order level. For a more comprehensive survey of the invertebrate fauna present, directly adjacent to each plot 30 beating samples (10 sapling replicates of each sapling species) were taken from randomly chosen saplings to ensure that the fauna on the research plots remained undisturbed. Beating samples were obtained by beating the saplings with a wooden club against a fabric funnel attached to a collecting jar. This resulted in a total of 520 beating samples. Samples were stored at −19°C until processing.

Sample processing and data analyses

Invertebrates were separated from plant material and debris and then preserved in 70% ethyl alcohol. When species level identification was impossible, individuals were assigned to the lowest possible taxonomic level (at least to order). All specimens, including the individuals observed in situ, were either grouped into the feeding guilds ‘chewers’, ‘suckers’, ‘predators’, and ‘parasitoids’, or classified as ‘others’ (ESM S3). The two groups of natural enemies, predators and parasitoids, were combined for further analyses and are for simplification hereinafter referred to as predators.

Data were analysed using the statistical software package R 2.6 (R Development Core Team; http://www.R-project.org). Normality of raw data was evaluated with Shapiro-Wilk tests followed by arcsine square-root transformation of all proportion data prior to further analyses. To analyse whether tree species generally differed in leaf area loss, one-way analysis of variance (ANOVA) was performed with tree species as a categorical explanatory variable, and a Tukey’s honestly significant difference test (Tukey HSD) as a post-hoc comparison.

To account for individual proportions of tree species as well as for the number of species (Magurran 2004), canopy tree diversity of the nine research plots was expressed as Shannon index based on stem counts of all individuals with a dbh >7 cm. Tree diversity a priori influences a range of other abiotic and biotic plot conditions (Mölder et al. 2006), and some of them might also impact the observed herbivory patterns. No relationship with photosynthetic active radiation (PAR) was found, but soil C/N ratios were higher in simple beech stands, whereas the number of molluscs was higher in the most diverse forest stands (ESM S2).

Linear mixed effects models (LMEs; Pinheiro and Bates 2000) with leaf area loss, frequency of mines, frequency of galls and predator abundance as response variables were fitted separately for all three tree species using maximum likelihood. The significance of the fixed-effect terms in each model was tested using conditional *F* tests with terms tested sequentially in the order in which they had been added to the model. LMEs are advantageous compared to simple ANOVA models because they allow the inclusion of multiple nested random effects terms to account for temporal and/or spatial pseudoreplication. Before construction of the maximal model, explanatory variables (Shannon index, number of sapling tree species, number of herbaceous plant species, PAR, soil C/N, proportion of tree species in the canopy, proportion of tree species in the understory, sapling height, sapling complexity) were analysed for correlations, and all variables with a pairwise correlation coefficient ≥0.6 were not included within the same model to minimize possible effects of multicollinearity. Shannon index was introduced as fixed variable after controlling for the variance explained by sapling complexity (number of primary branches). The maximal model was fitted with the following sequence: fixed effects = date, sapling complexity, Shannon index, Shannon index × date; random effects were included as differences between slopes (dates) and intercepts (plots). After fitting the maximal model, model simplification was accomplished by stepwise deletion of non-significant terms based on differences in Akaike’s

Table 1 Simplified linear mixed effects models performed on different types of leaf damage and percent predator abundance on three tree sapling species on forest plots in the Hainich National Park

Response variable	Effect	Beech				Norway maple				Sycamore maple			
		Num *df*	Den *df*	*F*	*p*	Num *df*	Den *df*	*F*	*p*	Num *df*	Den *df*	*F*	*p*
Leaf area loss													
	Date	1	8	49.15	<0.001	1	7	9.58	0.018	1	8	8.77	0.018
	Sapling complexity	–	–	–	†	–	–	–	†	1	7	26.59	0.001
	Shannon index	1	7	16.6	0.005	–	–	–	†	–	–	–	†
	Date × Shannon index	–	–	–	†	–	–	–	†	–	–	–	†
Frequency of mines													
	Date	1	8	31.9	<0.001								
	Sapling complexity	–	–	–	†	Not tested				Not tested			
	Shannon index	–	–	–	†								
	Date × Shannon index	–	–	–	†								
Frequency of galls													
	Date	1	8	15.38	0.004								
	Sapling complexity	–	–	–	†	Not tested				No significant terms			
	Shannon index	–	–	–	†								
	Date × Shannon index	–	–	–	†								
Predator abundance													
	Date	1	7	9.76	0.017	–	–	–	†				
	Sapling complexity	–	–	–	†	1	5	7	0.046	No significant terms			
	Shannon index	1	7	10.88	0.013	1	5	4.73	0.081				
	Date × Shannon index	1	7	10.44	0.014	–	–	–	†				

Num df numerator degrees of freedom, *Den df* denominator degrees of freedom, † removed during model simplification, *not tested* no observations made for response variable

Information Criterion (AIC) (Crawley 2007). AIC measures the lack of fit of the model; the model with the lower AIC is to be preferred (Burnham and Anderson 2002). If the difference in AIC between two models was smaller than 2, empirical support for the model with the lower AIC was assumed to be substantially better (Burnham and Anderson 2002). Results for each response variable and tree species are presented in Table 1. To ensure that the assumptions of all tests were met, model residuals were inspected for normality and homogeneity of variances.

Results

Leaf area loss of tree saplings

By the end of the observation season, leaf area loss was generally higher in both maple species compared to beech (one-way ANOVA, sum of squares = 0.1, mean of squares = 0.06, $F_{2,23} = 61.18$, $P < 0.001$). Beech saplings had an average loss of 1.5% leaf area per leaf, whereas leaf area loss was more than twice as high in Norway maple (3.6%, Tukey HSD, $P < 0.001$). Leaf area loss in sycamore maple was highest (five times higher compared to beech, 7.6%, Tukey HSD, $P < 0.001$).

Damage increased with season (LME, $F_{1,8} = 49.15$, $P < 0.001$) and the response pattern remained constant in June and August. In August, leaf area loss was roughly 50% lower in the most species-rich stands compared to the simple beech stands (Fig. 1a). Relating the damage to canopy tree diversity, leaf area loss on beech declined with increased tree species richness (LME, $F_{1,7} = 16.6$, $P = 0.005$; Fig. 1a). No diversity-related pattern was found for the two maple species, but leaf area loss in sycamore maple was positively related to sapling complexity (LME, $F_{1,7} = 26.59$, $P = 0.001$; Table 1).

Frequency and distribution of mines and galls

Mines were only observed on beech, while galls were abundant on beech and sycamore maple. Mines surveyed on beech were caused by larvae of two species of microlepidopteran moths, *Stigmella hemagyrella* Kollar and *Stigmella tityrella* Stainton (Lepidoptera: Nepticulidae). The percentage of leaves infested with mines of *Stigmella* sp. increased during the season from less than 0.3 to 7.2% (LME,

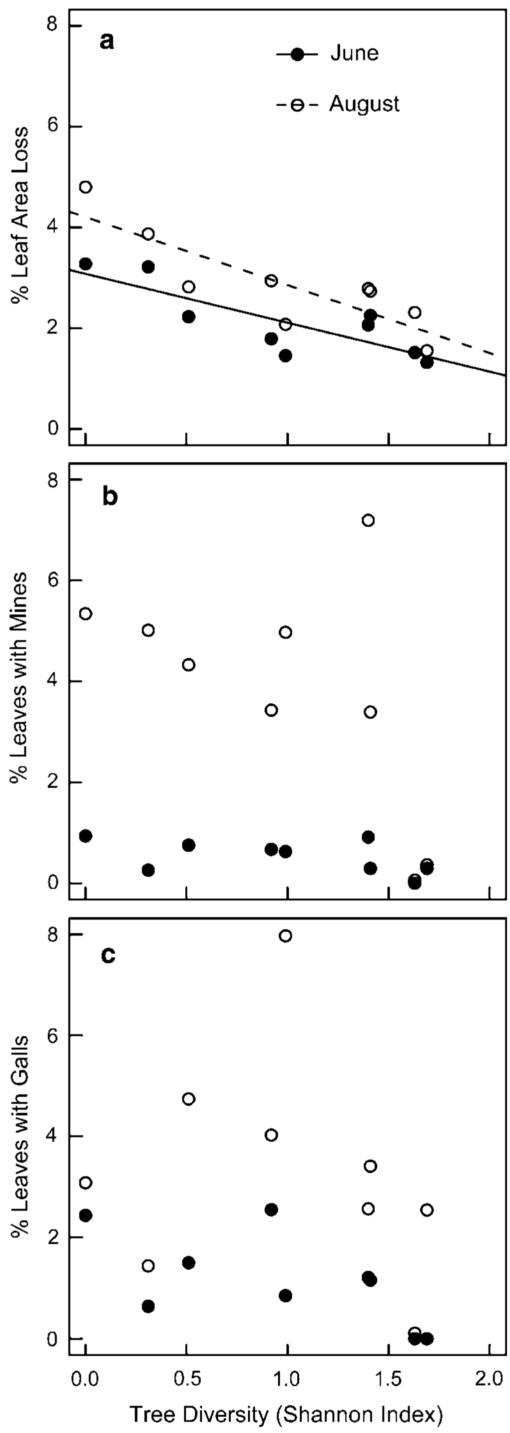

Fig. 1 Leaf damage of beech saplings (means per plot) across a tree diversity gradient ranging from monospecific beech to mixed forest stands in the Hainich National Park. **a** Percentage leaf area loss per leaf caused by leaf-chewing insects; **b** percentage of leaves infested with mines of *Stigmella* sp.; **c** percentage of leaves infested with galls of *Hartigiola annulipes* and *Mikiola fagi*. *Filled circles* June, *open circles* August

$F_{1,8} = 31.9$, $P < 0.001$; Fig. 1b). In the two most diverse forest stands, there was hardly any increase in mine frequency from June to August. Mine frequency did not correlate with canopy tree diversity (Table 1).

Galls on beech saplings were induced by two gall forming midges (Diptera: Cecidomyiidae), *Hartigiola annulipes* Hartig and *Mikiola fagi* (Hart.). The percentage of leaves infested with galls was higher in August compared to June (LME, $F_{1,8} = 15.38$, $P = 0.004$) and the overall pattern of distribution was similar for both months (Fig 1c). By the end of the season, gall frequency ranged from 0.1 up to 7.9% infested leaves, but was not related to canopy tree diversity. Galls on sycamore maple were induced by the gall-forming mite *Aceria macrorhynchus* Nalepa (Acari: Eriophyidae), but showed no response to the factors tested (Table 1).

Arthropod Community structure

In total, 2,593 arthropods were counted across all plots. Herbivorous and predatory species were grouped into four feeding guilds: leaf chewers, leaf suckers, predators and parasitoids (ESM S3). No adult leaf miners or gall formers were observed. Of all guilds, predators were most abundant (37.2%), while leaf suckers were the most abundant herbivore feeding guild (19.2%; Table 2). Parasitoids contributed 3.9% and leaf-chewing insects amounted to 4.5% of the total community (Table 2). Identified individuals that do not feed on trees, as well as predators that only prey on minute prey (e.g. predatory mites), were excluded from further analyses.

