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**Spatiotemporal patterns of insect diversity and
multitrophic interactions across a tree diversity gradient
in a Central European deciduous forest**

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„When you have seen one ant, one bird, one tree,
you have not seen them all.”

Edward O. Wilson

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CHAPTER

1

Introduction

Biodiversity & forest ecosystems in a changing world

Biodiversity research has become a key subject in modern ecology. Throughout the last decade, a plethora of studies has been conducted to elucidate the status quo and distribution of global biodiversity (Gaston 2000), to determine major threats (Purvis & Hector 2000), to link biodiversity with ecosystem functioning and services (Loreau *et al.* 2001, Hooper *et al.* 2005, Kremen 2005, Balvanera *et al.* 2006), and to stop biodiversity loss by applying appropriate conservation measures (Perfecto *et al.* 1997, Rundlöf *et al.* 2008). What is biodiversity, and why has it recently gained major attention of scientists around the globe?

The term “biodiversity” combines different perceptions of variety among organisms. According to the United Nations’ “Convention on Biological Diversity” (1992), it includes ecological diversity (=niche diversity), organismic diversity, and genetic diversity among individuals (Noss & Cooperrider 1994, Schellnhuber *et al.* 1999). The UN conference on the environment and development in Rio de Janeiro (1992) also acknowledged biodiversity as a natural resource, and determined its conservation as a keystone task for future sustainable development (Haila & Kouki 1994).

Biodiversity offers goods and services that are impossible to be replaced by man alone. If society remains unable to establish sustainability and fails in stopping the current biodiversity decline, ecosystem services such as pollination, provision of clean air and soil, biocontrol of pest outbreaks, continuity of biogeochemical cycles etc. will be lost (Ehrlich & Ehrlich 1992). Besides these apparent driving forces of the environment, biodiversity also has economic implications and serves as resource for food, industrial production (e.g. timber, medical goods), and recreation (Ehrlich & Ehrlich 1992).

Forest ecosystems, in tropical as well as in temperate regions, are believed to house the major proportion of global biodiversity (Carnus *et al.* 2006). As a result of global change, extensive timber logging, and conversion of forest to arable land for biofuel production, pristine forest habitats decline rapidly. According to the 2005 report of the Food and Agriculture Organisation of the United Nations (FAO), approximately 7.3 million hectares of forest are lost each year. Worldwide, only 30 % of surface area is still covered by natural or planted forest, and especially Central Europe exhibits only a minute fraction of large-scale forest habitats (FAO 2005). In Germany, although 30 % of land surface is forested, the proportion of old-growth natural forest equals zero (FAO 2005).

With the majority of pristine forest habitats already vanished and with prospect to future losses, it is of immediate importance to identify the contribution of the remaining forest

habitats to global diversity and ecosystem functioning. Since the late Holocene, European beech (*Fagus sylvatica* L.) and other deciduous trees should be naturally predominant in Central Europe (Tinner & Lotter 2006). Instead, for many years conifers have primarily been reforested (Puumalainen *et al.* 2003), and only recently sustainable forestry tries to re-establish a greater abundance and variety of deciduous tree species. For Central Europe and Germany in particular, the scope should thus lie on the last semi-natural deciduous forest habitats, which are scarce and widely scattered across a landscape otherwise dominated by agricultural land use.

Research on animal and plant communities in forest habitats has a long tradition in ecology, but nevertheless, blank spots remain on the map of global forest diversity. Although numerous examinations in tropical rainforests have illustrated that especially insects in the forest canopy are prime contributors to global biodiversity (Erwin 1982, Erwin 1988, Stork 1988, Novotny & Basset 2005, Dial *et al.* 2006), canopy research in temperate deciduous forests in Central Europe has long been neglected, and only a handful of published studies on a limited selection of arthropod taxa exists. (Kampichler & Teschner 2002, Goßner & Bräu 2004, Goßner & Ammer 2006, Goßner *et al.* 2007, Müller & Goßner 2007).

In the present study, we try to fill these blanks by relating diversity and function of canopy and understory insect communities to a semi-natural tree diversity gradient ranging from simple beech to mixed deciduous forest stands located in the Hainich National Park (Thuringia, Germany).

Umbrella project

The research conducted for this thesis was placed within the framework of the DFG (German Research Foundation) Research Training Group (“Graduiertenkolleg”) 1086, “The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests”. The multidisciplinary programme was aimed to link the work of 14 PhD students, who independently examined various topics of temperate forest biodiversity and ecosystem functioning. A complete list of all parameters investigated can be found in Leuschner *et al.* (in press), subprojects included:

Abiotic stand characteristics, biogeochemical cycles, and productivity

Stand structure and abiotic conditions are primarily set by the tree species present in the canopy layer. Analyses included soil moisture, soil carbon and nutrient content, local stand climate, and management history. Biogeochemical processes were examined and modelled from the soil up to the canopy, including rainfall precipitation and water cycling, nutrient fluxes, sap flow and canopy transpiration, litter decomposition, soil respiration, and primary plant production (stem increment, leaf and fine root production, etc.).

Biotic stand characteristic and interactions

Again, focus was laid on examining animal and plant communities from the soil up to the high canopy. Investigations ranged from analysing abundance and diversity of mycorrhizal fungi, herb layer plants, tree seedlings, and full-grown trees to soil mesofauna (oribatid mites), macrofauna (earthworms, ground beetles, isopods, spiders, snails), and canopy arthropods. Results for the latter including beetles, true bugs, bees and wasps are described in detail in chapter 2 to 4 of the present thesis. Biotic interactions like parasitism, herbivory of tree seedlings, and the abundance of herbivores and predators, as well as their functional relationships, are presented in chapter 4 and 5.

Economic evaluation

As mentioned earlier in this chapter, biodiversity offers services and goods of high economic impact and monetary value. Hence, to make the multidisciplinary survey complete, the willingness-to-pay for insurance values maintained by diverse forest stands (e.g. biocontrol of pest outbreaks) was investigated in a choice experiment and by random interviews.

Study area

All investigations were conducted in the the Hainich National Park. The park was established in 1997 and is located in the federal state Thuringia (Germany) in temperate Central Europe. It is described as Germany's largest connected semi-natural deciduous forest, and covers a total area of 16,000 ha (Nationalpark Hainich; <http://www.nationalpark-hainich.de>). In the past, the region belonged to the territory of the former German Democratic Republic, and has been used for many years as a military training site by Russian occupants. The latter ensured that most of the forest remained unmanaged for at least 40 years. In 1997, 7,600 ha have been put under permanent conservation and been declared National Park. In 2005, 12 permanent

research plots were set-up in the north-eastern part of the conservation zone close to the village Weberstedt, establishing a semi-naturally grown tree diversity gradient ranging from simple beech to mixed forest stands with up to 9 broadleaved tree species (Fig. 1.1 & Fig 1.2).



Fig. 1.1. Simple beech stand in the Hainich National Park in spring 2008 (photo: C. Scherber).



Fig. 1.2. Species-rich forest stand in the Hainich National Park in spring 2005 (photo: S. Schiele).

The tree species composition of the Hainich National Park is highly exceptional, and unlike other forest habitats in Germany, conifers are a minority group and frequently logged to regain a late successional stage of semi-natural deciduous forest. One can find many stands dominated by European beech (*Fagus sylvatica* L.), other tree species like lime (*Tilia* sp.) and ash (*Fraxinus excelsior* L.) also appear frequently, and the mix is enriched with species like hornbeam (*Carpinus betulus* L.), maple (*Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L.), cherry (*Prunus avium* L.), oak (*Quercus robur* L.) and elm (*Ulmus glabra* Huds.). Even the rare service tree (*Sorbus torminalis* L.) is present, and in total a maximum of 14 different tree species per hectare has been reported (Mölder *et al.* 2006).

Study system

Insects in the forest canopy and understory

Insects are the predominant taxon in terrestrial ecosystems by means of species richness, individual abundance, and biomass (Kremen 1993), and are of great importance for conservation management (Pearce & Venier 2006, Underwood & Fisher 2006). Estimations of global faunal diversity are closely interlinked with investigations on insect species richness, abundance, and host specificity (e. g. Erwin 1982, Erwin 1988, Erwin 1991, Longino 1994, Stork 1988), most of which have focused on forest canopy habitats in the tropics.

Species richness of arthropods has been reported to positively correlate with plant diversity (Gaston 1992, Siemann *et al.* 1998, Novotny *et al.* 2006). Habitat heterogeneity is usually enhanced in species-rich plant communities, resulting in a structurally more complex environment due to differences in plant architecture and increased availability of resources, offering a greater niche array and hence supporting a larger number of arthropod species (Humphrey *et al.* 1999, Hansen 2000, Hamer *et al.* 2003, Lassau & Hochuli 2008). Although studies exist comparing the richness of arthropod communities of different tree species (Mawdsley & Stork 1997), far less is known about how communities change if different sets of tree species combinations are considered. Reason for this might be the lack of availability of semi-natural forest stands within a single study region that are comparable by means of climate, elevation, soil conditions, and management history. Recently conducted investigations used gradients, for example of management intensity, to estimate effects of anthropogenic disturbance and land use on forest insect communities (Müller *et al.* 2008), but information on effects of plant diversity gradients has so far only been gained from experiments (Vehviläinen *et al.* 2006, Vehviläinen *et al.* 2007). Making use of the semi-

naturally established tree diversity gradient in the Hainich National Park, for the first time we examine species richness and distribution of three major taxa of canopy arthropods across a tree diversity gradient within a real-world forest ecosystem, and present data for beetles (Coleoptera), true bugs (Heteroptera), and cavity-nesting bees and wasps (Hymenoptera).

Beetles are believed to represent almost 40 % of all arthropods worldwide (Grove & Stork 2000). Up to now, ~400,000 species have been described, 5,600 thereof in Central Europe (Honomichl 1998). Attributable to a long history of research on this order, most species are well described, and identification is eased by the availability of well-established keys. Beetles are economically and environmentally important as pest and predator species in agriculture and forestry, and have thus received major attention in biodiversity assessments of agricultural habitats, grassland habitats, tropical, boreal, and also temperate forests (e.g. Batary *et al.* 2007, Bos *et al.* 2007, Clough *et al.* 2007, Jacobs *et al.* 2007, McGeoch *et al.* 2007, Müller *et al.* 2008).

While the latter allows for a comparison of our data with existing material, information is vastly lacking for the heteropteran fauna in forest habitats. Although true bugs comprise sap-sucking herbivores as well as predators, only very few studies on arboreal true bug communities exist (but see Goßner & Bräu 2004, Goßner *et al.* 2006). Even for other ecosystems, data for true bugs are scarce, and especially data on temporal and spatial turnover of true bug diversity do not exist. Our data will provide new insights into the community structure of this formerly neglected group.

Beetles, as well as true bugs, were sampled with non-baited flight interception traps suspended in individual tree crowns (Fig. 1.3a, b), which is a common method for random sampling of flying insects (e.g. Simon & Linsenmair 2001, Stork & Grimbacher 2006, Grimbacher & Catterall 2007), and allows for sufficient estimation of individual and species abundance within a certain area.



Fig. 1.3. a) Flight-interception trap, b) traps were mounted in the forest canopy (Photos: S. Schiele).

The inclusion of bees and wasps in our study resulted from a lack of data on how temperate forest habitats serve as a pool for hymenopteran diversity, including bees as pollinators of crop and wild plants, predatory wasps, and associated parasitoids. Due to anthropogenic habitat loss and fragmentation, pollinators like solitary bees decline rapidly, which has large-scale consequences on plant survival (Biesmeijer *et al.* 2006). Various studies have dealt with pollinator abundance and species richness in agricultural habitats (e.g. Gathmann *et al.* 1994, Kruess & Tscharntke 2002, Sheffield *et al.* 2008, Steffan-Dewenter & Schiele 2008), and tropical agroforestry has also gained major attention recently (e.g. Klein *et al.* 2006, Tylianakis *et al.* 2006). Up to now, not much is known how bee pollinators and predatory wasps utilise forest habitats as source for food, shelter, and reproduction. Especially species-rich forests house a variety of flowering plants offering nectar and pollen resources (Mölder *et al.* 2006), which we expected to impact hymenopteran abundance and species richness, thus linking our observations to the provision of ecosystem services. Besides distribution of species richness and individual abundance, information on biotic interactions between parasitoids and hosts was included in the present study, which is of importance for the evaluation and understanding of diversity on an ecosystem scale (Montoya *et al.* 2003). The latter was accomplished by using trap nests instead of flight interception traps for sampling. Trap-nests provide a standardised method of sampling communities of cavity-nesting bees and wasps

(Tschardtke *et al.* 1998), but up to now only two studies conducted in a temperate forest are known to the author (Taki *et al.* 2008b, Taki *et al.* 2008a), in which sampling was constricted to the understory. Here we give new insights in the spatial distribution of species by comparing vertical strata (canopy and understory habitats) across the tree diversity gradient (Fig. 1.4a,b).



Fig. 1.4. Trap nests in the a) forest understory, b) forest canopy (photos: S. Schiele).

Herbivory of tree saplings

While an assessment of arthropod diversity delivers valuable information for describing the fauna of a certain area, it is of special interest how arthropod communities interact with their environment, especially with regard to ecosystem functioning, e.g. resilience against pest outbreaks. Many recent biodiversity experiments have addressed this issue by investigating plant diversity-herbivory relationships. In various agricultural (Risch *et al.* 1983), grassland (Unsicker *et al.* 2006) and forest habitats (Jactel *et al.* 2005, Jactel *et al.* 2006, Jactel & Brockerhoff 2007, Kaitaniemi *et al.* 2007), reduced herbivory was observed with increased plant diversity. However, some authors found no effect at all (Scherber *et al.* 2006) or even increased herbivory with increased plant diversity (Vehviläinen *et al.* 2006), and information on which patterns appear in natural forests is completely lacking. Utilising the tree diversity gradient, we examined insect herbivory on beech, Norway maple and sycamore maple saplings in the forest understory. For a most comprehensive survey of possible patterns and processes, we estimated damage caused by leaf-chewing, leaf-mining and gall-forming insects, and also observed the insect fauna (predators and herbivores) present on each sapling. Although previous studies dealing with insect herbivory have mostly included a survey of the associated herbivore fauna, the assessment of predator abundance and diversity has long been neglected, especially in forest habitats (but see Vehviläinen *et al.* 2008).

Major hypotheses and chapter outline

The general scope of this thesis was to analyse the effects of canopy tree diversity on insect diversity, community structure, and herbivory patterns across various spatiotemporal scales.

In particular, we examined the following major hypotheses and questions:

Hypothesis 1: Insect species richness increases with increased canopy tree diversity.

- How does alpha, beta, and gamma diversity of insect communities change across spatiotemporal scales? (Chapter 2 & 3)
- How is species richness in functional groups and feeding guilds distributed across the tree diversity gradient? (Chapter 2, 3 & 4)
- How are trophic interactions within insect communities mediated by tree diversity? (Chapter 4)

Hypothesis 2: Herbivory decreases with increased canopy tree diversity.

- How does tree diversity impact insect herbivory on tree saplings in the forest understory (leaf area loss, galls, mines)? (Chapter 5)
- How is the abundance of predators and herbivores related to tree diversity and damage patterns? (Chapter 5)

Declaration of the author's own contribution to manuscripts with multiple authors

The chapters 2 to 5 are a series of manuscripts submitted to peer-reviewed journals. Stephanie Sobek is the overall author of all manuscripts presented in this thesis. She has personally developed the main ideas presented in the manuscripts, personally written all manuscripts, collected and analysed the data for all manuscripts, created tables, figures, and appendices, and contributed significantly to the sampling design. She is also responsible for correspondence with editors and reviewers.

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CHAPTER

2

Spatiotemporal changes of beetle communities across a tree diversity gradient

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Abstract

Plant and arthropod diversity are often related, but data on the role of mature tree diversity on canopy insect communities are only fragmentary. Here 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. We used flight interception traps to assess the beetle fauna of various tree species, and applied additive partitioning to examine spatiotemporal patterns of diversity. 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, 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. 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 fully conserve 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 turnover contributes more to beetle diversity than spatial turnover among different tree species or individuals.

Key words: 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 & Christ 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 emphasised 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 positively affect arthropod species richness (Vehviläinen *et al.* 2008). As a measure of host specificity in insects, May (1990) introduced the term “effective specialisation”. Effective specialisation *sensu* May (1990) is defined as the weighted quantity of an insect assemblage specialised to a certain host tree species. However, effective specialisation of beetles has been demonstrated to strongly depend 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 utilised 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 interrelation 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. Because no studies up to date exist that focus 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 characterised by low plant diversity (Ellenberg 1996, Mölder *et al.* 2008). They also appear generally homogenous (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 specialisation 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 β_{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 & field sites

Trees were sampled in Germany's largest coherent semi-natural broadleaved forest, the Hainich National Park, Thuringia. Established in 1997, 7,600 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 (MeteoMedia 2005). 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 x 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 2.1).

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 x 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 (6 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 x 50 m plots or in a 10 m wide corridor in the directly adjacent forest. Clearance of traps was accomplished every four weeks over a period of six 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 specialisation, feeding guild) was annotated based on details outlined in Böhme (2004) (Appendix 2.2), 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 non-parametric 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 2.1), 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 2.3). To test for linear relationships between tree diversity and the response variables (γ -diversity, α , β_{time} , β_{space} , factor levels of rarity, habitat specialisation, feeding guild) we used multiple regressions with type I sum of squares with beetle abundance and tree diversity (Shannon index) as explanatory variables. Count data were \log_{10} -transformed. Beetle 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 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 abundance to the actually observed number of species. Rarefaction has recently been criticised 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 abundance and tree diversity only. Beetle 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 2.2). 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 abundance ($F_{1,9} = 46.44$, $p < 0.001$, Fig. 2.1). 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.

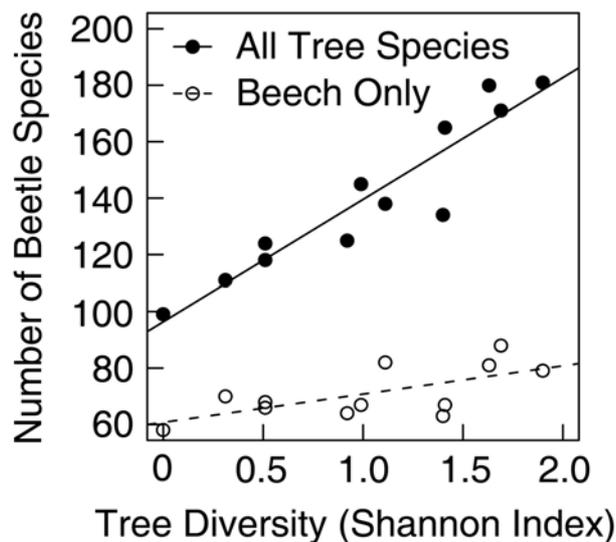


Fig. 2.1. Observed species richness (γ -diversity) of beetles across a tree diversity gradient in a Central European forest.

Table 2.1. Multiple regression analyses of species richness parameters for canopy beetles of various tree species across a tree diversity gradient in the Hainich National Park. Abundance= beetle abundance, Shannon Index = tree diversity of the sampled forest stands. [†] Temporal and spatial species turnover were not linked to turnover in beetle abundance, hence this variable was omitted from the model.

Response Variable	Effect	Model A: Abundance + Shannon Index			Model B: Shannon Index + Abundance		
		Multiple r2	F	p	Multiple r2	F	p
Observed Species Richness	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	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	Abundance [†]						
	Shannon Index	0.77	32.76	<0.001			
β_{space} -Diversity	Abundance [†]						
	Shannon Index	0.89	79.33	<0.001			

Table 2.2. Multiple regression analyses of species richness parameters for canopy beetles of beech trees across a tree diversity gradient in the Hainich National Park. Abundance= beetle abundance, Shannon Index = tree diversity of the sampled forest stands. † Temporal and spatial species turnover was not linked to turnover in beetle abundance, hence this variable was omitted from the model

Response Variable	Effect	Abundance + Shannon Index		
		Multiple r2	<i>F</i>	p
Observed Species Richness	Abundance		21.04	0.001
	Shannon Index	0.75	6.53	0.031
α -Diversity	Abundance [†]		16.66	0.003
	Shannon Index	0.65	0.02	0.9
β_{time} -Diversity	Abundance [†]			
	Shannon Index	0.11	1.19	0.3
β_{space} -Diversity	Abundance			
	Shannon Index	0.52	10.75	0.008

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: $F_{1,9} = 61.32$, $p < 0.001$, Abundance: $F_{1,9} = 90.32$, $p < 0.001$, Fig. 2.2a). Temporal turnover β_{time} also increased with increasing tree diversity ($F_{1,9} = 32.76$, $p < 0.001$, Table 2.1). 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 2.1). In contrast, temporal turnover β_{time} was higher if beech alone was analysed (Fig 2.2b), 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 2.2).

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 2.4), only relative spatial turnover on beech alone showed a slightly increasing linear relationship ($F_{1,9} = 5.17$, $p = 0.049$)

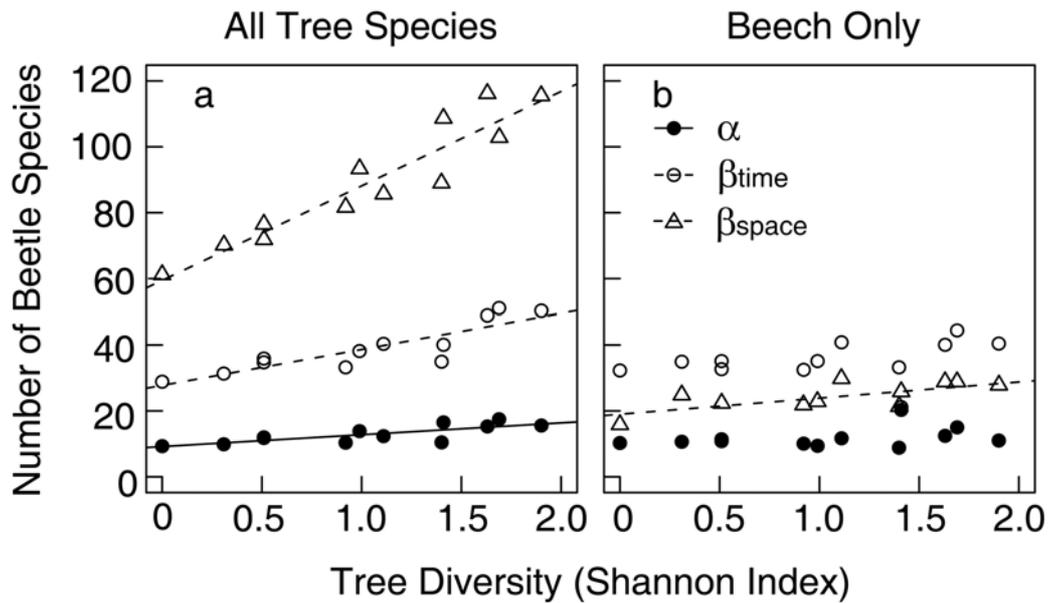


Fig. 2.2. α -, β_{time} - and β_{space} -diversity of beetle communities across a tree diversity gradient based on observed species richness per plot. a) All tree species sampled, regression slopes differ significantly (ANCOVA, $F_{2,30} = 33.71$, $p < 0.001$, b) beech only.

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 2.2). Both groups also constituted the majority of individuals (7,106 generalist individuals, 68.6 %; 2,405 forest individuals, 23.3 %). Less than 1 % of the species were identified as tourists specialised 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. 2.3a), the linear relationship of forest species to tree diversity was highly significant ($F_{1,9} = 41.67$, $p < 0.001$, Table 2.3). The number of forest species also increased linearly if beech alone was compared ($F_{1,9} = 7.84$, $p = 0.021$, Fig. 2.3b) while habitat generalists showed no significant response ($F_{1,9} = 4.77$, $p = 0.057$, Table 2.4).

Table 2.3. 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. Abundance= beetle abundance, Shannon Index = tree diversity of the sampled forest stands.

Response Variable		Model A: Abundance + Shannon Index			Model B: Shannon Index + Abundance			
		Effect	Multiple r2	F	p	Multiple r2	F	p
Habitat Generalists	Abundance		141.05			18.39		0.002
	Shannon Index	0.94	9.09	0.015	0.94	131.75		<0.001
Forest Species	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	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	Abundance		24.37	<0.001		15.07		0.004
	Shannon Index	0.91	61.62	<0.001	0.91	70.93		<0.001
Predators	Abundance		81.77	<0.001		6.1		0.036
	Shannon Index	0.91	6.51	0.031	0.91	82.18		<0.001
Herbivores	Abundance		0.62	0.452		1.27		0.288
	Shannon Index	0.76	28.47	<0.001	0.76	27.81		<0.001
Fungivores	Abundance		58.35	<0.001		13.12		0.006
	Shannon Index	0.88	7.55	0.023	0.88	52.77		<0.001

Based on the classification in Böhme (2004), the majority of species and individuals was denoted as common or only regionally rare (9,093 individuals, 87.8 %; 310 species, 73.5 %, Appendix 2.2), 76 species (18 %) as rare or very rare (1,043 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. 2.3c), and the response of rare species was highly significant ($F_{1,9} = 61.62$, $p < 0.001$, Table 2.3). A similar pattern was found for species on beech alone (Fig. 2.3d, common: $F_{1,9} = 7.66$, $p = 0.022$; rare: $F_{1,9} = 9.65$, $p = 0.013$).

Table 2.4. Multiple regression analyses of functional guild parameters for canopy beetles captured on beech trees across a tree diversity gradient in the Hainich National Park. Abundance= beetle abundance, Shannon Index = tree diversity of the sampled forest stands.

Response Variable	Effect	Abundance + Shannon Index		
		Multiple r2	F	p
Habitat Generalists	Abundance	0.77	25.96	<0.001
	Shannon Index		4.77	0.057
Forest Species	Abundance	0.61	6.33	0.033
	Shannon Index		7.84	0.021
Common Species	Abundance	0.71	14.5	0.004
	Shannon Index		7.66	0.022
Rare Species	Abundance	0.77	19.89	0.002
	Shannon Index		9.65	0.013
Predators	Abundance	0.72	12.96	0.006
	Shannon Index		9.78	0.012
Herbivores	Abundance	0.5	0.35	0.57
	Shannon Index		8.52	0.017
Fungivores	Abundance	0.45	4.41	0.065
	Shannon Index		2.99	0.117

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 2.2). Other feeding guilds each did not include more than 5 % of the observed species. In terms of abundance, herbivorous species were most common (3,194 individuals, 30.8 %), whereas one quarter of all individuals was fungivorous (2,782 individuals, 26.9 %) and one quarter predatory (2,588 individuals, 25 %). Among the herbivorous beetles, 48 species (40.3 %) were identified as wood feeders (1066 individuals, 38.3 %).

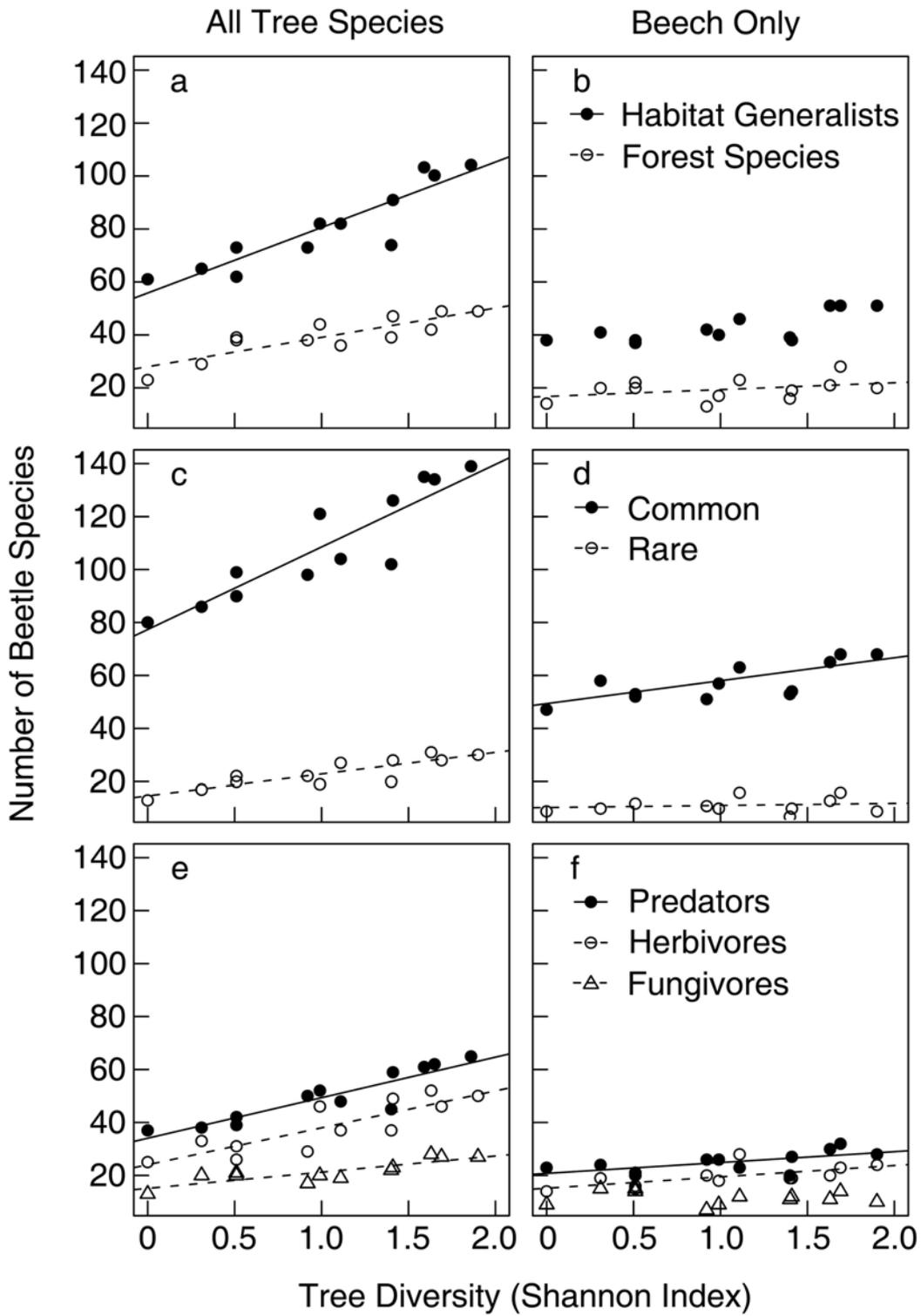


Fig. 2.3. Species richness of functional groups of beetles across a tree diversity gradient on various tree species. a & b) habitat specialisation, c & d) rarity, e & f) feeding guilds (a, c, e all tree species sampled, b, d, f beech only).

All three guilds showed a positive linear relationship to increased tree diversity (Fig. 2.3 e), with a highly significant response for herbivore species richness ($F_{1,9} = 58.35$, $p < 0.001$, Table 2.3), which were not influenced by differences in herbivore 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 2.5), 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 γ -diversity of beetles increased across the tree diversity gradient. α -diversity was mainly influenced by differences in 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 understory (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 (Lawton 1983, Southwood *et al.* 1982, Halaj *et al.* 1998, Halaj *et al.* 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 (I. Schmidt, pers. com.) as well as productivity (Jacob *et al.*, submitted) 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 also common and

generalist species preferred the more heterogenous 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 also 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 pairwise comparisons of i. e. managed/unmanaged stands, which currently dominate the available literature.

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Appendix 2.1

Tree diversity 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.