Both date (LME, $F_{1,7} = 9.76$, $P = 0.017$) and canopy tree diversity (LME, $F_{1,7} = 10.88$, $P = 0.013$) affected relative abundance of predators and parasitoids on beech saplings, but responses differed depending on observation of month (significant date × Shannon index interaction, LME, $F_{1,7} = 10.44$, $P = 0.014$, Fig. 2). In June, the percentage of predators increased with increasing tree diversity by

Table 2 Number of specimens and relative abundance (% of total) of different insect feeding guilds, sampled or observed on forest plots in the Hainich National Park

	June	August	Total	%
Leaf chewers	36	81	117	4.5
Leaf suckers	164	334	498	19.2
Predators	191	774	965	37.2
Parasitoids	51	51	102	3.9
Other	221	690	911	35.1
Total			2,593	99.9[a]

[a] The sum of the percentages falls below 100% due to rounding

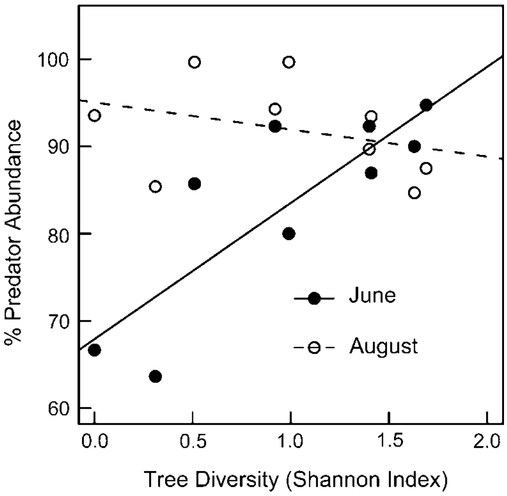

Fig. 2 Relative abundance of predators and parasitoids (per plot) on beech saplings across a tree diversity gradient ranging from monospecific beech to mixed forest stands in the Hainich National Park. *Filled circles* June, *open circles* August

roughly 1/3, but in August the abundance of predators and parasitoids decreased with increased tree diversity. The relative abundance of predators and parasitoids was generally high (ranging from 63.6 to 100% of the total community; Fig. 2).

No significant pattern was found for the relative abundance of predators and parasitoids on sycamore maple. The arthropod community on Norway maple was not affected by canopy tree species richness (LME, $F_{1,5} = 4.73$, $P = 0.081$; Table 1), but related to sapling complexity (LME, $F_{1,5} = 7$, $P = 0.046$; Table 1).

Discussion

Our data support the hypothesis that tree saplings in diverse forest stands are less susceptible to herbivory, but the response was strongly dependent on tree species identity, as well as on herbivore feeding guild. This result is consistent with findings in the boreal zone where no general reduction of herbivore damage in the canopy of mixed forest stands was observed (Koricheva et al. 2006; Vehviläinen et al. 2006, 2007). Vehviläinen et al. (2006) suggest that higher quantities of deciduous trees in conifer forests may explain why in some species-rich stands herbivore damage is not reduced as hypothesised. Deciduous trees have been found to attract more generalist herbivores than conifers. Due to possible dispersal of these generalists across various neighbouring tree species, herbivory rates in forest stands with a higher proportion of deciduous trees might show only subtle or no responses to increased tree species richness (Jactel et al. 2005). Our results do not fully support this assumption. We still found a decrease of leaf area loss on beech saplings, with beech saplings and mature beech trees decreasing in abundance across the deciduous tree diversity gradient—a pattern, which has been explained by mechanisms such as resource concentration (Tahvanainen and Root 1972; Root 1973). The Janzen-Connell hypothesis (Janzen 1970; Connell 1971) also predicts that survival of tree saplings improves with increased parental distance, because herbivores more easily disperse to conspecific saplings growing in dense patches, especially near parent trees. One of the prerequisites to apply these hypotheses is that the herbivores in question are specialists (Risch et al. 1983). The few leaf-chewing species identified in our study feed on various tree species, and cannot be categorised as specialists in the narrow sense of feeding only on one host plant. Nevertheless, some of these species such as *Dasychira pudibunda* (Lepidoptera: Lymantriidae) show a strong host preference for beech (Schwenke 1978). Such ecological preferences, rather than strict resource specialisation, might have effectively protected beech saplings from leaf area loss in species-rich forest stands.

Our results for miners and gall formers, though specialised insects, showed no evidence for associational resistance. Vehviläinen et al. (2007) suggest feeding preferences as a possible explanation for observed declines of leaf miners in boreal mixed stands, but did not find the same response for gall-forming and leaf-chewing insects. The inconsistent results for chewers, leaf miners and gall-forming insects in different forest types imply that feeding specialisation may be just one of several mechanisms shaping herbivory–tree diversity relationships.

Seasonality and population dynamics after initial colonisation may be important (Otway et al. 2005), but damage patterns in our study were consistent for all observed guilds at both observation dates. This is contrary to observations on deciduous trees in other forest ecosystems, where diversity effects for miners and leaf-chewing insects were more apparent early in the year and then reversed (Vehviläinen et al. 2007).

Examples for in situ top-down control of insect herbivores by predators in forest ecosystems of different diversity are scarce (Riihimaki et al. 2005), but have been shown in experiments (Jactel et al. 2006; Kaitaniemi et al. 2007). However, recent evaluations question the relevance of the enemies hypothesis in forest ecosystems, and relate predator abundance to the presence of certain tree species rather than to tree diversity as such (Schuldt et al. 2008; Vehviläinen et al. 2008). Here, predator abundance on beech saplings was high and increased in the species rich forest stands in June when the leaves where young. This supports the enemies hypothesis (Root 1973; Russell 1989) and suggests a diversity-related seasonal increase of top-down control, similar to observations in other ecosystems (Schmitz et al. 2000, Schmitz 2003).

Besides insect herbivores, molluscs also play an important role as herbivores in forest systems (Jennings and Barkham 1975a, b; Cote et al. 2005), and particularly maple is a known food resource for snails and slugs (Pigot and Leather 2008). Herbivory patterns in our examination could not be related to the abundance of snails and slugs at the time of observation, but the higher abundance of molluscs on the most species-rich plots (ESM S2) might be one reason why herbivore damage on maple was not affected by tree diversity. Both maple species were generally more attractive to invertebrate herbivores than beech, but data explaining why beech seems to be less palatable compared to other tree species are scarce. Further investigations should aim to test for species-specific defence mechanisms (e.g. phenolics, condensed tannin and toughness of leaves) or differences in nutrient availability when growing under the same conditions. Norway maple has previously been shown to have a high N content and thus a narrow C/N ratio in the foliage (Hilfreich 1991), which has been used to explain higher herbivore damage (Brötje and Schmidt 2005). The soil C/N ratios observed in our study were slightly increased in the simple beech stands, which was contrary to the observed higher herbivore load for beech on these plots. In addition, this should affect all tree species alike, unless differences exist in soil nutrient uptake and utilisation in the plant. Light availability was very low in all stands (0.7–2.7% of daylight intensity) and insufficient for further height growth of regeneration. Only the growth of *Fagus sylvatica* and *Fraxinus excelsior* was slightly sensitive to the marginally fluctuating irradiation (Mölder et al. 2009). Herbivores have previously been shown to be more active in forest gaps (Norghauer et al. 2008). But even though the simple beech stands we studied had higher PAR transmissivity by trend (Mölder et al. 2009), in these stands only beech saplings suffered more herbivore damage compared to saplings in the rather darker mixed forest stands. Differences in light availability amongst our forest stands might be too subtle to have any general effect on sapling herbivory, since we did not investigate fully sun-exposed gaps as did Norghauer et al. (2008).

In conclusion, our study reveals new insights into the effects of tree diversity on levels of herbivory, herbivore and predator abundances in selected tree species at the sapling stage. Tree diversity has only limited explanatory power for the observed patterns in herbivory or insect abundances. By contrast, the identity and abundance of the observed tree species and seasonal effects were much better predictors in many cases. Hence, according to our results, species identity effects may be more important than species diversity per se. While it is difficult to draw such strong conclusions from observational studies alone, it will be interesting to see if tree diversity experiments simulating temperate deciduous forests such as the BIOTREE experiment (Scherer-Lorenzen et al. 2007) will show similar trends.

Acknowledgements Financial support was obtained by the DFG (German Research Foundation) within the framework of the Research Training Group “Graduiertenkolleg 1086: The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests”. We thank Christoph Leuschner, Frank Thomas, Hermann Jungkunst and Stefan Fleck for coordination of the Research Training Group and also acknowledge Mascha Jacob, Karl M. Daenner, Anja Guckland, Catharina Meinen and Andreas Mölder for providing data on biotic and abiotic plot characteristics. We thank Kyle Rea for proofreading and two anonymous reviewers for helpful comments on the manuscript. All examinations complied with the current law in the country of performance.

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Electronic Supplementary Material

Appendix S1: Relative abundance of trees in the canopy (C, per plot) and saplings in the understory (U, per ha; see Mölder et al. 2009) on 9 deciduous forest plots of different diversity in the Hainich National Park.

Shannon Index	**0**		**0.31**		**0.51**		**0.99**		**0.92**		**1.4**		**1.41**		**1.69**		**1.63**	
Stratum	**C**	**U**	**C**	**U**	**C**	**U**	**C**	**U**	**C**	**U**	**C**	**U**	**C**	**U**	**C**	**U**	**C**	**U**
%																		
Acer campestre	-		-	-	-	0.2	-	-	-	-	-	-	-	-	2	1.4	-	0.4
Acer platanoides	-	-	-	20.9	1.9	6.3	0.8	61.0	1	34.4	3.7	40.0	0.9	32.6	4.1	28.2	6	65.2
Acer pseudoplatanus	-	20.3	1.9	18.0	-	15.2	1.5	11.0	1.5	19.3	1.8	23.0	3.4	33.2	2	13.4	1.2	15.8
Carpinus betulus	-	-	-	-	-	-	-	-	-	-	-	1.1	3.4	-	9.2	1.8	10.8	1.8
Fagus sylvatica	100	71.9	93.5	4.1	83.3	66.3	59.4	7.5	73.7	34.7	47.7	11.7	41.9	7.1	3.1	2.3	2.4	4.7
Fraxinus escelsior	-	1.6	1.9	56.4	-	8.9	33.1	16.0	12.9	11.2	13.8	22.3	16.2	27.1	7.1	44.8	13.3	9.3
Prunus avium	-	3.1	-	-	-	-	-	-	-	-	-	-	-	-	1	5.9	-	2.2
Quercus petraea	-	-	-	-	14.8	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus robur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.1	-	1.2	-
Sorbus aucuparia	-	3.1	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-
Tilia cordata	-	-	-	-	-	2.9	2.3	2.5	5.7	0.4	22	1.5	30.8	-	24.5	1.4	22.9	-
Tilia platyphyllos	-	-	2.8	0.6	-	-	1.5	1.5	5.2	-	11	0.4	3.4	-	42.9	0.7	41	-
Ulmus glabra	-	-	-	-	-	-	1.5	0.5	-	-	-	-	-	-	-	0.2	1.2	0.7

Appendix S2: Spearman rank correlations of biotic and abiotic plot characteristics with canopy tree diversity. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

	Canopy Tree Diversity (Shannon)	
Tree Species Understory	0.66	
Plant Species Understory	0.94	***
% Beech^{C}	-0.94	***
% Beech^{U}	-0.71	*
% Norway Maple^{C}	0.76	*
% Norway Maple^{U}	0.69	*
% Sycamore Maple^{C}	0.60	
% Sycamore Maple^{U}	0.09	
Stem Density	0.26	
PAR	-0.56	
Soil C/N	-0.74	*
Snails & Slugs^{J}	0.73	*
Snails & Slugs^{A}	0.53	

^{C}Canopy, ^{U}Understory, ^{J}June, ^{A}August

S3: Feeding guilds and classification of the insect community sampled/observed on forest plots in the Hainich Nationalpark.

Feeding guild	Associated taxa	Order	Family
Leaf chewers	Butterfly larvae	Lepidoptera	Lymantriidae
	Sawfly larvae	Hymenoptera	
	Leaf beetles	Coleoptera	Chrysomelidae
	Leaf weevils	Coleoptera	Curculionidae (Entiminae)
	Short-horned grasshoppers	Orthoptera	Acrididae
Leaf suckers	Leaf hoppers	Homoptera	Cicadellidae
	Frog hoppers	Homoptera	Cercopidae
	Sap-sucking true bugs	Heteroptera	
	Aphids	Homoptera	Aphidae
Predators	Spiders	Araneae	
	Predatory true bugs	Heteroptera	
	Robber flies	Diptera	Asilidae
	Scorpion flies	Mecoptera	Panorpidae
	Click beetles	Coleoptera	Elateridae
	Rove beetles	Coleoptera	Staphylinidae
	Earwigs	Dermaptera	
Parasitoids	Parasitic wasps	Hymenoptera	

Chapter 11

Effects of tree diversity on true bugs (Heteroptera)

published as:

Sobek S, Goßner M, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera). Ecological Entomology 34: 772–782.

Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera)

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Abstract. 1. Spatiotemporal patterns of canopy true bug diversity in forests of different tree species diversity have not yet been disentangled, although plant diversity has been shown to strongly impact the diversity and distribution of many insect communities.

2. Here we compare species richness of canopy true bugs across a tree diversity gradient ranging from simple beech to mixed forest stands. We analyse changes in community composition by additive partitioning of species diversity, for communities on various tree species, as well as for communities dwelling on beech alone.

3. Total species richness (γ-diversity) and α-diversity, and abundance of true bugs increased across the tree diversity gradient, while diversity changes were mediated by increased true bug abundance in the highly diverse forest stands. The same pattern was found for γ-diversity in most functional guilds (e.g. forest specialists, herbivores, predators). Temporal and even more, spatial turnover (β-diversity) among trees was closely related to tree diversity and accounted for ~90% of total γ-diversity.

4. Results for beech alone were similar, but species turnover could not be related to the tree diversity gradient, and monthly turnover was higher compared to turnover among trees.

5. Our findings support the hypothesis that with increasing tree diversity and thereby increasing habitat heterogeneity, enhanced resource availability supports a greater number of individuals and species of true bugs. Tree species identity and the dissimilarity of true bug communities from tree to tree determine community patterns.

6. In conclusion, understanding diversity and distribution of insect communities in deciduous forests needs a perspective on patterns of spatiotemporal turnover. Heterogeneity among sites, tree species, as well as tree individuals contributed greatly to overall bug diversity.

Key words. Beta diversity, biodiversity conservation, canopy arthropods, *Fagus sylvatica* L., functional groups, habitat heterogeneity.

Introduction

It has long been known that tree crowns in tropical forests house the key proportion of global insect diversity (Stork, 1988). Only more recently, the insect fauna of the forest canopy in temperate and boreal forests has gained major attention, and species diversity and distribution in these habitats has been assessed in a variety of studies (e.g. Ozanne, 1996; Thunes *et al*., 2003; Southwood *et al*., 2005; Ulyshen & Hanula, 2007). The majority of published studies focus on forest stands differing in management intensity, stand age, deadwood amount or other parameters. Furthermore, they include only a small selection of tree species, usually comparing deciduous with coniferous trees. Until now, information on deciduous

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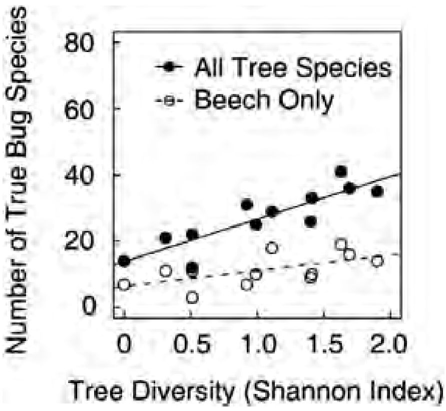

Fig. 1. γ

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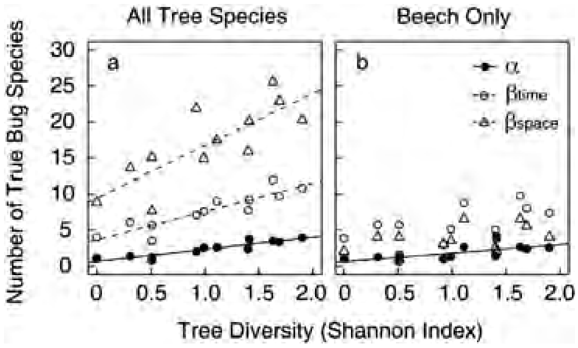

Fig. 2. α β β

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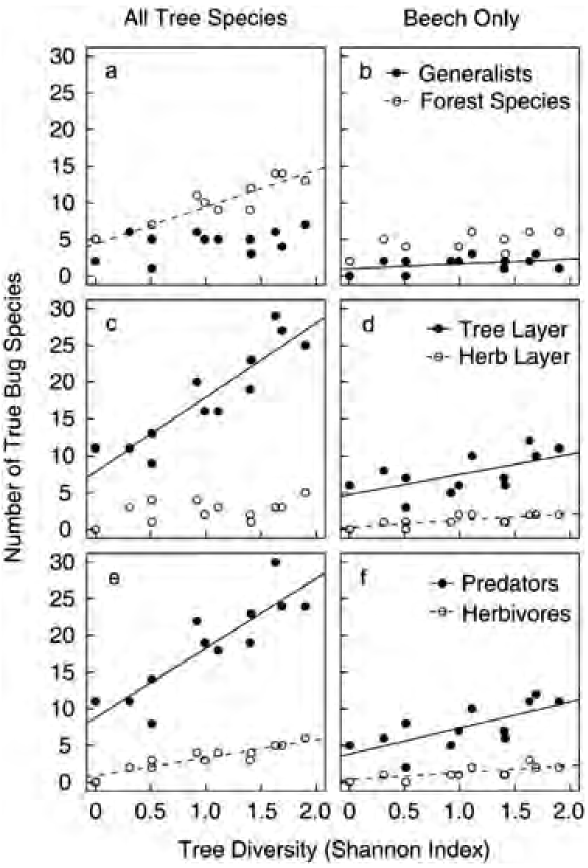

Fig. 3.

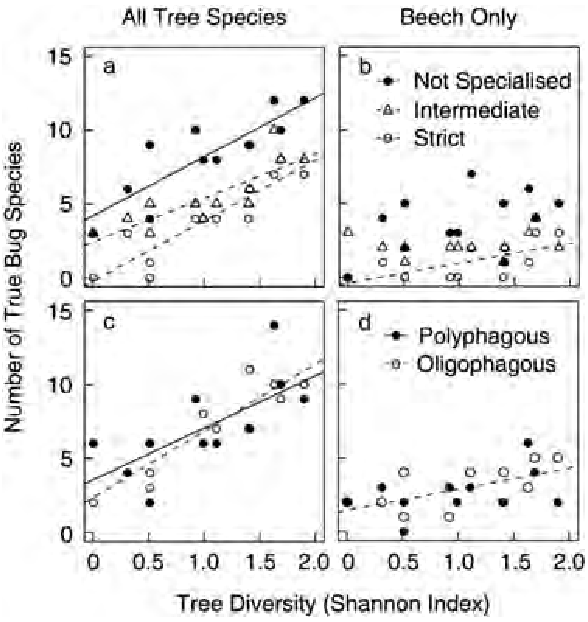

Fig. 4.

Discussion

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Acknowledgements

Supporting Information

Appendix S1.

Appendix S2.

Appendix S3.

Appendix S4.

Appendix S5.

Appendix S6.

References

Appendix S1: Tree diversity of 12 deciduous forest stands in the Hainich National Park and sampling success of local true bug communities. Stands ranking was based on increasing Shannon indices (tree diversity), rank 3 was assigned twice due to equal indices.

Shannon Index	Stand Ranking	% Beech	% Lime	% Sampling Success
0	1	100	0	70.6
0.31	2	93.5	2.8	73.7
0.51	3a	83.3	0	82.8
0.51	3b	87.5	3.6	63.8
0.92	4	73.7	10.8	65
0.99	5	59.4	2.3	73.2
1.11	6	60.6	12.1	79.5
1.4	7	47.7	33	70.6
1.41	8	41.9	34.2	70
1.63	9	2.4	63.9	75.5
1.69	10	3.1	67.4	73
1.9	11	13.2	37.9	76.4

Appendix S2: Species list of true bugs collected on various tree species in the canopy of forest stands across a tree diversity gradient in the Hainich National Park. Annotations to ecology based on Wachmann et al. (2004-2006). ^{D}deciduous, ^{H}host plant specialisation (food or habitat resource), ^{P}prey specialisation, ^{V}various tree species, ^{B}beech only, *because mainly adults were captured with flight interception traps, feeding guild classification is based on adult diet.

Species	Habitat	Stratum	Feeding Guild*	Specialisation^H	Specialisation^P	n^V	n^B
Acanthosoma haemorrhoidale	other	tree layer	other	not specialised	unknown	4	1
Acanthosomatidae sp.	unknown	unknown	unknown	unknown	unknown	1	1
Anthocoridae sp.	unknown	unknown	unknown	unknown	unknown	5	2
Anthocoris amplicollis	forest^D	other	carnivor	other	oligophagous	2	0
Anthocoris confusus	forest^D	tree layer	predator	other	oligophagous	90	21
Anthocoris nemoralis	forest^D	tree layer	predator	other	polyphagous	5	1
Berytinus minor	other	other	other	strict	unknown	1	0
Blepharidopterus angulatus	other	tree layer	other	intermediate	polyphagous	2	1
Campyloneura virgula	forest^D	tree layer	predator	not specialised	polyphagous	41	10
Carpocoris purpureipennis	other	herb layer	other	not specialised	unknown	1	1
Closterotomus biclavatus	other	other	predator	not specialised	other	8	2
Cremnocephalus alpestris	other	tree layer	predator	intermediate	oligophagous	1	0
Cyllecoris histrionius	forest^D	tree layer	predator	strict	polyphagous	1	0
Deraeocoris lutescens	other	tree layer	predator	other	polyphagous	708	171
Deraeocoris trifasciatus	forest^D	tree layer	predator	not specialised	polyphagous	3	0
Dicranocephalus agilis	other	herb layer	herbivore	intermediate	unknown	1	1
Dolycoris baccarum	no preference	herb layer	herbivore	not specialised	unknown	12	3
Dryophilocoris flavoquadrimaculatus	other	tree layer	predator	strict	polyphagous	3	0
Elasmostethus interstinctus	other	tree layer	other	intermediate	unknown	1	1
Elasmostethus minor	other	tree layer	other	strict	unknown	1	1
Eurydema oleracea	no preference	herb layer	herbivore	intermediate	unknown	1	0
Harpocera thoracica	other	tree layer	predator	strict	oligophagous	203	9
Himacerus apterus	no preference	other	predator	unknown	polyphagous	7	0
Isometopus intrusus	other	tree layer	predator	not specialised	polyphagous	5	0
Kleidocerys resedae	other	tree layer	other	intermediate	unknown	52	14
Loricula elegantula	other	tree layer	predator	unknown	polyphagous	6	5
Lygocoris contaminatus	other	tree layer	herbivore	intermediate	unknown	4	0
Lygocoris viridis	other	tree layer	predator	intermediate	unknown	7	0
Lygus pratensis	no preference	herb layer	herbivore	not specialised	unknown	19	10
Mermitelocerus schmidtii	other	tree layer	predator	intermediate	polyphagous	20	1
Mirinae sp.	unknown	unknown	unknown	unknown	unknown	1	1
Miris striatus	other	tree layer	predator	not specialised	polyphagous	12	1
Nabis pseudoferus	other	other	predator	unknown	unknown	70	23
Notostira erratica	other	herb layer	other	intermediate	unknown	1	1
Orius horvathi	no preference	other	predator	unknown	oligophagous	27	2
Orius laticollis	other	other	predator	other	oligophagous	4	0
Orius majusculus	other	other	predator	unknown	polyphagous	1	0
Orius minutus/vicinus	no preference	other	predator	unknown	polyphagous	77	13
Orthops basalis	no preference	herb layer	herbivore	intermediate	unknown	1	0
Orthops kalmii	no preference	herb layer	herbivore	intermediate	unknown	1	1
Orthotylinae sp.	unknown	unknown	unknown	unknown	unknown	5	0
Orthotylus marginalis	other	tree layer	predator	intermediate	polyphagous	19	2
Orthotylus nassatus	forest^D	tree layer	predator	intermediate	unknown	2	0
Orthotylus prasinus	forest^D	tree layer	herbivore	intermediate	unknown	1	0
Orthotylus tenellus	forest^D	tree layer	predator	intermediate	polyphagous	6	0
Orthotylus viridinervis	forest^D	tree layer	predator	strict	oligophagous	9	0