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

Appendix 2.2

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

Carabidae	<i>Agonum muelleri</i>	no preference	predator	common	2	1	
	<i>Amara communis</i>	other	other	common	1	1	
	<i>Amara familiaris</i>	no preference	other	common	3	2	
	<i>Amara lunicollis</i>	no preference	other	common	1	0	
	<i>Amara montivaga</i>	unknown	other	common	2	2	
	<i>Amara plebeja</i>	unknown	other	common	1	0	
	<i>Amara similata</i>	unknown	herbivore	common	5	2	
	<i>Bembidion quadrimaculatum</i>	unknown	predator	common	1	1	
	<i>Bradycellus verbasci</i>	unknown	other	common	1	0	
	<i>Calodromius spilotus</i>	forest	predator	common	1	0	
	<i>Calosoma inquisitor</i>	forest	predator	common	1	1	
	<i>Dromius agilis</i>	forest	predator	common	8	1	
	<i>Dromius fenestratus</i>	forest	predator	common	1	0	
	<i>Dromius quadrimaculatus</i>	forest	predator	common	168	46	
	<i>Dromius</i> sp.	unknown	predator	unknown	1	1	
	<i>Harpalus affinis</i>	no preference	other	common	1	1	
	<i>Limodromus assimilis</i>	no preference	predator	common	1	0	
	<i>Loricera pilicornis</i>	no preference	predator	common	8	3	
	<i>Microlestes minutulus</i>	unknown	predator	common	1	0	
	<i>Notiophilus biguttatus</i>	no preference	predator	common	3	0	
	<i>Platynus dorsalis</i>	unknown	unknown	unknown	1	0	
	<i>Pterostichus oblongopunctatus</i>	forest	predator	common	1	1	
	<i>Trechus quadristriatus</i>	no preference	predator	common	53	17	
	Cerambycidae	<i>Alosterna tabacicolor</i>	forest	herbivore	common	11	2
		<i>Anaglyptus mysticus</i>	forest	herbivore	rare	0	1
		<i>Grammoptera abdominalis</i>	forest	herbivore	rare	1	0
<i>Grammoptera ruficornis</i>		forest	herbivore	common	5	1	
<i>Leiopus nebulosus</i>		no preference	herbivore	common	17	1	
<i>Mesosa nebulosa</i>		no preference	herbivore	common	1	0	
<i>Oberea linearis</i>		no preference	herbivore	rare	0	1	
<i>Phymatodes testaceus</i>		no preference	herbivore	common	1	0	
<i>Pogonocherus hispidus</i>		no preference	herbivore	common	2	0	
<i>Rhagium mordax</i>		forest	herbivore	common	7	3	
<i>Saperda scalaris</i>		no preference	herbivore	common	1	0	
<i>Stenocorus meridianus</i>		no preference	herbivore	common	1	0	
<i>Stenostola dubia</i>		no preference	herbivore	common	15	2	
<i>Tetropium castaneum</i>		forest	herbivore	common	1	0	
<i>Tetrops starkii</i>		forest	herbivore	rare	9	0	
Cerylonidae		<i>Cerylon ferrugineum</i>	forest	other	common	28	8
	<i>Cerylon histerooides</i>	no preference	other	common	1	1	
Cholevidae	<i>Nargus velox</i>	forest	other	common	1	1	
	<i>Sciodrepoides watsoni</i>	no preference	other	common	4	0	
Chrysomelidae	<i>Aphthona euphorbiae</i>	unknown	herbivore	rare	54	9	
	<i>Aphthona venustula</i>	no preference	herbivore	common	1	0	
	<i>Chaetocnema concinna</i>	no preference	herbivore	common	0	1	
	<i>Cryptocephalus frontalis</i>	unknown	herbivore	rare	2	0	
	<i>Galeruca pomonae</i>	no preference	herbivore	common	1	0	
	<i>Galeruca tanacetii</i>	no preference	herbivore	common	2	1	
	<i>Longitarsus kutscherae</i>	no preference	herbivore	rare	2	1	
	<i>Longitarsus luridus</i>	no preference	herbivore	common	8	2	
	<i>Longitarsus parvulus</i>	no preference	herbivore	common	17	4	

	<i>Orsodacne cerasi</i>	no preference	herbivore	common	46	4
	<i>Oulema gallaeciana</i>	other	herbivore	common	254	85
	<i>Oulema melanopus</i>	no preference	herbivore	common	14	7
	<i>Phyllotreta atra</i>	no preference	herbivore	common	6	1
	<i>Phyllotreta nigripes</i>	no preference	herbivore	common	5	1
	<i>Phyllotreta vittula</i>	no preference	herbivore	common	6	6
Cisidae	<i>Cis bidentatus</i>	forest	fungivore	rare	1	0
	<i>Cis boleti</i>	no preference	fungivore	common	1	0
	<i>Ennearthron cornutum</i>	no preference	fungivore	common	3	0
	<i>Orthocis alni</i>	no preference	fungivore	common	6	1
Clambidae	<i>Clambus sp.</i>	unknown	fungivore	unknown	2	0
Cleridae	<i>Opilo mollis</i>	forest	predator	common	25	8
	<i>Tillus elongatus</i>	no preference	predator	common	1	0
Coccinellidae	<i>Adalia decempunctata</i>	no preference	predator	common	17	2
	<i>Calvia decemguttata</i>	no preference	predator	rare	1	1
	<i>Chilocorus renipustulatus</i>	no preference	predator	common	5	0
	<i>Coccinella septempunctata</i>	no preference	predator	common	5	1
	<i>Exochomus quadripustulatus</i>	no preference	predator	common	17	2
	<i>Halyzia sedecimguttata</i>	forest	fungivore	common	9	2
	<i>Propylea quatuordecimpunctata</i>	no preference	predator	common	11	1
	<i>Scymnus abietis</i>	no preference	predator	common	3	1
Colydiidae	<i>Synchita humeralis</i>	forest	fungivore	common	2	0
Corylophidae	<i>Orthoperus sp.</i>	forest	predator	unknown	3	0
	<i>Sacium pusillum</i>	no preference	predator	rare	13	2
	<i>Sericoderus lateralis</i>	other	predator	common	1	0
Cryptophagidae	<i>Atomaria analis</i>	no preference	other	common	43	7
	<i>Atomaria atricapilla</i>	no preference	other	common	267	82
	<i>Atomaria fuscata</i>	no preference	other	common	6	4
	<i>Atomaria lewisi</i>	no preference	other	common	2	0
	<i>Atomaria linearis</i>	no preference	other	common	124	43
	<i>Atomaria nigrirostris</i>	no preference	other	common	2	1
	<i>Atomaria puncticollis</i>	no preference	other	rare	1	1
	<i>Atomaria punctithorax</i>	no preference	other	rare	7	2
	<i>Atomaria pusilla</i>	no preference	other	common	1	0
	<i>Atomaria sp.</i>	unknown	other	unknown	9	4
	<i>Atomaria testacea</i>	no preference	other	common	13	6
	<i>Cryptophagus acutangulus</i>	no preference	other	common	1	0
	<i>Cryptophagus dentatus</i>	no preference	other	common	37	6
	<i>Cryptophagus intermedius</i>	unknown	other	rare	2	1
	<i>Cryptophagus pilosus</i>	no preference	other	common	23	6
	<i>Cryptophagus pubescens</i>	no preference	other	common	3	2
	<i>Cryptophagus scanicus</i>	no preference	other	common	8	1
	<i>Cryptophagus sp.</i>	unknown	other	unknown	1	0
	<i>Micrambe abietis</i>	forest	fungivore	common	2	0
Cucujidae	<i>Phloeostichus denticollis</i>	unknown	unknown	rare	8	0
Curculionidae	<i>Ceutorhynchus floralis</i>	no preference	herbivore	common	1	0
	<i>C.pallidactylus</i>	no preference	herbivore	common	8	6
	<i>Curculio glandium</i>	no preference	herbivore	common	11	1
	<i>Curculio pellitus</i>	other	herbivore	rare	1	0
	<i>Curculio pyrrhoceras</i>	other	herbivore	common	2	0
	<i>Curculio villosus</i>	other	herbivore	common	1	0

	<i>Furcipes rectirostris</i>	no preference	herbivore	common	2	3
	<i>Hypera venusta</i>	other	herbivore	common	2	0
	<i>Larinus planus</i>	unknown	unknown	unknown	1	1
	<i>Magdalis armigera</i>	forest	herbivore	common	1	0
	<i>Magdalis flavicornis</i>	no preference	herbivore	common	1	0
	<i>Phyllobius argentatus</i>	no preference	herbivore	common	31	14
	<i>Phyllobius calcaratus</i>	no preference	herbivore	common	1	0
	<i>Phyllobius maculicornis</i>	no preference	herbivore	common	1	0
	<i>Polydrusus mollis</i>	no preference	herbivore	common	4	2
	<i>Polydrusus pterygomalis</i>	no preference	herbivore	common	34	10
	<i>Polydrusus sericeus</i>	no preference	herbivore	common	17	2
	<i>Polydrusus undatus</i>	no preference	herbivore	common	28	9
	<i>Rhynchaenus fagi</i>	forest	herbivore	common	198	72
	<i>Sitona hispidulus</i>	no preference	herbivore	common	2	1
	<i>Sitona humeralis</i>	no preference	herbivore	common	1	1
	<i>Sitona lineatus</i>	no preference	herbivore	common	14	5
	<i>Sitona macularius</i>	no preference	herbivore	common	1	0
	<i>Sitona</i> sp.	unknown	herbivore	unknown	1	0
	<i>Stereonychus fraxini</i>	forest	herbivore	common	5	1
	<i>Strophosoma capitatum</i>	no preference	herbivore	common	1	0
	<i>S.melanogrammum</i>	no preference	herbivore	common	1	0
	<i>Tychius picirostris</i>	no preference	herbivore	common	0	1
Cybocephalidae	<i>Cybocephalus politus</i>	no preference	predator	rare	1	0
Dasytidae	<i>Aplocnemus nigricornis</i>	forest	predator	common	1	1
	<i>Dasytes aeratus</i>	no preference	predator	common	9	3
	<i>Dasytes cyaneus</i>	forest	predator	common	6	2
	<i>Dasytes niger</i>	no preference	predator	common	1	0
	<i>Dasytes plumbeus</i>	no preference	predator	common	69	17
	<i>Trichoceble memnonia</i>	forest	predator	rare	1	0
Dermestidae	<i>Attagenus pelli</i>	no preference	omni	common	1	0
	<i>Ctesias serra</i>	no preference	other	rare	3	1
	<i>Megatoma undata</i>	no preference	other	rare	15	4
Dytiscidae	<i>Agabus</i> sp.	unknown	predator	unknown	1	0
	<i>Graptodytes granularis</i>	no preference	other	common	1	0
	<i>Rhantus bistratus</i>	no preference	predator	rare	1	0
Elateridae	<i>Agriotes acuminatus</i>	no preference	herbivore	common	30	2
	<i>Agriotes gallicus</i>	unknown	herbivore	rare	1	1
	<i>Agriotes pallidulus</i>	no preference	herbivore	common	7	0
	<i>Agrypnus murina</i>	no preference	predator	common	2	0
	<i>Ampedus pomorum</i>	forest	herbivore	common	10	1
	<i>Athous bicolor</i>	no preference	herbivore	rare	2	1
	<i>Athous haemorrhoidalis</i>	no preference	herbivore	common	40	8
	<i>Athous subfuscus</i>	no preference	herbivore	rare	133	30
	<i>Athous vittatus</i>	no preference	herbivore	common	539	118
	<i>Calambus bipustulatus</i>	no preference	other	rare	8	1
	<i>Dalopius marginatus</i>	forest	other	common	44	11
	<i>Denticollis linearis</i>	no preference	other	common	10	3
	<i>Denticollis rubens</i>	forest	other	rare	6	2
	<i>Hemicrepidius hirtus</i>	no preference	herbivore	common	2	1
	<i>Hemicrepidius niger</i>	no preference	herbivore	common	1	0
	<i>Hypoganus inunctus</i>	forest	herbivore	rare	7	4

	<i>Kibunea minutus</i>	no preference	herbivore	common	1	0
	<i>Melanotus rufipes</i>	no preference	other	common	4	3
Erotylidae	<i>Dacne bipustulata</i>	no preference	fungivore	common	55	15
	<i>Triplax russica</i>	no preference	fungivore	common	2	0
	<i>Tritoma bipustulata</i>	unknown	fungivore	common	3	1
Eucnemidae	<i>Dirhagus lepidus</i>	forest	other	rare	2	0
	<i>Eucnemis capucina</i>	forest	other	rare	4	0
	<i>Hylis foveicollis</i>	forest	other	rare	2	0
	<i>Melasis buprestoides</i>	no preference	other	common	1	0
Helodidae	<i>Cyphon</i> sp.	unknown	herbivore	unknown	6	2
	<i>Cyphon variabilis</i>	unknown	herbivore	common	4	1
	<i>Prionocyphon serricornis</i>	no preference	other	common	10	2
Histeridae	<i>Carcinops pumilio</i>	no preference	other	common	1	0
	<i>Gnathoncus buyssoni</i>	no preference	other	rare	1	0
	<i>Plegaderus caesus</i>	forest	predator	common	1	0
Hydrophilidae	<i>Helophorus nubilus</i>	no preference	herbivore	common	1	0
Latridiidae	<i>Cartodere constricta</i>	no preference	fungivore	common	2	0
	<i>Cartodere nodifer</i>	no preference	fungivore	common	5	0
	<i>Corticaria abietorum</i>	forest	fungivore	rare	10	3
	<i>Corticaria elongata</i>	no preference	fungivore	common	4	0
	<i>Corticaria polypori</i>	forest	fungivore	rare	4	0
	<i>Corticaria umbilicata</i>	no preference	fungivore	common	2	2
	<i>Corticarina fuscula</i>	no preference	fungivore	common	6	2
	<i>Corticarina simulata</i>	no preference	fungivore	common	99	37
	<i>Corticinara gibbosa</i>	no preference	fungivore	common	2030	611
	<i>Enicmus atriceps</i>	forest	fungivore	rare	68	27
	<i>Enicmus fungicola</i>	forest	fungivore	common	1	0
	<i>Enicmus geminatus</i>	unknown	fungivore	rare	2	0
	<i>Enicmus histrio</i>	unknown	fungivore	common	5	2
	<i>Enicmus rugosus</i>	forest	fungivore	common	167	37
	<i>Enicmus transversus</i>	no preference	fungivore	common	35	13
	<i>Latridius hirtus</i>	unknown	fungivore	rare	63	23
	<i>Latridius minutus</i>	no preference	fungivore	common	2	0
	<i>Stephostethus alternans</i>	forest	fungivore	rare	4	1
Leiodidae	<i>Agathidium nigripenne</i>	forest	fungivore	common	57	10
	<i>Agathidium varians</i>	no preference	fungivore	common	59	6
	<i>Anisotoma humeralis</i>	forest	fungivore	common	3	0
Lucanidae	<i>Platycerus caraboides</i>	forest	herbivore	common	12	4
Malachiidae	<i>Charopus flavipes</i>	no preference	predator	common	1	0
	<i>Malachius bipustulatus</i>	no preference	predator	common	4	0
Melandryidae	<i>Anisoxya fuscula</i>	forest	other	rare	10	7
	<i>Orchesia fasciata</i>	no preference	fungivore	rare	1	0
	<i>Orchesia micans</i>	forest	fungivore	common	1	1
	<i>Orchesia minor</i>	forest	fungivore	common	19	4
	<i>Orchesia undulata</i>	forest	fungivore	common	5	1
	<i>Phloiotrya rufipes</i>	forest	other	rare	2	1
Monotomidae	<i>Monotoma longicollis</i>	no preference	unknown	common	1	1
	<i>Rhizophagus bipustulatus</i>	no preference	predator	common	85	23
	<i>Rhizophagus parvulus</i>	forest	predator	common	1	1
Mordellidae	<i>Mordellistena humeralis</i>	unknown	other	common	2	1
	<i>Mordellistena neuwaldeggiana</i>	no preference	other	common	40	12