Species	Habitat	Stratum	Feeding Guild*	Specialisation^H	Specialisation^P	n^V	n^B
Palomena prasina	no preference	other	herbivore	not specialised	unknown	8	1
Palomena viridissima	no preference	herb layer	herbivore	not specialised	unknown	3	2
Pentatoma rufipes	other	tree layer	predator	not specialised	unknown	101	28
Pentatomidae sp.	unknown	unknown	unknown	unknown	unknown	2	1
Peribalus vernalis	no preference	herb layer	herbivore	not specialised	unknown	1	0
Peritrechus nubilus	other	other	other	not specialised	unknown	1	0
Phylinae sp.	unknown	unknown	unknown	unknown	unknown	1	0
Phylus melanocephalus	forest^D	tree layer	predator	strict	oligophagous	10	2
Phytocoris dimidiatus	forest^D	tree layer	predator	not specialised	unknown	24	3
Phytocoris longipennis	forest^D	tree layer	predator	not specialised	unknown	7	3
Phytocoris populi	other	tree layer	predator	intermediate	polyphagous	8	0
Phytocoris sp.	unknown	unknown	unknown	unknown	unknown	3	1
Phytocoris tiliae	forest^D	tree layer	other	not specialised	unknown	43	19
Pinalitus cervinus	forest^D	tree layer	herbivore	not specialised	unknown	41	2
Plagiognathus chrysanthemi	other	herb layer	herbivore	not specialised	unknown	0	1
Psallus (Hylopsallus) sp.	unknown	unknown	unknown	unknown	unknown	1	0
Psallus (Psallus) sp.	unknown	unknown	unknown	unknown	unknown	16	7
Psallus ambiguus	forest^D	tree layer	predator	intermediate	polyphagous	5	0
Psallus flavellus/lepidus	forest^D	tree layer	predator	strict	oligophagous	40	0
Psallus mollis	forest^D	tree layer	predator	strict	oligophagous	12	0
Psallus perrisi/wagneri	forest^D	tree layer	predator	strict	oligophagous	137	24
Psallus pseudoplatani	other	tree layer	predator	strict	oligophagous	22	1
Psallus punctulatus	forest^D	tree layer	other	strict	oligophagous	2	0
Psallus varians	forest^D	tree layer	predator	intermediate	oligophagous	433	123
Rhabdomiris striatellus	other	tree layer	predator	other	polyphagous	9	0
Stenodema laevigata	no preference	herb layer	other	intermediate	unknown	5	0
Stenodema virens	other	herb layer	other	intermediate	unknown	1	0
Temnostethus pusillus	other	tree layer	predator	unknown	unknown	35	4
Tingis cardui	other	herb layer	herbivore	intermediate	unknown	3	0
Troilus luridus	other	tree layer	predator	unknown	polyphagous	4	0
Xylocoris galactinus	other	unknown	predator	unknown	polyphagous	1	0

Appendix S3: Spearman rank correlations of untransformed response (true bug species richness) and explanatory variables.

	True Bug Richness	True Bug Abundance	Tree Diversity (Shannon Index)	Stand Age	Stem Density	Tree Height	Crown Area	Plant Area Index	Deadwood m^3/m^2
True Bug Richness	1								
True Bug Abundance	0.89	1							
Tree Diversity (Shannon Index)	0.88	0.91	1						
Stand Age	-0.81	-0.77	-0.81	1					
Stem Density	0.45	0.23	0.34	-0.72	1				
Tree Height	-0.8	-0.79	-0.78	0.95	-0.63	1			
Crown Area	-0.54	-0.36	-0.49	0.84	-0.92	0.69	1		
Plant Area Index	0.51	0.62	0.65	-0.75	0.46	-0.69	-0.6	1	
Deadwood m^3/m^2	-0.57	-0.45	-0.36	0.66	-0.54	0.77	0.51	-0.21	1

Appendix S4: Relative contributions of α- and β-diversity to true bug species richness of communities sampled on various tree species in 12 forest plots across a tree diversity gradient. Values for beech alone are set in parentheses.

Forest Stand	% α	%β_{time}	%β_{space}
1	8 (15.5)	28.9 (56)	63.1 (28.6)
2	6.6 (11.4)	29.1 (52.3)	64.3 (36.4)
3a	6.7 (13.9)	29.4 (52.8)	63.9 (33.3)
3b	5.8 (11.4)	26 (52.3)	68.2 (36.4)
4	6.5 (14.3)	23 (42.9)	70.4 (42.9)
5	10.2 (13.3)	30.4 (51.7)	59.3 (35)
6	9 (14.8)	31.2 (49.1)	59.8 (36.1)
7	9.2 (15.7)	29.9 (56.5)	60.9 (27.8)
8	11.4 (41.7)	28 (38.3)	60.6 (20)
9	8.6 (14)	29.2 (51.8)	62.2 (34.2)
10	9.4 (15.1)	27.2 (50.5)	63.4 (34.4)
11	11.4 (18.5)	31 (53)	57.6 (28.6)

Appendix S5: Relative contributions of species abundance to functional guilds for canopy true bugs captured on various tree species across a tree diversity gradient in the Hainich National Park. Values for beech are set in parentheses.

Forest Stand	% Habitat Generalists	% Forest Species	Tree Layer Species	Herb Layer Species	Predators	Herbivores
1	14.3 (0)	35.7 (28.6)	78.6 (85.7)	0 (0)	78.6 (71.4)	0 (0)
2	28.6 (18.2)	28.6 (45.5)	52.4 (72.7)	14.3 (9.1)	52.4 (54.4)	9.5 (9.1)
3a	8.3 (0)	41.7 (66.7)	75 (100)	8.3 (0)	66.7 (66.7)	16.7 (0)
3b	22.7 (18.2)	31.8 (36.4)	59.1 (63.6)	18.2 (9.1)	63.6 (72.7)	13.6 (18.2)
4	19.4 (28.6)	35.5 (28.6)	64.5 (71.4)	12.9 (14.3)	71 (71.4)	12.9 (14.3)
5	20 (20)	40 (40)	64 (60)	8 (20)	76 (70)	12 (10)
6	17.2 (16.7)	31 (33.3)	55.2 (55.6)	10.3 (11.1)	62.1 (55.6)	13.8 (11.1)
7	19.2 (11.1)	34.6 (55.6)	73.1 (77.8)	7.7 (11.1)	73.1 (77.8)	11.5 (11.1)
8	9.1 (20)	36.4 (30)	69.7 (60)	3 (10)	69.7 (60)	12.1 (10)
9	14.6 (10.5)	34.1 (31.6)	70.7 (63.2)	7.3 (10.5)	73.2 (57.9)	12.2 (15.8)
10	11.1 (18.8)	38.9 (18.8)	75 (62.5)	8.3 (12.5)	66.7 (75)	13.9 (12.5)
11	20 (7.1)	37.1 (42.9)	71.4 (78.6)	14.3 (14.3)	68.6 (78.6)	17.1 (14.3)

Appendix S6: Relative contributions of species abundance to host plant and prey specialisation for canopy true bugs captured on various tree species across a tree diversity gradient in the Hainich National Park. Values for beech are set in parentheses. ^{H}host plant specialisation (food or habitat resource), ^{P}prey specialisation.

Forest Sstand	Strict^{H}	Intermediate^{H}	Not Specialised^{H}	Oligophagous^{P}	Polyphagous^{P}
1	0 (0)	21.4 (42.9)	21.4 (0)	14.3 (28.6)	42.9 (28.6)
2	14.3 (9.1)	19 (18.2)	28.6 (36.4)	19 (18.2)	19 (27.3)
3a	8.3 (0)	25 (33.3)	33.3 (66.7)	25 (33.3)	16.7 (0)
3b	0 (0)	22.7 (18.2)	40.9 (45.5)	18.2 (36.4)	27.3 (18.2)
4	12.9 (0)	16.1 (28.6)	32.3 (42.9)	29 (14.3)	29 (42.9)
5	16 (0)	16 (20)	32 (30)	32 (20)	24 (20)
6	13.8 (11.1)	17.2 (11.1)	27.6 (38.9)	24.1 (22.2)	20.7 (16.7)
7	15.4 (0)	19.2 (11.1)	34.6 (55.6)	26.9 (22.2)	26.9 (22.2)
8	18.2 (20)	18.2 (20)	27.3 (10)	33.3 (40)	21.2 (20)
9	17.1 (5.3)	24.4 (15.8)	29.3 (31.6)	24.4 (15.8)	34.1 (31.6)
10	22.2 (18.8)	22.2 (25)	27.8 (25)	25 (31.3)	27.8 (25)
11	20 (21.4)	22.9 (14.3)	34.3 (35.7)	28.6 (35.7)	25.7 (14.3)

Chapter 12

Effects of tree diversity on trap-nesting bees, wasps and their natural enemies

published as:

Sobek S, Tscharntke T, Scherber C, Schiele S, Steffan-Dewenter I (2009) Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? Forest Ecology and Management 258: 609–615

Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata?

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ARTICLE INFO

Article history:
Received 23 December 2008
Received in revised form 8 April 2009
Accepted 26 April 2009

Keywords:
Beech
Ecosystem functioning
Eumeninae
Habitat heterogeneity
Insects
Sphecidae
Trap nests
Vertical stratification

ABSTRACT

Bees and wasps provide important ecosystem services such as pollination and biocontrol in crop-dominated landscapes, but surprisingly little information is available on hymenopteran communities in temperate forest ecosystems. Species richness and abundance of bees and wasps can be hypothesised to increase with plant diversity, structural complexity, and availability of food and nesting resources. By experimentally exposing standardised nesting sites, we examined abundance and species richness of cavity-nesting bees (pollinators), wasps (predators) and their associated parasitoids across a tree diversity gradient in a temperate deciduous forest habitat. In addition, spatial distribution of individuals and species across forest strata (canopy vs. understory) was tested. Abundance and species richness was high for predatory wasps, but generally low for pollinators. Species-rich forest stands supported increased abundance, but not species richness, of pollinators and predatory wasps, and also increased abundance and species richness of natural enemies. In addition, the forests showed a distinct spatial stratification in that abundance of bees, wasps and parasitoids as well as parasitism rates were higher in the canopy than understory. We conclude that particularly the canopy in temperate forest stands can serve as an important habitat for predatory wasp species and natural enemies, but not bee pollinators. Enhanced tree diversity was related to increased hymenopteran abundance, which is likely to be linked to an increase in nesting and food resources in mixed forest stands.

1. Introduction

In tropical and temperate ecosystems alike, the forest canopy is known as a major source of insect diversity (Erwin, 1982, 1988; Stork, 1988; Novotny and Basset, 2005; Dial et al., 2006), and various authors have revealed differences in insect diversity and community composition across forest strata, regardless of the studied taxon (e.g. Le Corff and Marquis, 1999; Schulze et al., 2001; Fermon et al., 2005; Roisin et al., 2006). In rare cases no distinct stratification was observed (Stork and Grimbacher, 2006). The stratification of distinct forest layers like canopy and understory results in a vertical gradient of different abiotic conditions and biotic resources including light availability, temperature, wind exposure, as well as food and nesting site availability, which impacts the diversity and distribution of insect communities due to the provision of different microhabitats (see Schulze et al., 2001; Yanoviak et al., 2003 and references therein). The relative importance of canopy and understory communities to overall diversity patterns and processes might also be linked to tree diversity, but so far data on the effect of tree diversity on vertical stratification of insect communities is lacking.

Cavity-nesting bees and wasps have been shown to be a particularly useful model system for studying abundance and diversity of hymenopteran pollinators and predators (Tscharntke et al., 1998). Cavity-nesting communities comprise guilds such as pollinators (solitary bees), predators (solitary wasps) and associated parasitoids. They can be easily assessed experimentally by introducing above-ground nesting sites to quantify biodiversity patterns and trophic interactions. Linking biodiversity of a functional group such as parasitoids or pollinators with ecosystem functioning (i.e. parasitism and pollination) is a topical issue in ecology and has recently gained major attention (e.g. Kremen, 2005; Hooper et al., 2005; Bianchi et al., 2006; Priess et al., 2007; Ebeling et al., 2008; Höhn et al., 2008; Klein et al., 2008; Winfree et al., 2008).

Several studies have dealt with the abundance and diversity of cavity-nesting bees and wasps in temperate agricultural (e.g., Gathmann et al., 1994; Kruess and Tscharntke, 2002; Sheffield et al., 2008; Steffan-Dewenter and Schiele, 2008) or tropical agroforestry habitats (e.g. Klein et al., 2006; Tylianakis et al., 2006a,b). In contrast, data on cavity-nesting hymenopteran

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communities in temperate forest habitats are lacking (but see Taki et al., 2008a). This is remarkable, especially since the proximity to forest habitats has recently been shown to increase local abundance and diversity of cavity-nesting wasps (Holzschuh et al., 2009) and also bee pollinators (Taki et al., 2007) in agricultural habitats. Forests are hypothesised to provide resources such as deadwood nesting sites, which are otherwise not present in primarily cleared or simple landscapes. Hence, forest habitats are believed to house source populations of hymenopteran predators, which might spill over into adjacent agricultural habitats, eventually enhancing biocontrol (Tscharntke et al., 2005; Holzschuh et al., 2009).

Taki et al. (2008a,b) provide valuable information on community structure in the forest understory, but it remains ambiguous how cavity-nesting bees, wasps and their natural enemies are spatially distributed across forest types and strata. Until now, virtually nothing has been known about how the temperate forest canopy contributes to hymenopteran diversity.

Here, we present the first data on cavity-nesting hymenopterans and their natural enemies in the canopy and understory of a temperate forest habitat. The study was conducted in the Hainich National Park, Germany's largest coherent deciduous forest. We utilised a semi-natural, mature forest neighbourhood to *a priori* establish a tree diversity gradient ranging from simple beech to mixed forest stands comprising various deciduous tree species. This allowed us to analyse differences in stratification, and to directly relate our results to tree diversity of the sampled forest stands. Increased plant diversity has been linked to increases in species richness of various arthropod orders (Siemann et al., 1998) including cavity-nesting bees and wasps (Tscharntke et al., 1998), and might also influence trophic interactions such as parasitism. We hypothesise that abundance, species richness and parasitism rates of cavity-nesting bee and wasp communities increase with increased tree diversity due to enhanced resource availability (e.g. nesting resources, accessory food for parasitoids), and differ between forest layers (canopy vs. understory) due to microhabitat stratification.

Specifically, we address the following questions: (1) how abundant and species-rich are bee and wasp communities (hereafter referred to as hosts) and their associated parasitoids, and how are they distributed across the tree diversity gradient? (2) How are hosts and parasitoids spatially distributed across forest strata? (3) Are parasitism rates related to the tree diversity gradient? (4) Do parasitism rates differ between forest strata?

2. Materials and methods

2.1. Study area and field sites

Sampling was conducted in the Hainich National Park, Thuringia, which is Germany's largest coherent semi-natural broadleaved forest. Established in 1997, 7600 ha of forest (of a total area of 16,000 ha) are currently protected by federal law (National Park Hainich; http://www.nationalpark-hainich.de). To gain a late successional stage of deciduous forest, conifer removal is the only management practice conducted in the park. Sampled forest stands are located in the north-eastern part of the protected zone, south of the village of Weberstedt (approximately 51°1′N, 10°5′E).

The mild climate of the research area favours a high variety of deciduous tree species. The examined forest stands were dominated by beech (*Fagus sylvatica* L.), lime (*Tilia platyphyllos* Scop., *Tilia cordata* L.) and ash (*Fraxinus excelsior* L.). The study site has an elevation of 350 m a.s.l. and a temperate climate, with an average temperature of +7.5 °C (1973–2004, Deutscher Wetterdienst). Average annual temperature in 2006 was 9.4 °C (Meteomedia 2006). Mean annual precipitation is 590 mm (1973–2004, Deutscher Wetterdienst), and 518 mm in 2006 (Meteomedia 2006). The predominant soil type is stagnic luvisol on loess-limestone as parent material.

Trap nests were installed in 12 forest stands of different tree diversity, which were selected *a priori* to test for effects of a naturally occurring tree diversity gradient on arthropod communities and other biotic and abiotic variables (see Leuschner et al., 2009). All forest stands had remained undisturbed for more than 40 years since the last logging event, and shared major characteristics like soil type, flat elevation, and absence of canopy gaps. In each stand, a 50 m × 50 m core plot was fenced off for determination of tree diversity and for maintenance as long-term observation sites for follow-up projects. To account for the relative abundance of trees as well as for species richness, tree diversity of the plots was described as Shannon index based on stem counts of trees with a *dbh* (diameter breast height) >7 cm (Magurran, 2004). The selected forest stands represented a gradient ranging from simple beech to mixed forests with up to 11 deciduous tree species (i.e. *Acer platanoides* L., *Acer pseudoplatanus* L., *Carpinus betulus* L., *F. sylvatica* L., *F. excelsior* L., *Prunus avium* (L.), *Quercus robur* L., *Sorbus torminalis* L., *T. cordata* L., *T. platyphyllos* L., *Ulmus glabra* Huds).

2.2. Trap nest sampling and sample processing

Sampling of bees and wasps was accomplished using trap nests. Trap nests have been utilised in several studies in agricultural and tropical forest ecosystems to assess diversity of above-ground cavity-nesting bees and wasps as well as their natural enemies (e.g. Tscharntke et al., 1998; Klein et al., 2002). Each trap nest consisted of a pair of PVC tubes (each Ø10.5 cm) filled with a random mix of reed internodes (*Phragmites australis* (Cav). Trin. ex Steud.) ranging from 0.2 cm to approximately 1.0 cm in diameter. In contrast to random trapping with flight interception or Malaise traps, capture of tourist species can be eliminated by experimentally offering nesting resources which are only colonised by species capable of reproducing in a certain area (Tscharntke et al., 1998). The importance of the availability of appropriate nesting sites for the reproduction and establishment of insect populations within a certain habitat has been emphasised by various authors for cavity-nesting species (Gathmann et al., 1994; Horn and Hanula, 2004; Holzschuh et al., 2009). Furthermore, cavity-nesting species tend to breed in close proximity (i.e. several hundred meters) to the nesting site from which they originated (Tscharntke et al., 1998; Gathmann and Tscharntke, 2002; Steffan-Dewenter and Schiele, 2004; Tylianakis et al., 2006a,b). Hence, experimental exposure of these standardised nesting resources is particularly useful to describe communities of bees, wasps and their parasitoids within a defined habitat.

Trap nests were mounted in the canopy and understory of all forest stands. In total, 144 trap nests (12 trap nests per stand; 6 canopy trap nests, 6 understory trap nests) were installed in the centre of individual tree crowns using a crossbow, or mounted at chest height on wooden posts in the understory next to the sampled trees. The sampling scheme was based on the relative abundance of beech. In highly beech-dominated stands with up to four tree species (83–100% beech), trap nests were mounted only in beech (*F. sylvatica*). In stands with up to seven tree species and at least 48% beech, trap nests were installed in the three most dominant species (beech, lime (*Tilia* sp.), and ash (*F. excelsior*)), and in stands with up to 11 tree species and the proportion of beech decreasing below 42%, trap nests were installed in six tree species (beech, lime, ash, sycamore maple (*A. pseudoplatanus*), hornbeam (*C. betulus*) and either oak (*Q. robur*) or service tree (*S. torminalis*)). Sampled trees were randomly selected within the 50 m × 50 m plots or in the immediately adjacent forest. To quantify a possible nesting resource for hymenopteran hosts in each sampled forest stand, each main plot was equally divided into four quarters. The amount of deadwood (m^3/m^2) was assessed in 2007 within a randomly assigned circular subplot with a radius of 5 m within each quarter and then averaged per plot.

The trap nests were exposed over a period of 6 months starting in early May 2006, and harvested in late September of the same year. After retrieval, the traps were stored at 4 °C to initiate diapause. After a period of 5 months, the traps were visually inspected for internodes occupied with nests. Internodes with nests were dissected and the number of host brood cells, the number of brood cells infested with parasitoids and parasitoid eggs, as well as host and parasitoid morphospecies were recorded. The nests were then placed within individual glass vials and stored at room temperature for rearing. Upon emergence, all individuals were pinned and mounted for identification. Voucher specimens were deposited in an in-house collection (Agroecology, Georg-August-University Göttingen). When the condition of the material did not allow for species-level identification, specimens were assigned to other taxonomic levels (at least to family). Ichneumonid wasps were grouped into morphospecies.

2.3. Data analyses

Total species richness was calculated separately for each trap nesting guild (hosts and parasitoids) as accumulated number of species per plot and stratum (pooled across samples). Because of the low abundance and species richness of host bees (only three species were present), we pooled bees and wasps in all further analyses.

Using the lmer function in R (package lme4), we fitted generalised linear mixed effects models (GLMMs) to account for Poisson error distribution (response variables: abundance and species richness of hosts/parasitoids) and binomial error distribution (response variable: parasitism). A maximal model was fitted with the following sequence: fixed effects = deadwood m^3/m^2, Shannon index (tree diversity), stratum (canopy/understory), Shannon index × stratum. Random effects were included as differences between intercepts (i.e., different intercepts either for plots or for stratum nested within plots). The amount of deadwood (m^3/m^2) was included for hosts only to quantify availability of a possible nesting resource Model residuals were examined for meeting assumptions of normality and homoscedasticity.

Similarity of cavity-nesting host communities in different strata of different forest stands was determined using the Bray–Curtis similarity index. The data were transformed into a matrix of dissimilarity (1 minus Bray–Curtis; Zuur et al., 2007) and used as input for a metric multidimensional scaling of the different communities.

Bray–Curtis similarity indices were computed with EstimateS 8.0 (Colwell, 2006). Other statistical analyses were carried out using R, Version 2.6.2 (R Development Core Team 2007; http://www.R-project.org).