	<i>Mordellistena variegata</i>	unknown	other	common	21	4
	<i>Mordellochroa abdominalis</i>	no preference	other	common	28	2
Mycetophagidae	<i>Litargus connexus</i>	no preference	fungivore	common	80	21
	<i>Mycetophagus atomarius</i>	no preference	fungivore	common	1	0
	<i>Mycetophagus populi</i>	unknown	fungivore	common	8	6
	<i>Mycetophagus quadripustulatus</i>	unknown	fungivore	common	1	0
Nitidulidae	<i>Cryptarcha strigata</i>	forest	other	common	13	1
	<i>Cryptarcha undata</i>	forest	other	common	120	37
	<i>Eपुरaea marseuli</i>	forest	other	common	4	0
	<i>Eपुरaea melanocephala</i>	no preference	other	common	426	79
	<i>Eपुरaea unicolor</i>	no preference	other	common	2	0
	<i>Glischrochilus hortensis</i>	no preference	other	common	2	0
	<i>Meligethes aeneus</i>	no preference	herbivore	common	9	6
	<i>Meligethes nigrescens</i>	no preference	herbivore	common	1	0
	Nitidulidae sp.1	unknown	unknown	unknown	1	0
	<i>Soronia grisea</i>	no preference	other	common	127	32
Oedemeridae	<i>Ischnomera coerulea</i>	forest	herbivore	rare	3	2
	<i>Ischnomera cyanea</i>	forest	herbivore	common	1	0
	<i>Ischnomera sanguinicollis</i>	forest	herbivore	rare	1	0
Phalacridae	<i>Stilbus testaceus</i>	other	herbivore	common	0	1
Phloiophilidae	<i>Phloiophilus edwardsii</i>	forest	predator	rare	1	0
Pselaphidae	<i>Bibloporus bicolor</i>	forest	predator	rare	26	6
	<i>Bibloporus minutus</i>	forest	predator	rare	49	11
	<i>Bibloporus sp.</i>	forest	predator	rare	2	0
	<i>Trimium brevicorne</i>	forest	predator	common	8	2
	<i>Tychus niger</i>	unknown	predator	common	1	0
Ptiliidae	<i>Acrotrichis sp.</i>	unknown	fungivore	unknown	6	1
Ptinidae	<i>Ptinus rufipes</i>	forest	other	common	1	1
Pyrochroidae	<i>Pyrochroa coccinea</i>	forest	other	common	1	1
	<i>Schizotus pectinicornis</i>	forest	other	common	9	2
Rhynchitidae	<i>Byctisus betulae</i>	no preference	herbivore	common	0	1
	<i>Caenorhinus pauxillus</i>	no preference	herbivore	common	1	0
	<i>Deporaus betulae</i>	no preference	herbivore	common	3	0
	<i>Deporaus tristis</i>	forest	herbivore	rare	2	0
	<i>Lasiorrhynchites olivaceus</i>	no preference	herbivore	common	2	0
Salpingidae	<i>Lissodema cursor</i>	forest	predator	rare	12	2
	<i>Rabocerus gabrieli</i>	unknown	predator	rare	14	5
	<i>Salpingus planirostris</i>	no preference	predator	common	49	14
	<i>Salpingus ruficollis</i>	forest	predator	common	43	16
Scarabaeidae	<i>Aphodius fimetarius</i>	no preference	other	common	1	1
	<i>Aphodius granarius</i>	no preference	other	common	2	0
	<i>Aphodius prodromus</i>	no preference	other	common	2	0
	<i>Gnorimus nobilis</i>	no preference	herbivore	common	3	1
Scolytidae	<i>Cryphalus abietis</i>	forest	herbivore	common	1	0
	<i>Cryphalus sp.</i>	forest	herbivore	unknown	1	0
	<i>Crypturgus cinereus</i>	forest	herbivore	common	3	0
	<i>Dryocoetes autographus</i>	forest	herbivore	common	5	1
	<i>Ernoporicus caucasicus</i>	forest	herbivore	rare	2	1
	<i>Ernoporicus fagi</i>	forest	herbivore	common	330	131
	<i>Ernoporus tiliae</i>	forest	herbivore	common	2	1
	<i>Hylastes cunicularius</i>	forest	herbivore	common	1	0

	<i>Hylesinus crenatus</i>	forest	herbivore	common	4	1
	<i>Hylesinus oleiperda</i>	forest	herbivore	rare	2	0
	<i>Hylurgops palliatus</i>	forest	herbivore	common	1	0
	<i>Ips cembrae</i>	forest	herbivore	common	1	0
	<i>Ips typographus</i>	forest	herbivore	common	2	0
	<i>Leperisinus fraxini</i>	forest	herbivore	common	30	2
	<i>Pityogenes chalcographus</i>	forest	herbivore	common	57	12
	<i>Polygraphus grandiclava</i>	no preference	herbivore	common	0	1
	<i>Polygraphus poligraphus</i>	forest	herbivore	common	34	26
	<i>Scolytus carpini</i>	forest	herbivore	common	30	7
	<i>Scolytus intricatus</i>	forest	herbivore	common	7	8
	<i>Taphrorychus bicolor</i>	forest	herbivore	common	201	66
	<i>Xyleborus peregrinus</i>	forest	fungivore	rare	270	78
	<i>Xyleborus saxeseni</i>	no preference	fungivore	common	25	6
	<i>Xyleborus</i> sp.	unknown	fungivore	unknown	7	0
Scraptiidae	<i>Anaspis flava</i>	no preference	other	common	14	3
	<i>Anaspis frontalis</i>	no preference	other	common	16	1
	<i>Anaspis melanostoma</i>	no preference	other	rare	10	4
	<i>Anaspis rufilabris</i>	no preference	other	common	64	17
	<i>Anaspis thoracica</i>	no preference	other	common	63	13
Scydmaenidae	<i>Neuraphes elongatulus</i>	no preference	predator	common	3	1
	<i>Stenichnus bicolor</i>	forest	predator	rare	1	0
	<i>Stenichnus scutellaris</i>	forest	predator	common	1	1
Silvanidae	<i>Silvanus unidentatus</i>	forest	predator	common	1	0
	<i>Uleiota planata</i>	no preference	predator	common	3	1
Sphindidae	<i>Arpidiphorus orbiculatus</i>	no preference	fungivore	common	1	0
Staphylinidae	<i>Acrotona</i> sp.	unknown	predator	unknown	4	1
	<i>Aleochara bipustulata</i>	no preference	predator	common	4	1
	<i>Aleochara sparsa</i>	no preference	predator	common	28	5
	<i>Aleochara laevigata</i>	no preference	predator	rare	1	0
	<i>Aleochara sanguinea</i>	no preference	predator	common	1	0
	<i>Aleochara</i> sp.	unknown	predator	unknown	3	1
	<i>Aloconota gregaria</i>	no preference	predator	common	10	2
	<i>Amarochara bonnairei</i>	no preference	predator	rare	3	0
	<i>Amischa analis</i>	no preference	predator	common	3	0
	<i>Amischa decipiens</i>	no preference	predator	common	3	0
	<i>Amischa</i> sp.	no preference	predator	unknown	53	13
	<i>Anomognathus cuspidatus</i>	forest	predator	common	3	1
	<i>Anotylus inustus</i>	no preference	other	common	5	1
	<i>Anotylus rugosus</i>	no preference	other	common	1	0
	<i>Anotylus sculpturatus</i>	no preference	other	common	4	3
	<i>Anotylus tetracarinated</i>	no preference	other	common	19	6
	<i>Anthobium atrocephalum</i>	no preference	other	common	3	0
	<i>Anthophagus angusticollis</i>	unknown	predator	common	5	2
	<i>Atheta amplicollis</i>	unknown	predator	common	2	2
	<i>Atheta fungi</i>	no preference	predator	common	381	116
	<i>Atheta inquinula</i>	no preference	predator	common	4	2
	<i>Atheta nigra</i>	no preference	predator	common	0	1
	<i>Atheta palustris</i>	unknown	predator	common	1	1
	<i>Atheta</i> sp.	unknown	predator	unknown	74	28
	<i>Atheta</i> sp.1	unknown	predator	unknown	1	1

<i>Atheta sp.2</i>	unknown	predator	unknown	1	1
<i>Atheta triangulum</i>	no preference	predator	common	1	1
<i>Bolitobius castaneus</i>	no preference	predator	rare	1	0
<i>Bolitobius sp.</i>	no preference	predator	rare	1	0
<i>Bythinus burrelli</i>	no preference	predator	common	2	0
<i>Callicerus obscurus</i>	no preference	predator	common	1	1
<i>Carpelimus corticinus</i>	unknown	other	common	1	0
<i>Cypha longicornis</i>	no preference	predator	common	3	1
<i>Cypha curtula</i>	forest	predator	rare	19	1
<i>Euplectus karsteni</i>	no preference	predator	common	4	0
<i>Euplectus punctatus</i>	forest	predator	rare	3	1
<i>Euryusa optabilis</i>	forest	predator	common	2	1
<i>Eusphalerum luteum</i>	no preference	herbivore	common	65	14
<i>Eusphalerum minutum</i>	unknown	herbivore	common	6	4
<i>E.pseudaucupariae</i>	unknown	herbivore	rare	40	10
<i>Eusphalerum sp.</i>	unknown	herbivore	unknown	1	0
<i>Geostiba circellaris</i>	no preference	predator	common	3	0
<i>Haploglossa picipennis</i>	forest	predator	rare	1	0
<i>Haploglossa villosula</i>	no preference	predator	common	50	15
<i>Heterothops niger</i>	no preference	predator	common	1	0
<i>Holobus flavicornis</i>	no preference	predator	common	26	6
<i>Hypnogyra glabra</i>	no preference	predator	common	1	0
<i>Ischnoglossa sp.</i>	unknown	predator	rare	4	2
<i>Ischnosoma splendidum</i>	no preference	predator	common	4	1
<i>Lathrobium elongatum</i>	no preference	predator	common	3	0
<i>Leptacinus sp.</i>	unknown	predator	unknown	1	0
<i>Leptusa fumida</i>	forest	predator	common	10	2
<i>Leptusa ruficollis</i>	forest	predator	common	7	6
<i>Lesteva longoelytrata</i>	unknown	predator	common	4	2
<i>Liogluta nitidula</i>	no preference	predator	common	1	0
<i>Liogluta sp.</i>	unknown	predator	unknown	8	2
<i>Meotica sp.</i>	unknown	predator	rare	1	1
<i>Metopsia clypeata</i>	no preference	fungivore	rare	6	2
<i>Mycetoporus solidicornis</i>	no preference	predator	rare	1	0
<i>Ocalea sp.</i>	unknown	predator	unknown	1	0
<i>Oligota pusilima</i>	no preference	predator	unknown	0	1
<i>Oligota sp.</i>	unknown	predator	unknown	10	5
<i>Omalius caesum</i>	no preference	other	common	3	0
<i>Omalius rivulare</i>	no preference	other	common	1	0
<i>Oxypoda brevicornis</i>	no preference	predator	common	1	0
<i>Oxypoda sp.</i>	unknown	predator	unknown	2	1
<i>Philonthus carbonarius</i>	no preference	predator	common	16	7
<i>Philonthus cognatus</i>	no preference	predator	common	23	10
<i>Philonthus coracinus</i>	unknown	unknown	unknown	4	1
<i>Philonthus decorus</i>	forest	predator	common	1	0
<i>Philonthus rotundicollis</i>	no preference	predator	common	8	6
<i>Philonthus sp.</i>	unknown	predator	unknown	1	0
<i>Phloeopora corticalis</i>	no preference	predator	common	496	135
<i>Phloeopora testacea</i>	forest	predator	common	8	1
<i>Phyllodrepa floralis</i>	no preference	predator	common	1	1
<i>Phyllodrepa ioptera</i>	no preference	predator	common	15	5

	<i>Placusa atrata</i>	forest	predator	common	1	1
	<i>Placusa depressa</i>	forest	predator	common	2	0
	<i>Plataraea brunnea</i>	no preference	predator	common	7	2
	<i>Platystethus nitens</i>	no preference	other	common	7	1
	<i>Quedius brevicornis</i>	no preference	predator	rare	3	0
	<i>Quedius fuliginosus</i>	no preference	predator	common	1	1
	<i>Quedius invrae</i>	no preference	predator	common	1	0
	<i>Quedius maurus</i>	forest	predator	rare	24	7
	<i>Quedius ochripennis</i>	no preference	predator	common	2	0
	<i>Rugilus erichsoni</i>	no preference	predator	rare	0	1
	<i>Rugilus rufipes</i>	no preference	predator	common	1	0
	<i>Scaphisoma agaricinum</i>	other	fungivore	common	2	0
	<i>Silusa rubiginosa</i>	forest	predator	common	1	0
	<i>Stenus clavicornis</i>	no preference	predator	common	1	0
	<i>Stenus similis</i>	no preference	predator	common	1	1
	<i>Stichoglossa semirufa</i>	no preference	predator	rare	61	12
	<i>Tachinus</i> sp.	unknown	predator	unknown	2	0
	<i>Tachyporus atriceps</i>	no preference	predator	common	2	1
	<i>Tachyporus hypnorum</i>	no preference	predator	common	46	12
	<i>Tachyporus nitidulus</i>	no preference	predator	common	21	6
	<i>Tachyporus obtusus</i>	unknown	predator	common	3	0
	<i>Tachyporus solutus</i>	no preference	predator	common	8	4
	<i>Xantholinus linearis</i>	no preference	predator	common	19	7
Tenebrionidae	<i>Diaperis boleti</i>	forest	fungivore	common	13	3
	<i>Latheticus oryzae</i>	unknown	fungivore	rare	1	0
	<i>Palorus depressus</i>	no preference	other	rare	1	0
	<i>Platydema violaceum</i>	unknown	other	rare	1	0
Tetratomidae	<i>Tetratoma ancora</i>	unknown	fungivore	common	28	8
Throscidae	<i>Aulonothroscus brevicollis</i>	forest	herbivore	common	4	0
	<i>Trixagus dermestoides</i>	no preference	unknown	common	1	0
	<i>Trixagus</i> sp.	unknown	unknown	unknown	3	0
Trogossitidae	<i>Nemosoma elongatum</i>	no preference	predator	common	10	3

Appendix 2.3

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

	Beetle Richness	Beetle Abundance	Tree Diversity (Shannon)	Stand Age	Stem Density	Tree Height	Crown Area	Plant Index	Area	Deadwood m ³ /m ²
Beetle Richness	1									
Beetle 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 2.4

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 concurring 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 2.5

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 concurring Shannon indices.

Stand	Forest % Generalists	Habitat % Species	Forest % Species	Common % Species	Rare % 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

3

Room for more is in the mix: tree diversity drives spatiotemporal β -diversity of true bugs (Heteroptera)

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Abstract

The forest canopy is a major hot-spot of insect diversity, but almost nothing is known for functionally important and abundant taxa such as true bugs (Heteroptera). Spatiotemporal patterns of true bug diversity in forests of different tree diversity have not yet been disentangled, although plant diversity has been shown to strongly impact the diversity and distribution of many insect communities. 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. Total species richness (γ -diversity), α -diversity, and abundance of true bugs increased across the tree diversity gradient, but 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. Patterns for beech were similar, but species turnover could not be related to the tree diversity gradient, and on beech alone, monthly turnover was generally higher compared to turnover among trees. 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 in the more diverse forest stands. We conclude that simple beech stands lack capacity for conserving insect species richness of deciduous forest habitats, and show that tree species identity and the dissimilarity of true bug communities from tree to tree matters when analysing community patterns. To understand diversity and distribution of insect communities in forest habitats, future research needs a better integration of previously neglected groups and of the extensive spatiotemporal community changes involved.

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

Introduction

It has long been known that especially 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 conifer trees. Up to now, information on exclusively deciduous forest stands that *a priori* differ in tree diversity is lacking, and standwise canopy insect richness has rarely been linked to overall canopy tree diversity of the sampled stands. Especially spatiotemporal patterns of insect diversity in temperate deciduous forest monocultures have not yet been elucidated, and it remains unexplored how they compare to patterns in mixed stands within the same forest neighbourhood.

Most examinations of arthropod species richness in forest ecosystems have primarily been limited to a single spatial or temporal scale, which can lead to misleading results if differences occur elsewhere but not at the observed scale. Choosing the right scale is of particular importance to pinpoint diversity patterns, and some authors have recently reported noteworthy changes across multiple spatiotemporal scales by using trap-nesting bees and wasps (Tylianakis *et al.* 2005), or butterflies and beetles (Hirao *et al.* 2007) as model systems. As listed in Tylianakis *et al.* (2006), diversity of arthropods is largely scale-dependent and driven by various factors which change if larger spatial scales (e.g. regions) are compared to smaller spatial scales (e. g. single trees). Hence, faint differences in species richness across spatiotemporal scales might have previously remained undiscovered, especially for taxonomic groups that have not yet gained major attention among forest researchers, like true bugs (Heteroptera).

Whilst well-described taxa such as beetles or butterflies have a long tradition in being used as study systems in forest ecosystems, true bugs have up to now widely been neglected. The latter is surprising, because as a result of their high degree in host plant specialisation and based on their feeding habits as sucking insects, true bugs might respond differently to environmental gradients compared to the groups mentioned above. Moreover, this taxonomical bias apparently is limited to forest ecosystems. In other habitats, such as aquatic (Polhemus & Polhemus 2008) or agricultural ecosystems (Fauvel 1999), true bugs have

intensively been studied not only due to their important functional roles as predators and herbivores, but also because of their use as indicator group for overall arthropod species richness within one habitat (Duelli & Obrist 1998).

One approach to assess diversity across different scales in space and time is the additive partitioning of diversity (Lande 1996, Veech *et al.* 2002, Crist *et al.* 2003), which is a ubiquitously applied method to determine species turnover (β -diversity) of insect communities in various habitat types. By additive partitioning, diversity is split up in several components: γ -diversity (total diversity across several sampled units), α -diversity (average diversity within a single sampled unit), and β -diversity (difference between γ and α). Hence, higher β -diversity indicates increased differences in community composition, or in other words, a higher turnover of species in space or time (Clough *et al.* 2007).

Here we apply additive partitioning to canopy true bug diversity at multiple spatiotemporal scales across a tree diversity gradient ranging from simple beech to mixed deciduous forest stands. To our knowledge this is the first attempt to determine at which spatial or temporal scale the highest diversity occurs for this taxon, specifically in a forest habitat. Our analyses include true bug communities on various tree species in the mix as well as communities on single beech trees (*Fagus sylvatica* L.) across the gradient. Recently acknowledged as being the most important and successful plant species in Europe (Leuschner *et al.* 2006), it is of specific concern what role beech plays in maintaining arthropod diversity in temperate forest ecosystems.