3. Results

3.1. General community structure

In total, the trap nests were occupied with 3948 host brood cells. The majority of brood cells were built by five species of eumenid wasps (Hymenoptera: Eumeninae,

Table 1
GLMMs performed on number of brood cells (hosts), individuals (parasitoids), species richness and parasitism rates (hosts) of cavity-nesting hymenopteran species and their natural enemies across a tree diversity gradient in the Hainich National Park. d.f. = degrees of freedom, AIC = Akaike information criterion, BIC = Bayesian information criterion, logLik = log likelihood.

	d.f.	AIC	BIC	logLik	χ^2	*p*	Explanatory variable
Response variable: host brood cells							
Models							
lme1d: brood cells ~ (1 | plot)	2	668.74	671.1	332.37			
lme1c: brood cells ~ Shannon + (1 | plot)	3	663.61	667.15	328.81	7.13	**0.008**	Shannon (tree diversity)
lme1b: brood cells ~ Shannon + Stratum + (1 | plot)	4	269.48	274.19	130.74	396.13	<**0.001**	Stratum
lme1a: brood cells ~ Shannon × Stratum + (1 | plot)	5	222.69	228.58	106.35	48.79	<**0.001**	Stratum × Shannon
lme1: brood cells ~ DeadWood + Shannon × Stratum + (1 | plot)	6	223.33	230.4	105.66	1.36	0.243	Deadwood
Response variable: host species							
Models							
lme2d: host species ~ (1 | plot)	2	27.63	29.99	−11.82			
lme2c: host species ~ Shannon + (1 | plot)	3	26.62	30.15	−10.31	3.01	0.083	Shannon (tree diversity)
lme2b: host species ~ Shannon + stratum + (1 | plot)	4	22.41	27.12	−7.21	6.21	**0.013**	Stratum
lme2a: host species ~ Shannon × stratum + (1 | plot)	5	23	28.89	−6.5	1.41	0.235	Stratum × Shannon
lme2: host species ~ DeadWood + Shannon × stratum + (1 | plot)	6	24.66	31.72	−6.33	0.34	0.559	Deadwood
Response variable: parasitoid individuals							
Models							
lme3c: parasitoid individuals ~ (1 | plot)	2	174.61	176.96	−85.3			
lme3b: parasitoid individuals ~ Shannon + (1 | plot)	3	170.2	173.73	−82.1	6.4	**0.011**	Shannon (tree diversity)
lme3a: parasitoid individuals ~ Shannon + stratum + (1 | plot)	4	73.24	77.95	−32.61	98.96	<**0.001**	Stratum
lme3: parasitoid individuals ~ Shannon × stratum + (1 | plot)	5	53.56	59.45	−21.78	21.67	<**0.001**	Stratum × Shannon
Response variable: parasitoid species							
Models							
lme4c: parasitoid species ~ (1 | plot)	2	23.53	25.89	−9.77			
lme4b: parasitoid species ~ Shannon + (1 | plot)	3	20.17	23.7	−7.08	5.37	**0.021**	Shannon (tree diversity)
lme4a: parasitoid species ~ Shannon + stratum + (1 | plot)	4	16.29	21	−4.1	5.88	**0.015**	Stratum
lme4: parasitoid species ~ Shannon × stratum + (1 | plot)	5	18.09	23.98	−4.05	0.2	0.656	Stratum × Shannon
Response variable: parasitism							
Models							
lme5c: parasitism ~ (1 | plot)	2	57.78	60.14	−26.89			
lme5b: parasitism ~ Shannon + (1 | plot)	3	59.75	63.28	−26.88	0.03	0.853	Shannon (tree diversity)
lme5a: parasitism ~ Shannon + stratum + (1 | plot)	4	54.93	59.64	−23.47	6.82	**0.009**	Stratum
lme5: parasitism ~ Shannon × stratum + (1 | plot)	5	52.65	58.54	−21.33	4.28	**0.039**	Stratum × Shannon

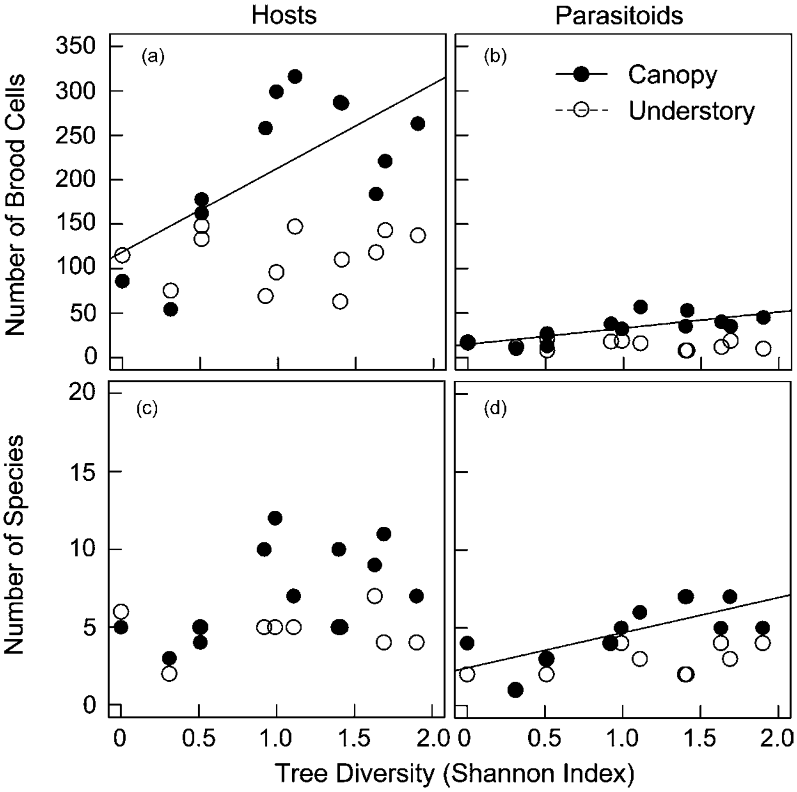

Fig. 1. Stratification of trap nesting bees and wasps and their natural enemies across a tree diversity gradient. (a and b) Number of brood cells or parasitoid individuals in the canopy and understory, (b and c) species richness in the canopy and understory (a, c hosts; b, d parasitoids).

1776 cells (45.1%), Appendix 1), followed by seven species of sphecid wasps (Hymenoptera: Sphecidae, 1272 cells (32.2%)) and one spider wasp species (Hymenoptera: Pompilidae, 548 cells (13.9%)). Solitary cavity-nesting bees were less species-rich (three species) than wasps and showed the lowest abundance of only 347 (8.8%) brood cells. A total of 566 brood cells were occupied by 14 species of natural enemies, the majority thereof being hymenopteran parasitoids (12 species in seven families, Appendix 2).

3.2. Stratification of cavity-nesting communities and parasitism

Hosts were significantly more abundant in the canopy (216.2 ± 24.5, $\chi^2 = 396.13$, d.f. = 4, $p < 0.001$, Table 1) compared to the forest understory (112.8 ± 8.9), and abundance in the canopy increased significantly across the tree diversity gradient ($\chi^2 = 7.13$, d.f. = 3, $p = 0.008$, Fig. 1a). Neither canopy or understory communities responded significantly to deadwood availability, in either abundance or species richness, nor was species richness significantly related to tree diversity ($\chi^2 = 3.01$, d.f. = 3, $p = 0.083$, Fig. 1c).

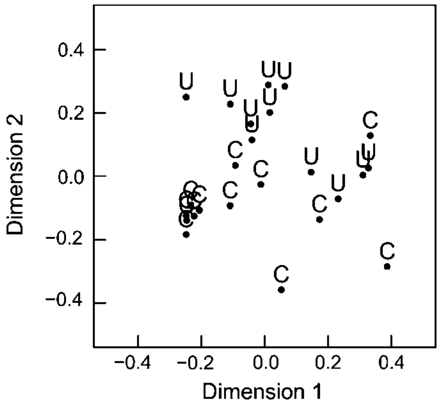

Fig. 2. Metric multidimensional scaling (based on Bray–Curtis similarity) of cavity-nesting bee and wasp host communities across a tree diversity gradient. C = canopy, U = understory.

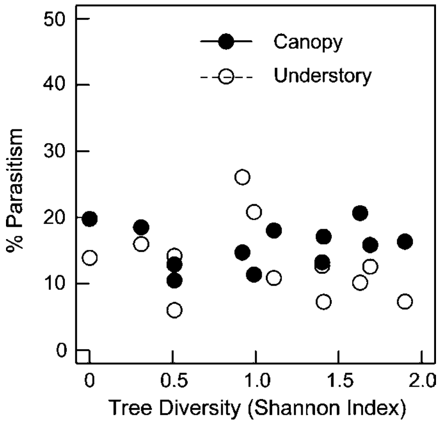

Fig. 3. Proportion of hymenopteran brood cells parasitised by natural enemies in the canopy and understory across a tree diversity gradient in a Central European deciduous forest.

Parasitoids were more abundant (33.5 ± 4.3) and species rich (4.8 ± 0.5) in the canopy compared to the understory (14 ± 1.4; $\chi^2 = 98.96$, d.f. = 4, $p < 0.001$, Fig. 1b, and 2.8 ± 0.3, $\chi^2 = 5.8$, d.f. = 4, $p = 0.015$, Fig. 1d). In the canopy, abundance and species richness increased significantly with increased tree species richness (parasitoid abundance: $\chi^2 = 6.4$, d.f. = 3, $p = 0.011$, Fig. 1b, parasitoid species richness: $\chi^2 = 5.37$, d.f. = 3, $p = 0.021$, Fig. 1d).

Multidimensional scaling of Bray–Curtis similarity illustrated that species composition of hosts differed between the canopy and understory (Fig. 2). Parasitism rates also differed between strata (canopy 15.8 ± 0.9%, understory 13.2 ± 1.7%; $\chi^2 = 6.82$, d.f. = 4, $p = 0.009$, Table 1), but did not respond to the tree diversity gradient (Fig. 3).

4. Discussion

The relationship between abundance or species richness of cavity-nesting communities and plant diversity is little known and most available data concern herbaceous plants (Gathmann et al., 1994; Tscharntke et al., 1998; Sheffield et al., 2008). Although tree species richness, and with it increased habitat heterogeneity and resource availability, has been shown to increase species richness of arthropods, for example in ants and parasitic wasps (e.g. Ribas et al., 2003; Sperber et al., 2004), cavity-nesting taxa may respond differently. Our results show that increased tree diversity of deciduous forest stands enhanced abundance, but not species richness, of cavity-nesting bees and wasps. The increased abundance of hosts in diverse forest stands might be a result of a greater availability of nesting sites and food resources.

Tree diversity determined various biotic and abiotic characteristics of the sampled study sites, such as species richness and density of understory vegetation which increased across the *a priori* set tree diversity gradient (Mölder et al., 2006). Highly structured, heterogeneous vegetation, as found in the most diverse forest stands in contrast to the simple beech stands, provides various resources like food and sites for reproduction, colonisation, and overwintering of arthropods (Lawton, 1983), which can be expected to support a more abundant, even though not significantly more diverse, cavity-nesting community. However, rather than tree species richness *per se*, species identity of certain trees in the mix might impact community composition and brood cell abundance, and thus result in a sampling effect. Less shade tolerant tree species in the species-rich forest stands, such as ash and oak, have a more open crown architecture and also tend to accumulate higher amounts of suspended deadwood compared to beech, which dominated the species-poor stands in our study. Data on the diversity of insect communities in single-species stands of tree species such as ash or oak are lacking, because monocultures of these species in real-world forest ecosystems are scarce, but oak has been shown to be of exceptional importance for the diversity and distribution of insect communities in other forest habitats (Müller and Goßner, 2007).

Surprisingly, understory deadwood amount within stands had no effect on abundance or species richness of cavity-nesting host species. This indicates that rather than deadwood amount as such, a higher diversity of prey items or the variability of actual deadwood nesting sites might have been of importance for the diversity and stratification of the observed cavity-nesting communities. The forest stands showed a distinct spatial stratification in that abundance of bees, wasps, parasitoids, and parasitism rates were higher in the canopy than understory. Cavity-nesting species utilise abandoned galleries of saproxylic beetles for nesting, and deadwood suspended in the canopy might serve as an important nesting site resource as opposed to deadwood on the forest floor, which is often covered with leaf litter and might represent unsuitable microclimatic conditions due to low temperature and high humidity. Beetle abundance and species richness within trophic guilds in the canopy (i.e. herbivores including wood feeding species) increased across the tree diversity gradient (Sobek et al., 2009), which could result in a higher availability and size diversity of galleries and exit holes in the canopy. Prey items, such as caterpillars and spiders, deposited as food sources for cavity-nesting wasp larvae within the brood cells, might follow a similar pattern of increased abundance in the canopy compared to the understory. Several studies conducted in temperate forest habitats have found lepidopteran larvae to be more abundant in the canopy compared to the understory (e.g. Le Corff and Marquis, 1999; Murakami et al., 2005). To test these hypotheses and to reveal the mechanisms behind the observed stratification patterns, future research should aim for data on suspended deadwood, microclimatic factors such as temperature, humidity, and exposure to wind and sun, stratification of plant and insect biomass, and observations of foraging behavior in cavity-nesting species.

Interestingly, the number of host bee species observed in this study was considerably low compared to studies conducted in agricultural or grassland habitats (excluding parasitic bees, three species vs. at least 13 species (e.g. Steffan-Dewenter, 2003; Steffan-Dewenter and Leschke, 2003; Albrecht et al., 2007), but higher than in North American temperate forests (no bees, Taki et al., 2008b). Rather than on high floral diversity as such, bees often depend more on the density of floral resources (Höhn et al., submitted for publication-a). Even though understory plant cover and species richness increased across the tree diversity gradient (Mölder et al., 2006), the mere number of available flowering resources might have simply not been enough to sustain a diverse and abundant community. In the most diverse forest stands of our study, understory vegetation was generally dense and dominated by non-flowering plants such as tree saplings, which overgrew available flowers resulting in reduced accessibility for pollinators. Hence, limited availability and accessibility of pollen and nectar resources appeared to make continuous forest habitats rather unsuitable for cavity-nesting bees, even though the availability of nesting sites might be enhanced compared to other habitat types.

Parasitoid abundance and species richness was related to tree diversity and showed a distinct stratification between canopy and understory. Even though higher trophic levels do not directly depend on the same resources as their hosts (nesting sites, floral resources), they are indirectly connected to these forest stand resources by availability of suitable hosts, in terms of numbers and species. In our study, the majority of parasitoids were linked to only one or two host species (Appendix 2), which indicates a highly specialised parasitoid community (Ebeling, 2008). Parasitism rates differed between forest strata and were slightly higher in the canopy compared to the understory. A stratification of parasitism rates could not be shown for a solitary cavity-nesting wasp species (Eumeninae) in a tropical forest habitat (Höhn et al., submitted for publication-b), and might in our case be related to a slightly more diverse parasitoid community in the canopy.

In conclusion, species-rich forest stands showed increased abundance of cavity-nesting hymenopterans, which might enhance provision of ecosystem services like pollination and biocontrol of herbivores (e.g. aphids, lepidopteran caterpillars) within the forest stand as well as in adjacent arable land (Holzschuh et al., 2009), even though species richness was not increased. Furthermore, temperate forest stands show a distinct vertical stratification of hymenopteran abundance and species composition, most likely linked to a greater availability of nesting sites and food resources in the forest canopy. Hence, we conclude that tree diversity in temperate forests might be a predictor of insect distribution patterns and associated processes such as parasitism.

Acknowledgements

This study gained financial support by the DFG [German Research Foundation] within the Research Training Group “Graduiertenkolleg 1086: The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests”. We highly acknowledge Christoph Leuschner, Frank Thomas, Hermann Jungkunst and Stefan Fleck for group coordination and also thank Mascha Jacob, Karl M. Daenner and Mareen Gollnow for providing data on stand characteristics. Our special thanks go to Andreas Dittrich, Martin Erren, Tobias Gebauer, Martin Goßner, Friedrich Rathing and Ulrich Simon for assistance with field work, and Nick Swant for proof-reading of the manuscript.

Appendix 1. List of cavity-nesting bee and wasp species collected in the canopy and understory of forest stands across a tree diversity gradient in the Hainich National Park. n^C = number of individuals captured in the canopy, n^U = number of individuals captured in the understory, n^P = number of observed parasitoid species.

Family/subfamily	Species	n^C	n^U	n^P
Colletidae	*Hylaeus communis*	295	32	2
Colletidae	*Hylaeus confusus*	0	9	0
Megachilidae	*Megachile ligniseca*	11	0	1
Eumeninae	*Ancistrocerus antilope*	9	0	1
Eumeninae	*Ancistrocerus trifasciatus*	985	599	8
Eumeninae	*Discoelius zonalis*	162	0	2
Eumeninae	*Symmorphus debilitatus*	6	0	0
Eumeninae	*Symmorphus gracilis*	10	10	0
Pompilidae	*Dipogon subintermedius*	271	277	4
Sphecidae	*Crossocerus binotatus*	11	5	2
Sphecidae	*Nitela spinolae*	38	7	1
Sphecidae	*Passaloecus corniger*	54	5	3
Sphecidae	*Passaloecus insignis*	64	4	2
Sphecidae	*Passaloecus* sp.	1	0	0
Sphecidae	*Psenulus pallipes*	73	10	3
Sphecidae	*Rhopalum clavipes*	42	72	1
Sphecidae	*Trypoxylon clavicerum*	562	324	8

Appendix 2. List of natural enemies of cavity-nesting hymenopterans collected in the canopy and understory of forest stands across a tree diversity gradient in the Hainich National Park. n^C = number of individuals captured in the canopy, n^U = number of individuals captured in the understory, n^H = number of observed host species.

(Morpho)species	n^C	n^U	n^H
Braconidae 1	1	0	1
Chrysididae	10	5	2
Chrysis ignita agg.	68	7	1
Coelioxys alata	3	0	1
Diptera	0	7	1
Gasteruption assectator	18	0	1
Ichneumonidae	24	12	2
Ichneumonidae 1	30	2	4
Ichneumonidae 2	39	7	4
Ichneumonidae 3	2	0	1
Ichneumonidae 4	111	86	3
Ichneumonidae 5	1	0	1
Ichneumonidae 6	0	1	1
Ichneumonidae 7	0	1	1
Megatoma undata	52	3	8
Melittobia acasta	41	36	4
Not identified	2	1	2

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General discussion and Conclusions

General discussion

In this thesis, we experimentally manipulated components of plant biodiversity and climate change, and we investigated the effects of gradients in landscape structure and tree biodiversity on ecosystem processes. Overall, we started off with a general framework, asking whether global change affected biodiversity and trophic interactions in the widest sense. The thesis was subdivided into four sections, each with their own specific hypotheses. What can we conclude from these findings? Which general patterns have emerged, given the variety of study systems and approaches?

Some may argue that answering these questions would require a meta-analysis of the different experiments conducted within the framework of this thesis (e.g. Cardinale et al. 2006; Cardinale et al. 2011; Quijas et al. 2010; Schmid et al. 2010). However, we believe that a thorough look at the findings presented in the individual chapters should suffice to extract some generalizations, and to provide further outlook on future research. The following discussion therefore starts with separate treatments of each of the four sections of this thesis, after which some general conclusions shall be drawn.

1 Plant biodiversity effects on biological invasions, herbivore performance and multitrophic interactions

This whole section made use of a plant biodiversity experiment - that is, a sown gradient in plant species richness, established on former arable land. The main advantage of such an approach is that gradients in plant species richness are essentially independent of abiotic gradients (Schmid and Hector 2004). Thus, a biodiversity experiment allows one to investigate species richness effects in isolation from other confounding factors. However, some important caveats of such an experimental approach need to be taken into account.

One of the most severe limitations of such experiments is the necessity to maintain the plant biodiversity gradients through weeding (for a recent example see Pfisterer et al. 2004). While weeding ensures that the diversity levels on every plot match the experimental design, it also causes soil disturbances. The question that needs to be asked is, therefore, whether it is likely that some of the findings presented in Section 1 are actually artifacts of weeding (see Huston 1997, the “classical” critique of biodiversity experiments in general). For this purpose, we tested whether the weeding effort per plot (expressed in person-weeding hours) was significantly correlated with plant biodiversity. These correlation analyses showed that there was a significant, yet only weakly negative correlation between log-transformed plant species richness, and weeding hours (Spearman´s rho=-0.37, P<0.001, df=80). Hence, weed invasion into monocultures was clearly stronger than weed invasion into mixtures. Now the critical question would be: Is it likely that the increased weeding disturbance caused to monocultures had a negative influence on the findings presented in this thesis? For example, how likely is it that weeding disturbance influenced the success of plant invaders? Clearly, we found that Knautia arvensis (our test invader) performed worse in species-rich mixtures. If weeding would be the cause, then the opposite pattern should be expected. Similarly, we found no plant species richness effects on performance of the grasshopper Chorthippus parallelus. Hence, it is unlikely that weeding effects played a significant role in this case. Finally, in our study on multitrophic interactions, weeding effects cannot be completely ruled out, especially for components of the belowground subsystem. Unfortunately, the experiments had no “disturbance control” treatment; this would be an important treatment that should be included in future biodiversity experiments.

Another caveat of biodiversity experiments such as the Jena Experiment is the artificiality of the actual plant mixtures used, and the random extinction scenario that is simulated by such an experiment (Leps 2004). However, generalizations would be more difficult if a non-random extinction scenario had been used - and a random extinction scenario by definition creates species combinations that don´t necessarily need to make sense in the “real world”.

Overall, we can conclude from the experiments presented in Section 1, that plant species richness matters to some processes, but not to all. For example, we showed clearly that invasion resistance increases with plant species richness. We also clearly demonstrated that this is likely to be caused by belowground interactions, such as root competition, or interactions with other belowground organisms. A similiar pattern emerged from our study on the effects of plant biodiversity on multitrophic interactions (Scherber et al. 2010): We found clear negative trends, for example for plant invader abundance, and invader species richness. Many other organisms and their interactions were, however, positively influenced by plant species richness. We have shown that a potential mechanism for these observed effects is bottom-up control. Because plants were the trophic level that was manipulated in this experiment, it is a reasonable assumption that plant species richness influences adjacent trophic levels more directly and more strongly than more distant trophic levels. An important generalization that can be drawn here is that plant biodiversity effects dampen with increasing trophic level and with increasing degree of omnivory. These findings now need to be tested in other study systems, and coupled with manipulations of other trophic levels.

2 Effects of global climate change on herbivore performance and above-belowground interactions

Similar to Section 1, we used a unified experimental installation for both chapters presented in this section. Here, too, the experimental approach chosen should be critically discussed. For example: How well did the treatments resemble the desired levels of global change? Clearly, FACE experiments are not the only way to study effects of elevated CO2 on ecosystems (Hendrey and Miglietta 2006). The CO2 pipes used in this system created some gradients in CO2 concentration from the edge to the center of each octagon (see also Bunce 2011). However, very high CO2 concentrations were only measured within a few centimeters off the pipes, and concentrations towards the center of the plot were homogenously distributed (see Figure 4 in Mikkelsen et al. 2008). The warming treatment (through passive night-time warming) could also have had some side-effects on the heathland community, for example by altering winter snow cover on the plots. However, the curtains were always withdrawn when precipitation occurred, and it is therefore unlikely that any artifacts of the experimental installations occurred. By introducing insects at low densities into individual cages, we avoided problems of increased densities of herbivores in global change treatments, as has been reported recently, e.g., by Moise and Henry (2010). The insect herbivores used were all locally present and abundant. However, the experiments described were both only short-term, and it is therefore not possible to draw conclusions about the long-term dynamics. Nevertheless, some interesting generalizations can be drawn from both experiments conducted. First, both experiments showed that herbivore performance or herbivory were negatively influenced by elevated CO2 (as has been shown also in a recent review by Stiling and Cornelissen 2007). This means that future climatic conditions may have adverse effects on insect herbivores in general. Second, climate change drivers interacted in both experiments, making predictions based on manipulations of single drivers difficult. In addition, above-belowground interactions, mediated by plants, were strongly altered by CO2 and drought (with only weak effects of warming). Nutrient cycling, in particular in nitrogen-limited systems, may be strongly influenced by climate change (see a recent publication on this by Larsen et al. 2011), and interactions between the above- and the belowground subsystem will be altered accordingly.