We expect communities of true bugs in simple beech stands to be more similar to each other than to communities in species rich stands, although diversity of communities on single beech trees within an otherwise mixed forest neighbourhood might also increase due to species spillover. To test our hypothesis, we apply an analysis of the distribution and species richness of functional groups and feeding guilds across the tree diversity gradient as well as additive partitioning of true bug diversity.

In particular, we test the following predictions with regard to effects of tree diversity on species richness and community composition of true bugs: (i) Habitat complexity has often been found to positively correlate with arthropod species richness (Humphrey *et al.* 1999, Hansen 2000, Hamer *et al.* 2003, Lassau & Hochuli 2008), hence we expect species richness of true bugs to be higher in more diverse forest stands as a result of increased structural complexity. (ii) Many true bug species show a high degree of host plant affiliation, either as food or habitat resource (Wachmann *et al.* 2004, Goßner 2008). In line with increased abundance of tree and herb layer plant species in the most diverse forest stands, we presume

higher true bug species turnover (β -diversity) in these habitats, due to increased abundance of specialists and forest-dwelling species restricted to particular tree species as habitat or food resource. (iii) For the same reason, we assume that seasonal turnover (β_{time}) contributes less to overall diversity compared to spatial turnover (β_{space}) between trees.

Materials and Methods

Study site description

Sampling was carried out in the Hainich National Park, which is located in Central Germany (Thuringia) north of the city of Eisenach. With a total area of 16,000 ha (7,600 ha designated as national park), the area is depicted as Germany's largest remaining semi-natural deciduous forest (Nationalpark Hainich; <http://www.nationalpark-hainich.de>). Prior to the German Reunion, the area was used as a military training site and has in large parts remained unmanaged for at least 60 years, resulting in a late-successional state of deciduous temperate forest which has been declared national park in 1997. The region has a mild 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 in 2005 was 9 °C, annual precipitation in 2005 was 601 mm (MeteoMedia 2005).

A major characteristic of the Hainich National Park is the lack of conifers in favour of a wide variety of deciduous tree species. Besides stands dominated by European beech (*Fagus sylvatica* L.), mixed forests with a high proportion of lime (*Tilia cordata* L., *Tilia platyphyllos* Scop.) and ash (*Fraxinus excelsior* L.) can also be found, and further deciduous tree species like hornbeam (*Carpinus betulus* L.), maple (*Acer pseudoplatanus* L., *Acer platanoides* L., *Acer campestre* L.), oak (*Quercus robur* L.), elm (*Ulmus glabra* Huds.), cherry (*Prunus avium* L.) and service tree (*Sorbus torminalis* L.) add variety to the mix.

For the present study, 12 forest stands of different tree diversity were chosen for examination, thereby establishing a tree diversity gradient ranging from simple beech to mixed forest stands with up to 11 deciduous tree species. All stands exhibited equal site characteristics in terms of soil (stagnic luvisol on loess-limestone as parent material), flat elevation, absence of canopy gaps and timespan since last management event (40 years).

Tree diversity of each stand was determined by recording tree species and individual abundance in a 50 x 50 sampling plot. To account for species richness and evenness (Magurran 2004), tree diversity in all subsequent analyses will be expressed as Shannon index based on stem counts of individuals with a diameter breast height (dbh) > 7 cm (Appendix 3.1).

Sampling design

True bugs were sampled with flight interception traps mounted in the forest canopy. Flight interception traps are commonly used to capture flying insects in forest habitats (e.g. Goßner *et al.* 2007, Müller *et al.* 2008). The traps consisted of two translucent polycarbonate panes (60 x 40 cm), which were arranged cross-shaped to maximise the probability that insects flying in from any direction hit one of the panes in flight. The insects then either drop down into a funnel leading to lower collecting jar, or fly up the window pane into a funnel attached to an upper collecting jar, both filled with ethylene-glycol (1:1 diluted with water) as a killing and preserving liquid.

Across all forest stands, 72 traps (six traps per stand) were suspended in the centre of individual tree crowns using a crossbow and following a sampling design based on the proportion of beech. In beech dominated stands (83-100% beech) with a maximum of 3 other tree species, only beech (*Fagus sylvatica*) was sampled, in stands with at least 48 % beech and up to six other tree species, the three most dominant species were sampled (beech, lime (*Tilia* sp.), ash (*Fraxinus excelsior*), and in stands with the relative abundance of beech declining below 42 % and up to ten other tree species, 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 chosen on the 50 x 50 m plots or in the directly adjacent neighbourhood. To include a comparison of single beech trees across the gradient, four supplementary traps were mounted in beech trees of the four most diverse forest stands. Analyses for beech alone were then derived from two randomly drawn/sampled trees per stand. All traps were cleared in intervals of four weeks over a period of six months (May to October 2005).

Sample processing

All true bugs were separated from bycatches, debris and plant material and preserved in 70 % ethyl alcohol. All specimens were identified to species level, except for some damaged and juvenile individuals that were assigned to higher taxonomic levels. Alcohol preserved voucher specimens were stored in the in-house collection (Agroecology, Georg-August-University Göttingen). Every species was supplied with additional information on habitat specialisation, stratum preference, adult feeding guild (predators: zoophagous species and zoophytophagous species with predominantly zoophagous diet during adult stage, herbivores: strictly phytophagous species and zoophytophagous species with predominantly phytophagous diet during adult stage), host plant specialisation (food or habitat resource) and prey specialisation

as outlined in Rabitsch *et al.* (in press) (Appendix 3.2). Feeding guilds were classified based on adult diet because flight-interception traps predominantly sample imagines.

Statistical analyses

Data analyses were conducted separately for six sampled trees per stand (beech or a mix of species), or for two sampled beech trees per stand. Observed species richness (γ -diversity) of true bugs was expressed as accumulated number of species per stand (pooled over space and time). We applied a non-parametric species richness estimator (first order Jackknife) to calculate sampling success, which was similar across the gradient (64-83 % of estimated species, Appendix 3.1).

Additive partitioning of γ -diversity was conducted for each forest stand following 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).

Relationships of the response variables (γ -diversity, rarefied γ -diversity, α , β_{time} , β_{space} , species richness in functional guilds) with tree diversity were tested with multiple regression models. To reach assumption of normality and homogeneity of variance, count data were \log_{10} transformed and proportional data arcsine-squareroot transformed prior to calculation of the model. Models were calculated using type I sum of squares with (1) true bug abundance and (2) tree diversity (Shannon index) as explanatory variables. The study was *a priori* designed to test effects of tree diversity. Tree diversity controlled several other biotic and abiotic plot characteristics (Appendix 3.3) which hence were not included in the statistical models for reasons of multicollinearity. True bug abundance data was included for correction of sample size. In the analyses of various tree species per forest stand, true bug abundance was strongly positively affected by tree diversity (Pearson's $\rho = 0.91$, $p < 0.001$), hence we tested different sequences of variables entered to the model. The same accounted for beech alone (Pearson's $\rho = 0.84$, $p < 0.001$). For each response variable, models were fitted separately, 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 homogeneity of variance. Computation of first order Jackknife estimates was compiled with EstimateS 8.0 (Colwell 2006). The remaining statistical analyses were carried out with R, Version 2.6.2 (R Development Core Team 2007; <http://www.R-project.org>).

Results

True bug community

In total, 2,431 individuals and 76 species were trapped within a period of six months in 2005 (Appendix 3.2). The most common species was *Deraeocoris lutescens* Schilling (708 individuals, 29.1 %), followed by *Psallus varians* Herrich-Schaeffer (433 individuals, 17.8 %) and *Harpocera thoracica* Fallén (203 individuals, 8.4 %). The remaining 73 species (96.1 %) each contributed less than 5 % to the total of sampled individuals, 21 species (27.6 %) were singletons. On beech trees, 522 individuals and 43 species and were captured, 18 (41.9 %) species thereof singletons (Appendix 3.2). Again, the predator *Deraeocoris lutescens* was most abundant (171 individuals, 32.8 %), but only two other species, *Psallus varians* (123 individuals, 23.6 %) and *Pentatoma rufipes* L., reached abundance levels above 5 % (28 individuals, 5.4 %). The vast majority of species on beech remained below 1 % in abundance (31 species, 72.1 %).

Species richness and additive partitioning of diversity

Observed species richness (γ -diversity) was not affected by tree diversity after controlling for increased individual abundance across the gradient (Abundance: $F_{1,9} = 51.88$, $p < 0.001$, Shannon index: $F_{1,9} = 0.51$, $p = 0.495$, Table 3.1). Nevertheless, the number of observed species tripled with increased tree diversity (Fig. 3.1), and the effect was significant when tree diversity was introduced to the multiple regression model first (Shannon index: $F_{1,9} = 47.11$, $p < 0.001$, Abundance: $F_{1,9} = 5.28$, $p = 0.047$, Table 3.1). Considering beech only, the number of observed true bug species also tripled across the gradient (Fig. 3.1), but the response to tree diversity was again primarily controlled by increased individual abundance (Shannon index, $F_{1,9} = 8.36$, $p = 0.018$, Abundance: $F_{1,9} = 47.11$, $p < 0.001$, Table 3.1).

The same effect explained increased α -diversity across the sampled forest stands (Shannon index: $F_{1,9} = 280.23$, $p < 0.001$, Abundance: $F_{1,9} = 36.57$, $p < 0.001$, Table 3.1). Both β_{time} - (Shannon index: $F_{1,9} = 45.79$, $p < 0.001$, Table 3.1) and β_{space} -diversity (Shannon index: $F_{1,9} = 18.05$, $p = 0.001$, Table 3.1) also increased across the tree diversity gradient, but spatial turnover β_{space} -diversity responded more strongly (ANCOVA, $F_{2,30} = 7.11$, $p = 0.003$).

Table 3.1. Multiple regression analyses of species richness parameters for canopy true bugs across a tree diversity gradient in the Hainich National Park. Values for beech alone are set in parentheses. † Temporal and spatial species turnover was not linked to turnover in true bug abundance, hence this variable was omitted from the model

Response Variable	Effect	Model A: Abundance + Shannon Index			Model B: Shannon Index + Abundance		
		Multiple r2	<i>F</i>	p	Multiple r2	<i>F</i>	p
γ -Diversity	Abundance		51.88 (14.06)	<0.001 (0.005)		5.28 (5.72)	0.047 (0.04)
	Shannon Index	0.85 (0.61)	0.51 (0.01)	0.495 (0.906)	0.85 (0.61)	47.11 (8.36)	<0.001 (0.018)
α -Diversity	Abundance		313.78 (49.79)	<0.001 (<0.001)		36.57 (23.01)	<0.001 (<0.001)
	Shannon Index	0.97 (0.85)	3.02 (0.02)	0.116 (0.901)	0.97 (0.85)	280.23 (26.79)	<0.001 (<0.001)
β_{time} -Diversity	Abundance [†]						
	Shannon Index	0.82 (0.31)	45.79 (4.5)	<0.001 (0.06)			
β_{space} -Diversity	Abundance [†]						
	Shannon Index	0.64 (0.19)	18.05 (2.4)	0.001 (0.152)			

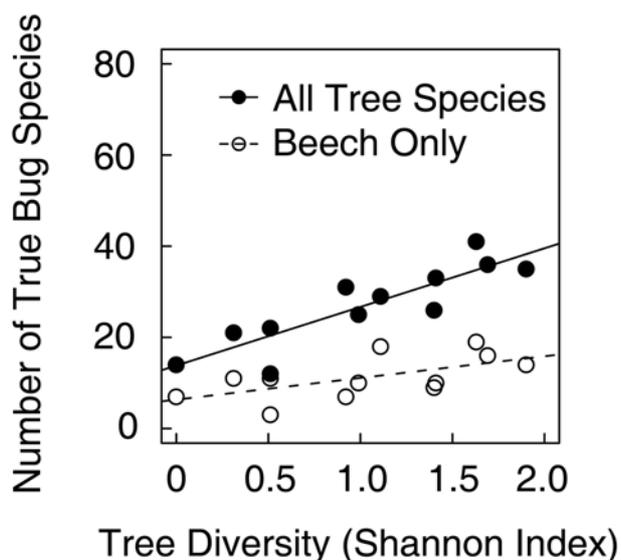


Fig. 3.1. Observed species richness (γ -diversity) of true bugs across a tree diversity gradient in a Central European deciduous forest.

Including all tree species in the analysis, spatial turnover contributed more to γ -diversity than temporal turnover (Fig. 3.2a), but the pattern reversed if beech alone was considered (Fig 3.2b). For beech trees, temporal and spatial turnover of true bug species did not respond to tree diversity, even if tree diversity was introduced to the model first (β_{time} : Shannon index: $F_{1,9} = 4.5$, $p = 0.06$; β_{space} : Shannon index: $F_{1,9} = 2.4$, $p = 0.152$, Table 3.1). No proportional change in the contribution of α -, β_{time} - or β_{space} - to total γ -diversity within each forest stand was observed, neither for all tree species nor for beech alone (Appendix 3.4).

Community composition & species richness of functional groups

Analysing all examined tree species, approximately one quarter of the sampled true bug species were associated with deciduous forest as habitat type (21 species, 27.6 %, Appendix 3.2). The rest of the species were more generalistic and did not prefer any particular habitat, (12 species, 15.8 %) or could be linked to other habitat types, most of them forest habitats but not strictly or primarily deciduous (43 species, 56.6%). Species bound to deciduous forest also contributed the majority of individuals (914 individuals, 37.6 %), whereas only 162 individuals (6.7 %) were found to be habitat generalists. This pattern remained constant if beech alone was taken into account (10 (23.3 %) forest species, 208 (39.8 %) individuals; 7 (15.2 %) habitat generalists, 32 (6.1 %) individuals, Appendix 3.2).

Table 3.2. Multiple regression analyses of functional guild species richness for canopy true bugs captured on various tree species across a tree diversity gradient in the Hainich National Park. Values for beech alone are set in parentheses.

		Model A: Abundance + Shannon Index			Model B: Shannon Index + Abundance		
Response Variable	Effect	Multiple r2	F	p	Multiple r2	F	p
Habitat Generalists	Abundance		10.64 (36.98)	0.01 (<0.001)		7.16 (30.06)	0.025 (<0.001)
	Shannon Index	0.55 (0.81)	0.57 (0.54)	0.47 (0.481)	0.55 (0.81)	4.04 (7.46)	0.075 (0.023)
Forest Species	Abundance		86.42 (5.7)	<0.001 (0.04)		7.1 (2.36)	0.026 (0.159)
	Shannon Index	0.91 (0.39)	3.03 (<0.01)	0.116 (0.973)	0.91 (0.39)	82.35 (3.34)	<0.001 (0.1)
Tree Layer Species	Abundance		66.32 (8.24)	<0.001 (0.018)		4.74 (1.76)	0.058 (0.218)
	Shannon Index	0.88 (0.48)	2.3 (0.19)	0.164 (0.674)	0.88 (0.48)	63.88 (6.68)	<0.001 (0.03)
Herb Layer Species	Abundance		7.76 (25.67)	0.021 (<0.001)		4.57 (7.28)	0.061 (0.024)
	Shannon Index	0.46 (0.75)	<0.01 (1.97)	0.996 (0.194)	0.46 (0.75)	3.18 (20.36)	0.108 (0.001)
Predators	Abundance		65.73 (15.74)	<0.001 (0.003)		8.83 (3.44)	0.016 (0.097)
	Shannon Index	0.88 (0.64)	0.28 (0.44)	0.613 (0.523)	0.88 (0.64)	57.17 (12.74)	<0.001 (0.006)
Herbivores	Abundance		75.77 (16.72)	<0.001 (0.003)		7.33 (6.13)	0.024 (0.008)
	Shannon Index	0.91 (0.66)	14.81 (0.67)	0.004 (0.433)	0.91 (0.66)	83.25 (11.26)	<0.001 (0.035)

The number of forest species and habitat generalists found on various tree species increased across the tree diversity gradient (Fig. 3.3a), but both groups were again controlled by increased individual abundance in the most species rich forest stands compared to the simple beech stands. Forest species responded significantly to the tested variables (Shannon index: $F_{1,9} = 82.35$, $p < 0.001$, Abundance: $F_{1,9} = 7.1$, $p = 0.026$, Table 3.2), while a relationship of habitat generalists to tree diversity remained only marginally significant, even if tree diversity was introduced to the multiple regression model first (Shannon index: $F_{1,9} = 4.04$, $p = 0.075$, Abundance: $F_{1,9} = 7.16$, $p = 0.025$, Table 3.2). The opposite was found if beech alone was analysed (Fig. 3.3b). Here, forest species showed only a significant response to individual abundance if it was introduced to the model first, and no relationship with tree diversity at all (Shannon index: $F_{1,9} = 3.34$, $p = 0.1$, Abundance: $F_{1,9} = 2.36$, $p = 0.159$, Table 3.2), whereas the number of habitat generalists increased across the gradient (Shannon index: $F_{1,9} = 7.46$, $p = 0.023$, Abundance: $F_{1,9} = 30.06$, $p < 0.001$, Table 3.2).