3 Landscape composition, habitat identity, and multitrophic interactions

In this section, we changed both the study system, and the spatial scale of observation - moving from local-scale plant-herbivore interactions to more indirect effects occurring on a landscape scale. However, the general approaches chosen in this section are similar to the phytometer and sampling approaches used in Section 1. The main difference between the experiments performed in Section 3 and the previous two sections is the degree of artificiality and experimental control: While the experiments in Section 1 and 2 were highly controlled and rather artificial, the experiments of Section 3 (and the following) are more observational, yet also more realistic. This increase in realism comes at the expense of experimental control: The main explanatory variables in Section 3 are fixed a priori as far as possible, but they are not experimental treatments in the pure sense. Thus, the main question that needs to be addressed is whether the relationships reported in this section were causal or not. However, we used a common phytometer approach, uncoupling the observed findings from local abiotic differences (introduced by Clements and Goldsmith 1924; see also Gibson 2002), and the landscape gradients chosen were selected a priori (see, among others, Steffan-

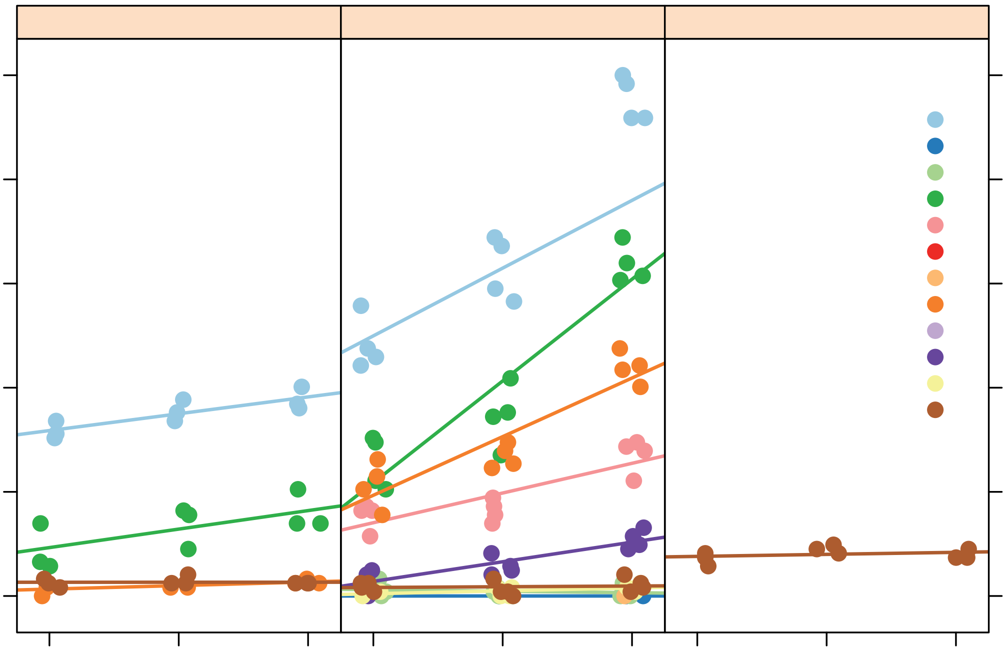

Figure 1 Combined results from the tree biodiversity experiments covered in Section 4. There are striking similarities between these results and those obtained in the grassland biodiversity experiment described in Section 1. Future studies should aim at integrating these findings, detection of generalizable patterns, and development of a unifying theory of biodiversity and multitrophic interactions. The y axis shows standardized response variables (scaled to [0;1]). DL1,2,3 Levels in tree species richness. Data source: DFG-GRK1086 database. Dataset contributors (among others): S.Sobek, N. Fahrenholz, C. Fornacon, A. Mölder, C. Leuschner, M. Schaefer, G. Gleixner, S. Fleck, M. Jacob, N. Weland, A. Schuldt, C. Platner, S. Cesarz.

Dewenter et al. 2002). Thus, we can be confident that the findings reported in this section represent causal relationships. Yet, another problem especially with the rape pollen beetle experiments conducted is that these experiments were performed rather late in the season. However, this is unlikely to be a major problem, because beetles did oviposit on the mustard phytometers, and larvae showed normal development. Thus, while there was some phenological difference between larvae developing on oilseed rape, and larvae developing on our experimental phytometer plants, these differences are not likely to be problematic.

In general, the results presented in Section 3 clearly show that local herbivore and parasitoid populations on wild plants are influenced by landscape structure, and that there are complex inter-annual interactions between crop and noncrop habitats. Spillover effects between crops and wild plants should be taken into account in future studies (Rand et al. 2006). The findings also emphasize the importance of conducting research for longer periods, i.e. also after the cessation of flowering of oilseed rape in the landscape. In addition, we proposed a new sampling approach for populations of insect pests and biocontrol agents; future research will show how suitable such a grid sampling approach is in comparison to other established approaches.

4 Tree biodiversity and multitrophic interactions

This section differed from all previous ones, because we used a natural biodiversity gradient, rather than artificially created plots, for all experiments and observations. Thus, we used a system in long-term equilibrium to test for biodiversity effects. While a direct comparison between results obtained in grassland, and results obtained in deciduous forest ecosystems, is clearly not possible, it is nevertheless interesting to search for similarities and differences. However, several things need to be born in mind. The biodiversity gradient in the Hainich National Park was neither independent nor random - in essence, it was a gradient in beech (*Fagus sylvatica*) abundance, crossed with a gradient in tree species richness. Assuming constant tree density per unit area, such an approach is similar to a replacement series design, as has frequently been used, for example, in plant competition studies (Morin 2011). In a replacement series design, the proportions of species in a mixture change, while density remains constant. Consequently, tree species richness and beech proportion are not independent in the studies presented in Section 4. However, in "natural" ecosystems, randomness and non-independence can almost never be assumed. Hence, the results obtained and presented in Section 4 are realistic at the expense of experimental control. In ecological experiments in general, it is almost impossible to maximize realism, generality and precision at the same time (see the extensive discussions on this, e.g., in Hairston 1989, Underwood 1997 or Morin 1999).

Now for the comparisons between tree biodiversity effects, and grassland biodiversity effects. In Section 1, we had proposed a general hypothesis on how plant species richness should affect multitrophic interactions. The general pattern that had emerged in those studies was that herbivores reacted more strongly than carnivores, parasitoids or omnivores to plant species richness; this pattern had been found both in the aboveground- and in the belowground subsystem, possibly pointing at an existing general mechanism generating these biodiversity effects.

We tested for similarities between the datasets presented in Section 4, and the datasets analysed in Section 1 (see Figure 1, opposite page). For this purpose, we additionally analyzed data on the belowground subsystem. Surprisingly, we found very similar patterns between both datasets: In both cases, herbivores and carnivores reacted more strongly to plant species richness than did parasitoids or omnivores. The responses of the belowground subsystem were also, in both cases, weaker than aboveground. While these steps of analyses are still preliminary, it would be fascinating to see such general patterns emerging.

A possible mechanism explaining plant biodiversity patterns in both datasets could be that plant communities´ structural complexity increases with plant species richness - for example, more surface area or volume could be available for biotic interactions between plants and herbivores. Likewise, the diversity of chemical compounds released by plants (aboveground volatiles, or belowground root exudates and rhizodeposits) could increase with plant species richness, attracting more first-order consumers and their predators, parasitoids and pathogens. Clearly, much more research into these areas would be necessary, with a new generation of biodiversity experiments and observational studies.

5 General conclusions

We have shown that global change components (such as climate change, land-use change) can change biodiversity and trophic interactions. We have also shown that biodiversity loss may greatly impede trophic interactions and change overall food web structure of ecological systems. Most analyses and results presented in this thesis have shown that the relationships are more complex than generally anticipated, and that most observed processes act in network structures rather than in isolation. It is therefore vital to account for such network structures by employing suitable statistical methods, but also to design new experiments with knowledge about the network structure of ecological systems at hand. We need to move away from pure "reponse variable - explanatory variable" thinking to a systems perspective of the world around us. As human activities act in concert, so do global change components. Now it is time to decide which of the many global environmental changes want to address first. A good starting point would be land-use change, because it strongly affects species, communities and ecosystems, and because it happens at an unprecedented pace. Similarly, preservation of plant biodiversity is a good basis for conservation as a whole, because primary producers form the basis of life on Earth.

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Summary

Summary

Anthropogenic global change may affect different compartments of the biosphere, atmosphere, or hydrosphere. In particular, increasing atmospheric concentrations of carbon dioxide, anthropogenic changes to biogeochemical cycles, or land-use changes have been identified as particularly important components of global change.

In this thesis, we study the effects of human-caused environmental change on ecosystems. In particular, the effects of climatic and land-use changes are addressed. In addition, we address the loss of biological diversity, and the subsequent effects of biodiversity loss on ecosystem processes, such as biological invasions or trophic interactions. The thesis is structured into four subsections.

Section 1 covers biodiversity effects on invasion resistance, herbivore performance, and multitrophic interactions.

Section 2 investigates effects of climate change on plant-herbivore and above-belowground interactions.

Section 3 is about landscape structure, multitrophic interactions and biological control.

Finally, **Section 4** covers effects of tree biodiversity on multitrophic interactions.

While all results are presented as individual chapters, some unifying experimental approaches were followed; we experimentally manipulated (i) plant species and functional richness and composition (The Jena Experiment); (ii) atmospheric Carbon dioxide concentration, drought, warming and herbivory (CLIMAITE Experiment);(iii) Landscape composition and habitat identity and (iv) tree species richness along a natural gradient in the Hainich National Park.

We found that (i) plant biodiversity consistently affected ecosystem processes, (ii) multitrophic interactions were bottom-up controlled by plant species richness, (iii) Herbivores reacted more strongly than carnivores, parasitoids or omnivores to changes in plant biodiversity, (iv) global climate change drivers interactively affect herbivore performance and above-belowground interactions and (v) landscape composition and habitat identity can be important predictors of herbivore performance and biological control.

Our findings show that protecting plant species richness (and plant biodiversity in the wider sense) can be a good basis for conservation of other organisms and their interactions.

Our climate change studies also show that we need a better understanding of global change effects on above-belowground interactions and terrestrial nutrient cycling in order to improve the predictions of predictive climatic models.

Overall, future research should aim at experimentally manipulating organism species richness or abundance at multiple trophic levels, combined with manipulations of multiple drivers of anthropogenic environmental change.

Acknowledgements

Acknowledgements

I would wish to express my special gratitude to Teja Tscharntke for the opportunity to write this thesis in his lab, for scientific freedom and open-mindedness, and for lots of inspirations during the last years. I would also wish to thank the members of the Agroecology working group, in particular

David Gladbach and Max von Fragstein for ideas, discussions and advice with artwork, Jochen Fründ for stimulating discussions, the (former) BSc, MSc and PhD students Stephi Sobek, Mareen Gollnow , Christoph Rothenwöhrer, Ellie Vockenhuber, Georg Everwand, Christine Venjakob, Verena Rösch, Urs Kormann, Tatiane Beduschi, and Claudia Normann for lots of inspirations and field expertise, our technicians Susanne Jahn and Susanne Schiele, as well as our secretary Jutta Gilles for support in many ways, my post-doc colleagues Alexandra-Maria Klein, Yann Clough, Péter Batáry and Carsten Thies for interesting discussions and fabulous collaboration, our IT team for setting up an excellent working environment (Friedrich Sundmacher, Thomas Oesterreich, Jan Tönjes and Siggi).

I´d also like to express my special thanks to my (former and recent) Jena colleagues, in particular Wolfgang Weisser (now in Munich), Sylvia Creutzburg, Sybille Unsicker (Jena), Jule Heimann geb. Specht and Anett Oswald and Peter N. Mwangi (Nairobi) for help with field work.

Thank you to Søren Christensen, Karen Stevnbak Andersen, Claus Beier and Inger Kappel Schmidt for the great collaboration with you at the CLIMAITE experiment - two chapters of my habilitation thesis would be missing without you!

I´d also wish to thank Geoff M. Gurr (Australia) for kindly allowing me to contribute a book chapter to his “Biodiversity and Insect Pests” book that is contained in this thesis.

From the statistics side, I´d like to thank Mick Crawley, Bernhard Schmid, Andy Hector and Winnie Voigt for challenging but fruitful discussions about covariates, path analysis and other related topics.

A thesis such as this would not be possible without the love of my parents Jörg and Traudl, my wife Julia and my children Paul and Lisa - I just wish to thank you for everything.

Parts of this research were funded by the DFG (FOR 456, FOR 1451, GRK 1644, GRK 1086), by the European Union (7th Framework Programme, INCREASE Infrastructure), by the VILLUM KANN RASMUSSEN Foundation, and by Air Liquide Danmark A/S.

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