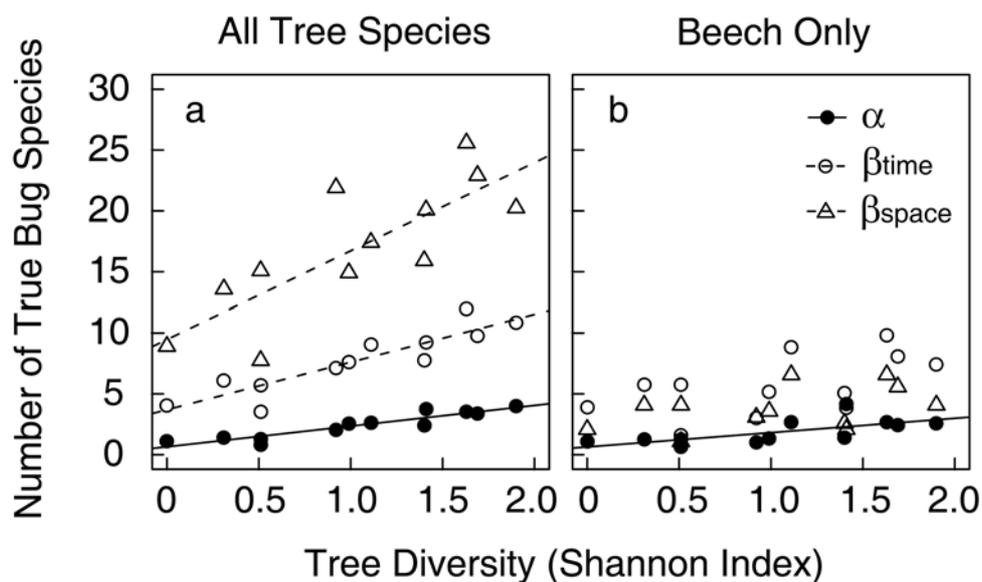


Fig. 3.2. α -, β_{time} - and β_{space} -diversity of true bug communities across a tree diversity gradient based on observed species richness per plot. a) All tree species sampled, regression slopes differ significantly (ANCOVA, $F_{2,30} = 7.11$, $p = 0.003$), b) beech only.

Concerning stratification, the majority of species and individuals found on various tree species were found to be associated with the tree layer (42 species (55.3 %), 2139 individuals (88 %), Appendix 3.2), while only a small fraction was contributed to tourist species typically dwelling in the forest herb layer (13 species (17.1 %), 50 individuals (3.9 %), Appendix 3.2). Yet again, the gross proportions remained consistent if beech alone was considered (tree

layer: 24 species (55.8 %), 448 individuals (85.8 %), herb layer: 8 species (18.6 %), 20 individuals (3.8 %)). Tree dwelling species showed a positive linear relationship to increased tree diversity (Fig. 3.3c), but only if tree diversity was introduced to the multiple regression model before controlling for individual abundance (Shannon index: $F_{1,9} = 63.88$, $p < 0.001$, Abundance: $F_{1,9} = 4.74$, $p = 0.058$, Table 3.2). Neither individual abundance nor tree diversity influenced species richness of herb layer species (Shannon index: $F_{1,9} = 3.18$, $p = 0.108$, Abundance: $F_{1,9} = 4.57$, $p = 0.061$, Table 3.2). If beech alone was considered, species richness of both tree layer dwelling species (Shannon index: $F_{1,9} = 6.68$, $p = 0.03$, Abundance: $F_{1,9} = 1.76$, $p = 0.218$, Table 3.2) and herb layer dwelling species (Shannon index: $F_{1,9} = 20.36$, $p < 0.001$, Abundance: $F_{1,9} = 7.28$, $p = 0.024$, Table 3.2) increased across the gradient (Fig. 3.3d), but effects were only apparent when tree diversity entered the model first. Assorted to feeding guilds, the majority of species found on all trees was described as predatory according to the feeding ecology of adults (41 species, 53.9 %, Appendix 3.2). In contrast, only 13 (17.1 %) species were annotated as strictly herbivorous. By means of individual abundance, predators were also most common (2185 individuals, 89.9 %), whereas only 96 (3.9 %) of all individuals belonged to the herbivore guild. Communities on beech exhibited the same distribution of herbivores and predators (herbivores: 8 (18.6 %) species, 21 (4 %) individuals; predators: 21 (48.8 %) species, 449 (86 %) individuals, Appendix 3.2). The number of predators as well as of herbivores increased across the tree diversity gradient (Fig. 3.3e), but only species richness of herbivores showed a significant response to tree diversity after previously controlling for increased individual abundance (Abundance: $F_{1,9} = 75.77$, $p < 0.001$, Shannon index: $F_{1,9} = 14.81$, $p = 0.004$, Table 3.2). A similar pattern was found for species richness on beech alone (Fig. 3.3f), although here the herbivore guild did not respond to tree diversity if individual abundance was entered to the model first (Abundance: $F_{1,9} = 16.72$, $p = 0.003$, Shannon index: $F_{1,9} = 0.67$, $p = 0.433$, Table 3.2).

Most true bug species and individuals captured on various tree species exhibited an intermediate degree of host plant specialisation (22 (28.9 %) species, 575 (23.7 %) individuals, Appendix 3.2). 12 (15.8 %) species were highly specialised on a single plant species or genus (441 (18.1 %) individuals), and 18 (23.7 %) species were not specialised at all (334 (13.7 %) individuals), thus being capable of dwelling on a variety of plant genera. Similar proportions of species and individuals were found on beech alone (5 (11.6 %) strict species, 37 (7.1 %) individuals; 9 (20.9 %) intermediate species, 145 (27.8 %) individuals; 15 (34.9 %) non-specialised species, 87 (16.7 %) individuals, Appendix 3.2).

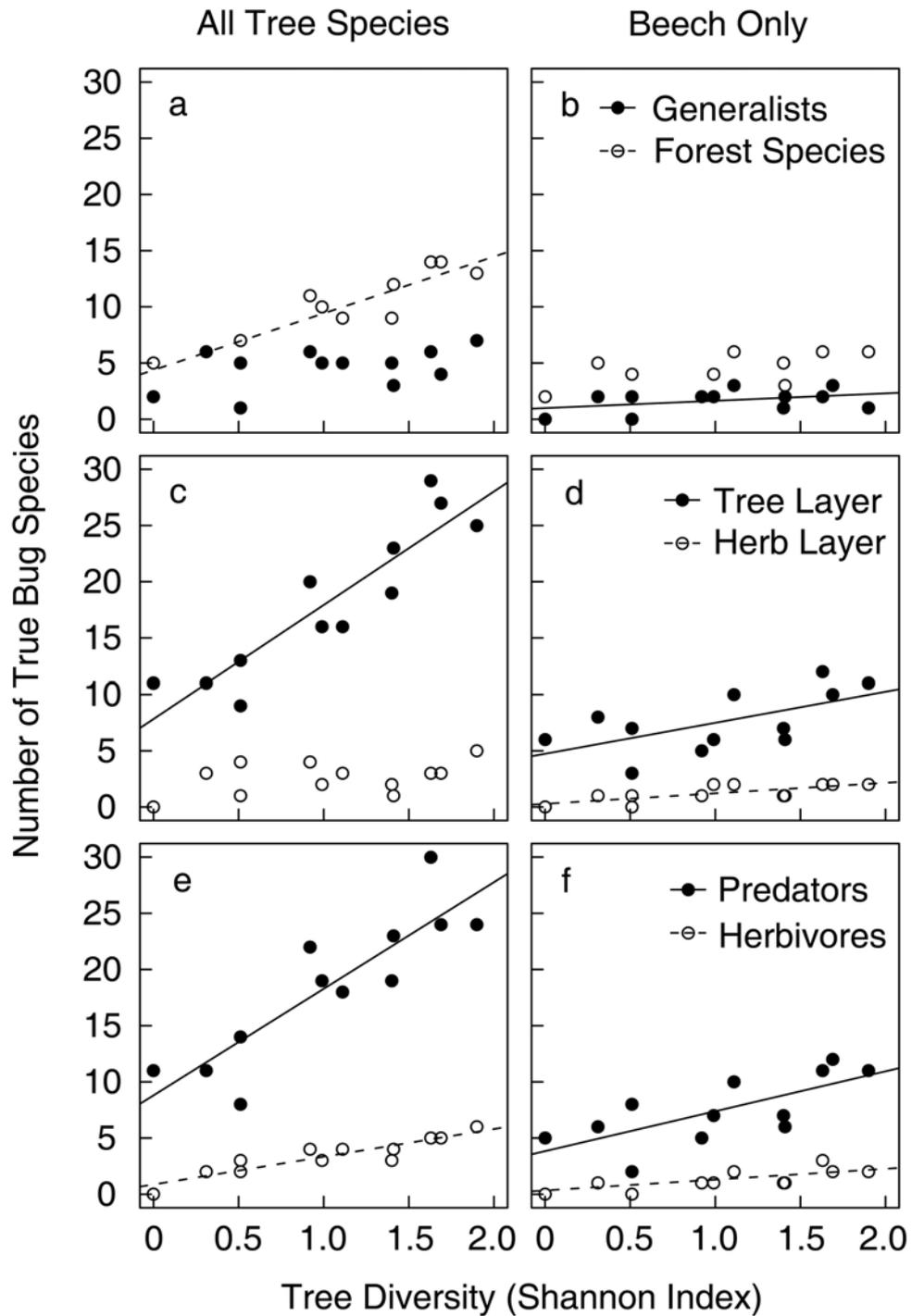


Fig. 3.3. Species richness of functional groups of true bugs across a tree diversity gradient on various tree species. a & b) habitat specialisation, c & d) stratification specialisation, e & f) feeding guilds (a, c, e all tree species sampled, b, d, f beech only).

Table 3.3. Multiple regression analyses of 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 alone are set in parentheses. ^Hhost plant specialisation (food or habitat resource), ^Pprey specialisation.

		Model A: Abundance + Shannon Index			Model B: Shannon Index + Abundance		
Response Variable	Effect	Multiple r2	F	p	Multiple r2	F	p
Species Richness of	Strict ^H Species		97.09 (42.24)	<0.001 (<0.001)		9.39 (19.47)	0.013 (0.002)
	Shannon Index	0.92 (0.83)	5.15 (0.85)	0.05 (0.379)	0.92 (0.83)	92.85 (23.63)	<0.001 (<0.001)
Intermediate ^H Species	Abundance		20.42 (7.23)	0.001 (0.025)		0.93 (8.46)	0.359 (0.017)
	Shannon Index	0.72 (0.5)	2.56 (1.87)	0.143 (0.205)	0.72 (0.5)	22.05 (0.64)	0.001 (0.445)
Not Specialised ^H Species	Abundance		36.05 (7.52)	<0.001 (0.023)		3.24 (3.94)	0.105 (0.078)
	Shannon Index	0.8 (0.46)	0.55 (0.04)	0.477 (0.849)	0.8 (0.46)	33.36 (3.62)	<0.001 (0.09)
Oligophagous ^P Species	Abundance		43.8 (19.37)	<0.001 (0.002)		2.66 (9.42)	0.138 (0.013)
	Shannon Index	0.84 (0.68)	3.78 (0.16)	0.084 (0.702)	0.84 (0.68)	44.93 (10.11)	<0.001 (0.011)
Polyphagous ^P Species	Abundance		6.2 (3.01)	0.034 (0.117)		0.06 (1.5)	0.809 (0.252)
	Shannon Index	0.48 (0.29)	2.01 (0.72)	0.19 (0.418)	0.48 (0.29)	8.15 (2.24)	0.019 (0.169)

In the analyses of various tree species combined, species richness in all groups increased across the tree diversity gradient (Fig. 3.4a), but only strictly specialised true bugs responded to tree diversity after previous control for increased individual abundance (Abundance: $F_{1,9} = 97.09$, $p < 0.001$, Shannon index: $F_{1,9} = 5.15$, $p = 0.05$, Table 3.3). Effects were similar but less significant if beech alone was considered (Fig. 3.4b). Even if tree diversity was introduced to the model first, intermediately specialised (Shannon index: $F_{1,9} = 0.64$, $p = 0.445$, Abundance: $F_{1,9} = 8.46$, $p = 0.017$, Table 3.3) and non-specialised species (Shannon index: $F_{1,9} = 3.64$, $p = 0.09$, Abundance: $F_{1,9} = 3.94$, $p = 0.078$, Table 3.3) did not respond at all, and only strictly specialised species were significantly affected by the tree diversity gradient (Shannon index: $F_{1,9} = 23.63$, $p < 0.001$, Abundance: $F_{1,9} = 19.47$, $p = 0.002$, Table 3.3).

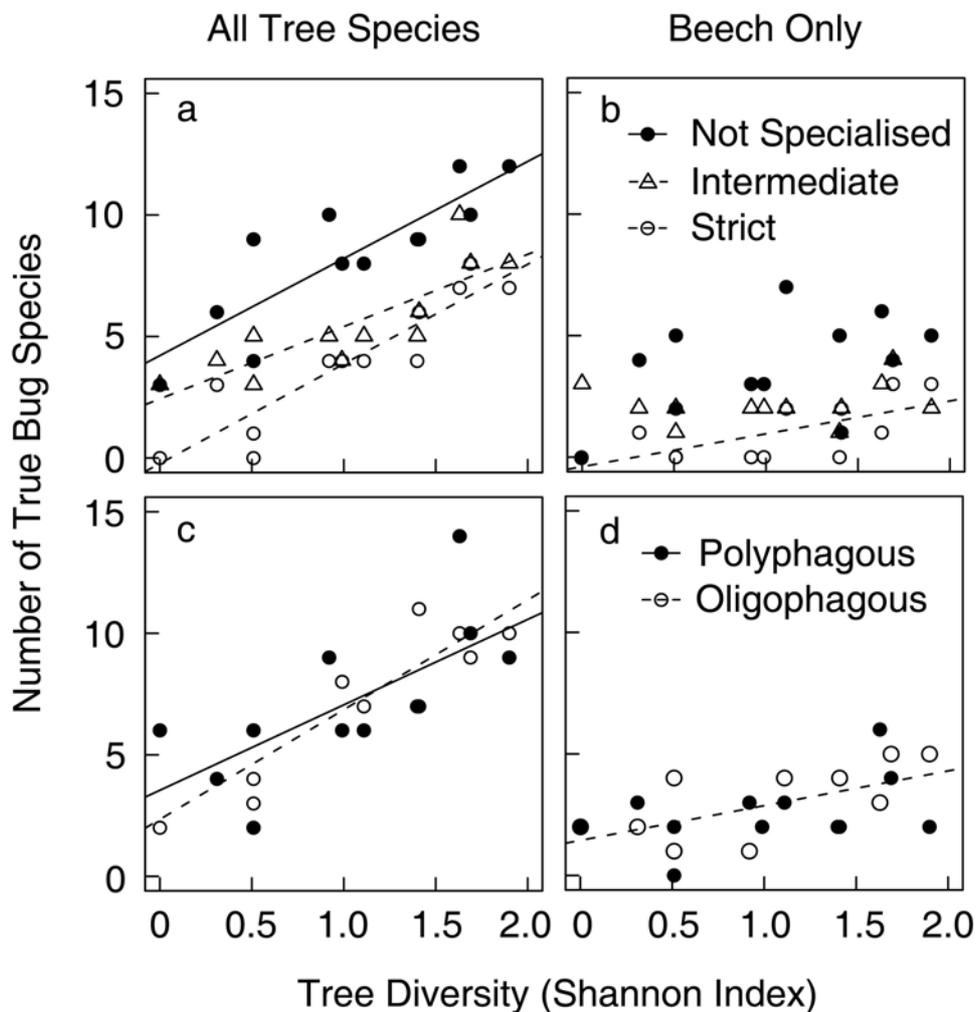


Fig. 3.4. Species richness of functional groups of true bugs across a tree diversity gradient on various tree species. a & c) host plant specialisation, b & d) prey specialisation, (a, c all tree species sampled, b, d beech only).

No predatory true bug species were found to be strictly dependent on a single prey species. In contrast, most individuals found on various tree species were oligophagous with a specialisation on several prey taxa (14 species (34.1%), 998 (45.7 %) individuals), or polyphagous and capable of feeding on high variety of prey (20 (48.8 %) species, 941 (43.1 %) individuals, Appendix 3.2). Results were similar if beech alone was taken into account (8 polyphagous species (38.1 %), 204 individuals (45 %), 8 oligophagous species (38.1 %), 184 individuals (41 %), Appendix 3.2). For various tree species (Fig. 3.4c), both oligophagous true bug species richness (Shannon index: $F_{1,9} = 44.93$, $p < 0.001$, Abundance: $F_{1,9} = 2.66$, $p = 0.138$, Table 3.3) and polyphagous true bug species richness were found to increase with the tree diversity gradient, but only if Shannon index was introduced to the model first (Shannon index: $F_{1,9} = 8.15$, $p = 0.019$, Abundance: $F_{1,9} = 0.06$, $p = 0.809$, Table 3.3). Considering beech alone (Fig. 3.4d), a similar response in oligophagous species was only found if tree diversity was introduced to the model first (Shannon index: $F_{1,9} = 10.11$, $p = 0.011$, Abundance: $F_{1,9} = 9.42$, $p = 0.013$, Table 3.3), but even then species richness of polyphagous species was not affected (Shannon index: $F_{1,9} = 2.24$, $p = 0.169$, Abundance: $F_{1,9} = 1.5$, $p = 0.252$, Table 3.3).

No differences or specific patterns in proportional species richness could be determined for any of the groupings or guilds within each forest stand across the gradient (Appendix 3.5 & 3.6), neither if all tree species were analysed, nor beech alone.

Discussion

Overall γ -diversity of true bugs increased across the tree diversity gradient as hypothesised. However, rather than tree diversity as such, increased abundance of true bugs in the most species-rich forest stands turned out to primarily account for increased species richness of this taxon. The same pattern was exhibited by species richness in most functional guilds. When additive partitioning of true bug diversity was performed, α -diversity also was primarily influenced by differences in true bug abundance rather than by tree diversity, and the mean number of species per tree and month was only slightly higher in the more diverse forest stands. Regression slopes were much steeper for spatiotemporal species turnover, and both β_{time} and β_{space} showed a strong response to tree diversity. β -diversity contributed roughly 90 % to total γ -diversity, which stresses the importance of species turnover between individual trees, tree species and months for diversity estimates. For a reliable determination of arthropod diversity across habitat gradients, sufficient sampling effort, both in space and time,

is crucial (Tylianakis *et al.* 2005). As our results illustrate, focusing on a single tree species abundant in all stands (here beech) would have been vastly misleading, indicating that β_{time} contributes more to true bug diversity than β_{space} , with neither of them responding to tree diversity. This pattern was reversed if simply more replicates (here trees) or more tree species were included in the analyses. In particular, spatial turnover between tree individuals of the same species was surprisingly high, which only became apparent when six instead of two beech trees were compared in the most simple forest stands. The latter result is unexpected, because forest stands primarily consisting of beech on first sight appear to be a much more continuous habitat compared to forest stands consisting of various tree species. Hence we presumed that spatial turnover would play a minor role in the more simple stands. Although plant identity and diversity strongly promotes species richness of associated arthropods (Siemann 1998, Siemann *et al.* 1998, Brändle *et al.* 2001, Haddad *et al.* 2001), spatial turnover seems to be controlled by individual differences among trees of the same species as well. Lindo & Winchester (2008) found high species turnover among conspecific trees for oribatid mites, and one explanation for this was limited dispersal due to low mobility of these organisms. In contrast to mites, true bugs are a lot more mobile, and in simple beech stands high β_{space} -diversity is unlikely to be mediated by host specialisation. It is crucial to investigate how microhabitat conditions of individual trees differ and whether this leads to a patchy distribution of true bug species, which in turn increases β_{space} -diversity even among conspecific individuals, thereby mediating overall γ -diversity.

With tree diversity *a priori* set as controlling variable, how can observed differences in true bug richness across the gradient be explained? In our study, canopy tree diversity determined various biotic and abiotic plot characteristics and structural parameters (e.g. plant area index, stem density), which were highly correlated with the Shannon index of the sampled forest stands. Not only the number of true bug species was increased with increasing tree diversity, but also the number of individuals captured in the most diverse forest stand was enhanced and highly correlated with the Shannon index. Highly structured vegetation, such as a high variety of tree species with different traits, provides a high variety of resources and sites for reproduction, colonisation, and overwintering (Lawton 1983). Compared with simple beech stands, diverse forest stands most likely offer a greater array of niches, which in turn can enhance true bug abundance and with it diversity.

The increase in structural complexity mediated by tree diversity resulted in greater habitat heterogeneity, which has been suggested as an overarching factor determining animal species richness regardless of taxon or habitat type (Tews *et al.* 2004). Additionally, different tree

species themselves differ in architecture, bark texture, branching complexity, leave abundance and other features. Hence, micro-climate, shelter-availability and accessibility differs for various tree species, and the resulting niches can support different sets of arthropod abundance and diversity (Lawton 1983, Southwood *et al.* 1982, Halaj *et al.* 1998, Halaj *et al.* 2000, Goßner & Ammer 2006). Although most species captured were not dependent on a particular host plant as habitat or food resource, the number of species with intermediate or strict host affiliation strongly increased across the gradient, indicating the importance of availability of certain tree or plant species and the associated structures. If the latter are lacking, a high proportion of species will vanish.

Some authors could not find a relationship of insect richness and habitat complexity when flight interception traps in forests were used (Lassau *et al.* 2005), but this might be due spatial (low number of traps, restriction to understory) and temporal sampling bias. For beetles, Lassau *et al.* (2005) suggest easier accessibility of the traps in more simple habitats as reason for the lack of differences in species richness compared to complex habitats. Sampling bias due to more barrier-free flight-paths might explain some of the species richness we observed by sampling oak and maple, because the crowns of these trees appeared to be more open in contrast to other tree species. Nevertheless, we can diminish this objection by comparing beech alone, which had similarly structured crowns on all sampled plots, but still reflected differences of true bug richness across the tree diversity gradient. Moreover, taxa might respond differently to gradients of plant diversity and habitat structure in general, which highlights the necessity to include previously neglected taxa like true bugs in biodiversity survey.

Concerning functional guilds, forest species, and in particular, tree-dwelling species, were most abundant in the traps and distinctly responded to the tree diversity gradient, whereas habitat generalists were less species-rich and showed a weaker response. This illustrates that true bugs in deciduous forest show a distinct stratification in species distribution. Further research is needed to investigate community patterns in other strata and how they compare to patterns observed in the canopy. Abundance and species richness of predators and herbivores would be of particular interest with regard to ecosystem functioning (herbivory and biocontrol) in the forest understory.

In the canopy, predators were generally more species-rich compared to herbivores, and species richness of predators also increased with the tree diversity gradient. Predator richness of true bugs has been linked to vegetation structure (Zurbrügg & Frank 2006), and intra-guild predation might decrease in highly structured vegetation due to a greater availability of

refuges (Morris 2000, Finke & Denno 2002, Corkum & Cronin 2004). This mechanism only holds true for generalist predators, and is legitimate to be applied here since none of the species observed was highly specialised or restricted to a single prey species. For the same reason, increased habitat complexity positively affects individual abundance of predators (Langellotto & Denno 2004), but this does not necessarily mean that as a cascading effect, herbivores become less abundant and species-rich. As illustrated by the increase in herbivore species richness across the tree diversity gradient, the lower trophic levels might also profit from resource availability and shelter, which might limit top-down control (Sanders *et al.* 2008).

We conclude that the additive partitioning of diversity across space and time is a necessary tool to evaluate diversity of insect communities, in particular if it is desired to determine what contributes most to the total observed diversity within one habitat. Here, species turnover β_{space} between tree species and tree individuals has been shown to be of great importance for increasing diversity of true bug communities, which has direct implications for forest management. Simple beech stands alone only insufficiently conserve regional species richness of true bugs, which can only be maintained by a mix of different tree species and individuals. This ensures habitat heterogeneity and increased microhabitat abundance supporting a higher load of true bug individuals, and with it a greater number of species. Tree diversity, by means of species identity and individual identity, hence indirectly controls several factors that in turn influence species richness of true bug communities. We show that species rich deciduous forests are of particular importance for forest dependent true bug species, which rely on certain tree species as food or reproductive resource. The current intensification of forestry leads to increased habitat loss, habitat fragmentation and reduced habitat complexity (Kouki *et al.* 2001, Larsson & Danell 2001, Hirao *et al.* 2007, Müller & Goßner 2007), eventually resulting in forests unsuitable to maintain a true bug community dependent on a diverse mix of deciduous trees and niches.

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Appendix 3.1

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 3.2

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 Rabitsch *et al.* (2008). ^Ddeciduous, ^Hhost plant specialisation (food or habitat resource), ^Pprey specialisation, ^Vvarious tree species, ^Bbeech 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
<i>Acanthosoma haemorrhoidale</i>	other	tree layer	other	not specialised	unknown	4	1
<i>Acanthosomatidae</i> sp.	unknown	unknown	unknown	unknown	unknown	1	1
<i>Anthocoridae</i> sp.	unknown	unknown	unknown	unknown	unknown	5	2
<i>Anthocoris amplicollis</i>	forest ^D	other	carnivor	other	oligophagous	2	0
<i>Anthocoris confusus</i>	forest ^D	tree layer	predator	other	oligophagous	90	21
<i>Anthocoris nemoralis</i>	forest ^D	tree layer	predator	other	polyphagous	5	1
<i>Berytinus minor</i>	other	other	other	strict	unknown	1	0
<i>Blepharidopterus angulatus</i>	other	tree layer	other	intermediate	polyphagous	2	1
<i>Campyloneura virgula</i>	forest ^D	tree layer	predator	not specialised	polyphagous	41	10
<i>Carpocoris purpureipennis</i>	other	herb layer	other	not specialised	unknown	1	1
<i>Closterotomus biclavatus</i>	other	other	predator	not specialised	other	8	2
<i>Cremnocephalus alpestris</i>	other	tree layer	predator	intermediate	oligophagous	1	0
<i>Cyllocoris histrionius</i>	forest ^D	tree layer	predator	strict	polyphagous	1	0
<i>Deraeocoris lutescens</i>	other	tree layer	predator	other	polyphagous	708	171
<i>Deraeocoris trifasciatus</i>	forest ^D	tree layer	predator	not specialised	polyphagous	3	0
<i>Dicranocephalus agilis</i>	other	herb layer	herbivore	intermediate	unknown	1	1
<i>Dolycoris baccarum</i>	no preference	herb layer	herbivore	not specialised	unknown	12	3
<i>Dryophilocoris flavoquadrimaculatus</i>	other	tree layer	predator	strict	polyphagous	3	0
<i>Elasmotethus interstinctus</i>	other	tree layer	other	intermediate	unknown	1	1
<i>Elasmotethus minor</i>	other	tree layer	other	strict	unknown	1	1
<i>Eurydema oleracea</i>	no preference	herb layer	herbivore	intermediate	unknown	1	0
<i>Harpocera thoracica</i>	other	tree layer	predator	strict	oligophagous	203	9
<i>Himacerus apterus</i>	no preference	other	predator	unknown	polyphagous	7	0
<i>Isometopus intrusus</i>	other	tree layer	predator	not specialised	polyphagous	5	0
<i>Kleidocerys resedae</i>	other	tree layer	other	intermediate	unknown	52	14
<i>Loricula elegantula</i>	other	tree layer	predator	unknown	polyphagous	6	5
<i>Lygocoris contaminatus</i>	other	tree layer	herbivore	intermediate	unknown	4	0
<i>Lygocoris viridis</i>	other	tree layer	predator	intermediate	unknown	7	0
<i>Lygus pratensis</i>	no preference	herb layer	herbivore	not specialised	unknown	19	10
<i>Mermitelocerus schmidtii</i>	other	tree layer	predator	intermediate	polyphagous	20	1
<i>Mirinae</i> sp.	unknown	unknown	unknown	unknown	unknown	1	1
<i>Miris striatus</i>	other	tree layer	predator	not specialised	polyphagous	12	1
<i>Nabis pseudoferus</i>	other	other	predator	unknown	unknown	70	23
<i>Notostira erratica</i>	other	herb layer	other	intermediate	unknown	1	1
<i>Orius horvathi</i>	no preference	other	predator	unknown	oligophagous	27	2
<i>Orius laticollis</i>	other	other	predator	other	oligophagous	4	0
<i>Orius majusculus</i>	other	other	predator	unknown	polyphagous	1	0
<i>Orius minutus/vicinus</i>	no preference	other	predator	unknown	polyphagous	77	13
<i>Orthops basalis</i>	no preference	herb layer	herbivore	intermediate	unknown	1	0
<i>Orthops kalmii</i>	no preference	herb layer	herbivore	intermediate	unknown	1	1
<i>Orthotylinae</i> sp.	unknown	unknown	unknown	unknown	unknown	5	0

<i>Orthotylus marginalis</i>	other	tree layer	predator	intermediate	polyphagous	19	2
<i>Orthotylus nassatus</i>	forest ^D	tree layer	predator	intermediate	unknown	2	0
<i>Orthotylus prasinus</i>	forest ^D	tree layer	herbivore	intermediate	unknown	1	0
<i>Orthotylus tenellus</i>	forest ^D	tree layer	predator	intermediate	polyphagous	6	0
<i>Orthotylus viridinervis</i>	forest ^D	tree layer	predator	strict	oligophagous	9	0
<i>Palomena prasina</i>	no preference	other	herbivore	not specialised	unknown	8	1
<i>Palomena viridissima</i>	no preference	herb layer	herbivore	not specialised	unknown	3	2
<i>Pentatoma rufipes</i>	other	tree layer	predator	not specialised	unknown	101	28
<i>Pentatomidae</i> sp.	unknown	unknown	unknown	unknown	unknown	2	1
<i>Peribalus vernalis</i>	no preference	herb layer	herbivore	not specialised	unknown	1	0
<i>Peritrechus nubilus</i>	other	other	other	not specialised	unknown	1	0
<i>Phylinae</i> sp.	unknown	unknown	unknown	unknown	unknown	1	0
<i>Phylus melanocephalus</i>	forest ^D	tree layer	predator	strict	oligophagous	10	2
<i>Phytocoris dimidiatus</i>	forest ^D	tree layer	predator	not specialised	unknown	24	3
<i>Phytocoris longipennis</i>	forest ^D	tree layer	predator	not specialised	unknown	7	3
<i>Phytocoris populi</i>	other	tree layer	predator	intermediate	polyphagous	8	0
<i>Phytocoris</i> sp.	unknown	unknown	unknown	unknown	unknown	3	1
<i>Phytocoris tiliae</i>	forest ^D	tree layer	other	not specialised	unknown	43	19
<i>Pinalitus cervinus</i>	forest ^D	tree layer	herbivore	not specialised	unknown	41	2
<i>Plagiognathus chrysanthemii</i>	other	herb layer	herbivore	not specialised	unknown	0	1
<i>Psallus (Hylopsallus)</i> sp.	unknown	unknown	unknown	unknown	unknown	1	0
<i>Psallus (Psallus)</i> sp.	unknown	unknown	unknown	unknown	unknown	16	7
<i>Psallus ambiguus</i>	forest ^D	tree layer	predator	intermediate	polyphagous	5	0
<i>Psallus flavellus/lepidus</i>	forest ^D	tree layer	predator	strict	oligophagous	40	0
<i>Psallus mollis</i>	forest ^D	tree layer	predator	strict	oligophagous	12	0
<i>Psallus perrisi/wagneri</i>	forest ^D	tree layer	predator	strict	oligophagous	137	24
<i>Psallus pseudoplatani</i>	other	tree layer	predator	strict	oligophagous	22	1
<i>Psallus punctulatus</i>	forest ^D	tree layer	other	strict	oligophagous	2	0
<i>Psallus varians</i>	forest ^D	tree layer	predator	intermediate	oligophagous	433	123
<i>Rhabdomiris striatellus</i>	other	tree layer	predator	other	polyphagous	9	0
<i>Stenodema laevigata</i>	no preference	herb layer	other	intermediate	unknown	5	0
<i>Stenodema virens</i>	other	herb layer	other	intermediate	unknown	1	0
<i>Temnostethus pusillus</i>	other	tree layer	predator	unknown	unknown	35	4
<i>Tingis cardui</i>	other	herb layer	herbivore	intermediate	unknown	3	0
<i>Troilus luridus</i>	other	tree layer	predator	unknown	polyphagous	4	0
<i>Xylocoris galactinus</i>	other	unknown	predator	unknown	polyphagous	1	0

Appendix 3.3

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

	True Bug Richness	True Bug Abundance	Shannon Index Trees	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							
Shannon Index Trees	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 3.4

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 3.5

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	% Generalists	Habitat % Species	Forest Tree Species	Layer Herb Species	Layer 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 3.6

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. ^Hhost plant specialisation (food or habitat resource), ^Pprey specialisation.

Forest Stand	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

4

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

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(submitted)

Abstract

Bees and wasps provide important ecosystem services such as pollination and biocontrol in crop-dominated landscapes, but surprisingly few 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 the mixed forest stands.

Key words: beech, ecosystem functioning, Eumeninae, habitat heterogeneity, Hymenoptera, insects, solitary bees and wasps, Sphecidae, trap nests, parasitism, parasitoids, bottom-up control

Introduction

In tropical and temperate ecosystems alike, the forest canopy is known as a major source of insect diversity (Erwin 1982, Erwin 1988, Stork 1988, Novotny & 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 & Marquis 1999, Schulze *et al.* 2001, Fermon *et al.* 2005, Roisin *et al.* 2006). In a few cases no distinct stratification was observed (Stork & Grimbacher 2006), and the relative importance of canopy and understory communities to overall diversity patterns and processes may be linked to tree diversity.

Cavity-nesting bees and wasps have been shown to be a particularly useful model system for studying abundance and diversity using 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 with ecosystem functioning (i.e. parasitism) 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, 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 & Tscharntke 2002, Sheffield *et al.* 2008, Steffan-Dewenter & Schiele 2008) or tropical agroforestry habitats (e.g. Klein *et al.* 2006, Tylianakis *et al.* 2006). In contrast, data on cavity-nesting hymenopteran 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.*, in press) 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.*, in press).

Taki *et al.* (2008a, 2008b) 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. Up to now, virtually nothing is

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 analyze 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 (Tschardt *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 strata (canopy vs. understory).

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) Do parasitism rates relate to the tree diversity gradient? (4) Do parasitism rates differ between forest strata?

Materials and Methods

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, 7,600 ha of forest (of a total area of 16,000 ha) are currently protected by federal law (Nationalpark 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 placed in the north-eastern part of the protected zone south of the village 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), 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.*, in press). 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 x 50 m plot was fenced for determination of tree diversity. 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., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Prunus avium* (L.), *Quercus robur* L., *Sorbus torminalis* L., *Tilia cordata* L., *Tilia platyphyllos* L., *Ulmus glabra* Huds.).

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 aboveground cavity nesting bees and wasps and their natural enemies (e. g. Tscharrntke *et al.* 1998; Klein *et al.* 2002). The trap nests consisted of two paired PVC tubes (each \varnothing 10.5 cm) filled with a random mix of reed internodes (*Phragmites australis* (Cav.) Trin. ex Steud.) ranging from 0.2 cm to approximately 1 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 to reproduce in a certain area (Tscharrntke *et al.* 1998). Furthermore, cavity nesting species tend to breed in close proximity to the nesting site they originated from. Hence, experimental exposure of these standardised nesting resources are 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 breast height on wooden posts in the understory next to the sampled tree. 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 in beech (*Fagus 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.), ash (*Fraxinus 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 (*Acer pseudoplatanus*), hornbeam (*Carpinus betulus*) and either oak (*Quercus robur*) or service tree (*Sorbus torminalis*)). Sampled trees were randomly selected within the 50 x 50 m plots or in the directly adjacent forest. To quantify a possible nesting resource for hymenopteran hosts, the amount of deadwood [m^3/m^2] was measured within four circular subplots with a radius of 5 m.

The trap nests were exposed over a period of six 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 five months, the traps were inspected visually 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 number of parasitoid eggs, as well as host and parasitoid morphospecies was recorded. The nests were then placed in 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.

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 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 x 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 data 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>).

Results

General community structure

In total, the trap nests were occupied with 3,948 host brood cells. The majority of brood cells was built by five species of eumenid wasps (Hymenoptera: Eumeninae, 1776 cells (45.1 %), Appendix 4.1), followed by seven species of sphecid wasps (Hymenoptera: Sphecidae, 1,272 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 was occupied by 14 species of natural enemies, the majority thereof hymenopteran parasitoids (12 species in seven families, Appendix 4.2).

Stratification of cavity-nesting communities and parasitism

Hosts were significantly more abundant in the canopy (216.2 ± 24.5 , $\chi^2 = 396.13$, $df = 4$, $p < 0.001$, Table 4.1) compared to the forest understory (112.8 ± 8.9), and abundance in the canopy increased significantly across the tree diversity gradient ($\chi^2 = 7.13$, $df = 3$, $p = 0.008$, Fig. 4.1a). Canopy as well as understory communities did not respond significantly to deadwood availability, neither by means of abundance nor by species richness, and species richness was also not related to tree diversity ($\chi^2 = 3.01$, $df = 3$, $p = 0.083$, Fig. 4.1c).

Table 4.1. 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 Nationalpark. Df = degrees of freedom, AIC = Akaike information criterion, BIC = Bayesian information criterion, logLik = log likelihood.

Response Variable: Host Brood Cells							
Models:	Df	AIC	BIC	logLik	χ^2	p	Explanatory Variable
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 x 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 x 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 x Shannon
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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 x 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 x Shannon

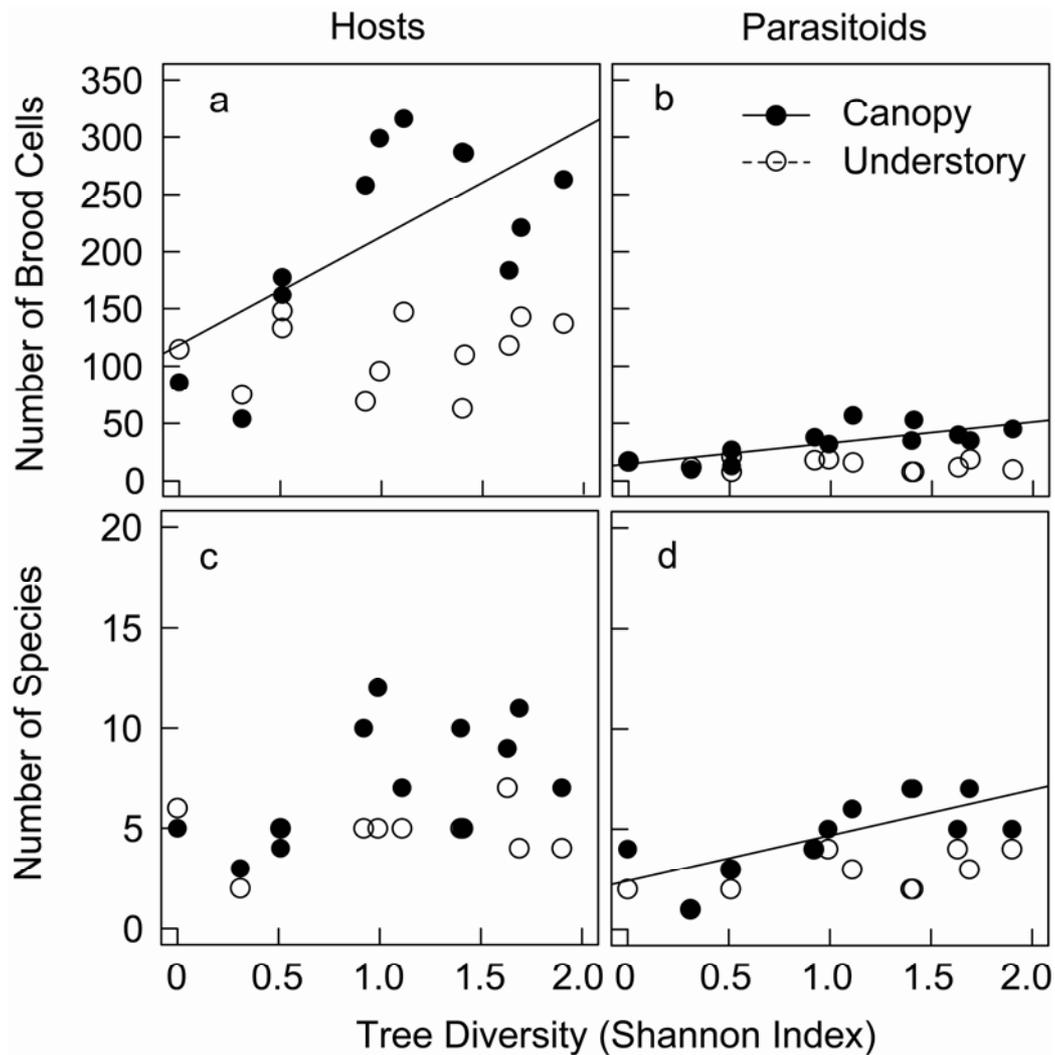


Fig. 4.1. Stratification of cavity-nesting bees and wasps and their natural enemies across a tree diversity gradient. a and b) Number of brood cells or parasitoid individuals in the canopy and understory, b and c) species richness in the canopy and understory. (a, c hosts, b, d parasitoids).

Parasitoids were more abundant in the canopy (33.5 ± 4.3) compared to the understory (14 ± 1.4 ; $\chi^2 = 98.96$, $df = 4$, $p < 0.001$, Fig. 4.1b), and abundance as well as species richness in the canopy increased significantly with increased tree species richness (parasitoid abundance: $\chi^2 = 6.4$, $df = 3$, $p = 0.011$, Fig. 4.1b, parasitoid species richness: $\chi^2 = 5.37$, $df = 3$, $p = 0.021$, Fig. 4.1d). More species of parasitoids were observed in the canopy (4.8 ± 0.5) compared to the understory (2.8 ± 0.3 , $\chi^2 = 5.8$, $df = 4$, $p = 0.015$, Fig. 4.1d).

Multidimensional scaling of Bray-Curtis similarity illustrated that species composition of hosts differed between the canopy and understory (Fig. 4.2). Parasitism rates also differed between strata (canopy 15.8 ± 0.9 %, understory 13.2 ± 1.7 %; $\chi^2 = 6.82$, $df = 4$, $p = 0.009$, Table 4.1), but did not respond to the tree diversity gradient (Fig. 4.3).

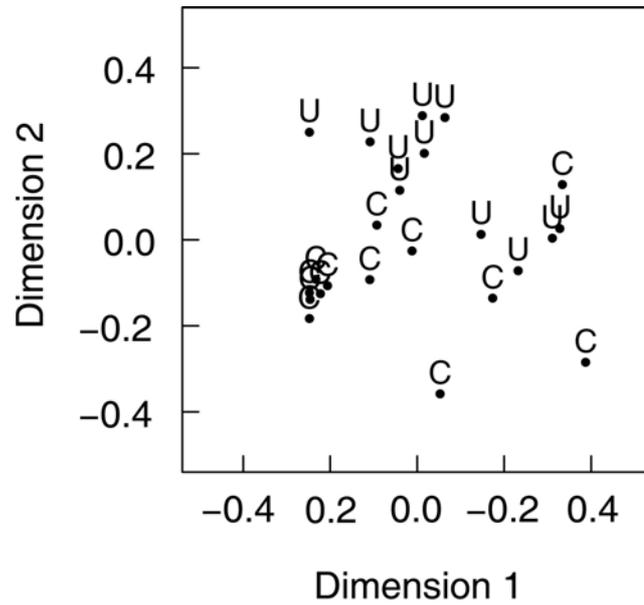


Fig. 4.2. Metric multidimensional scaling (based on Bray-Curtis-similarity) of cavity-nesting bee and wasp host communities across a tree diversity gradient. C = canopy, U = understory.

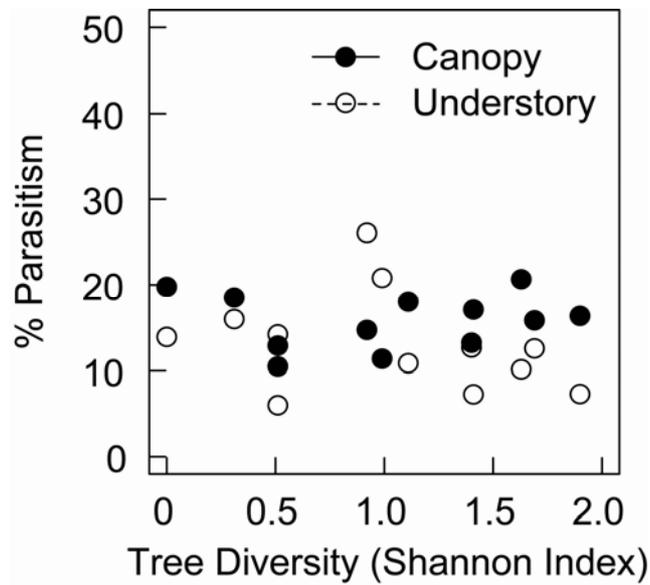


Fig. 4.3. Proportion of hymenopteran brood cells parasitised by natural enemies in the canopy and understory across a tree diversity gradient in a Central European deciduous forest.

Discussion

Our results show that increased tree diversity of deciduous forest stands enhanced abundance, but not species richness, of cavity-nesting bees and wasps. 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. 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 more diverse, cavity-nesting community.

The relationships between abundance or species richness of cavity-nesting communities and plant diversity is little known (but see Gathmann *et al.*, 1994, Tscharncke *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. The increased abundance of hosts in diverse forest stands as observed in our study might be a result of a greater availability of nesting sites and food resources. Surprisingly, the deadwood amount within stands had no effect on abundance or species richness of cavity-nesting host species. This indicates that rather than deadwood as such, a higher diversity of prey items or the quality of actual deadwood nesting sites might have been of importance. Cavity nesting species utilize abandoned galleries of saproxylic beetles for nesting, and especially deadwood suspended in the canopy might serve as an important nesting-site resource as opposed to deadwood on the forest floor. Beetle abundance in the canopy increased across the tree diversity gradient (Sobek *et al.*, submitted), and prey such as caterpillars and spiders may follow a similar pattern.

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 & Leschke 2003, Albrecht *et al.* 2007), and even lower 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 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 like 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 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 was linked to only one or two host species (Appendix 2). 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 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), even though species richness was not increased. Furthermore, temperate forest stands show a distinct stratification of hymenopteran abundance and species composition, most likely related to a greater availability of nesting-sites and food resources in the forest canopy. Hence we conclude that tree diversity in temperate forests is a predictor of insect distribution patterns and associated processes such as parasitism.

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Appendix 4.1

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

Appendix 4.2

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
<i>Chrysis ignita</i> agg.	68	7	1
<i>Coelioxys alata</i>	3	0	1
Diptera	0	7	1
<i>Gasteruption assectator</i>	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
<i>Megatoma undata</i>	52	3	8
<i>Melittobia acasta</i>	41	36	4
Not identified	2	1	2

CHAPTER

5

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

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(submitted)

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 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 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 & 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 & 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 & Brockerhoff 2007). According to data from other invertebrate herbivores (e.g. molluscs), diversity-herbivory relationships are not controlled by plant diversity in the local neighbourhood, 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 & Root 1972, Karban 2007, Sholes 2008), can be explained with two well-established concepts: the resource concentration hypothesis (Tahvanainen & 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 & 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 & Fegan 2007), and during ontogeny defensive plant traits are subject to change (Boege & 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 & 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 & 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.*, in press).

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 & 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, hence, 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 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 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 (Meteoedia 2006). Mean annual precipitation is 590 mm (1973-2004, Deutscher Wetterdienst), and was 518 mm in 2006 (Meteoedia 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 (Appendix 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., *Tilia cordata* Mill. (both Tiliaceae) and *Fraxinus excelsior* L. (Oleaceae). The species *Carpinus betulus* L. (Betulaceae), *Acer campestre* L., *Acer platanoides* L., *Acer 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 have not been logged for at least 40 years. On each site, an observation plot measuring 50 x 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 x 5 m subplots inside each 50 x 50 m main plot (Mölder *et al.* 2009), while herbaceous plant species were identified in the 5 x 5 m subplots and additionally in a larger 20 x 20 m subplot per 50 x 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 (*Acer 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 (Appendix 5.1, 5.2).

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 x 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, 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 x 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' (Appendix 5.3). 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 2007; <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 9 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 (Appendix 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 x 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 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 two, 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 5.1. 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 (ANOVA, $F_{2,23} = 61.18$, $p < 0.001$, Fig. 5.1). 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. 5.2a). 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. 5.2a). 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 5.1).

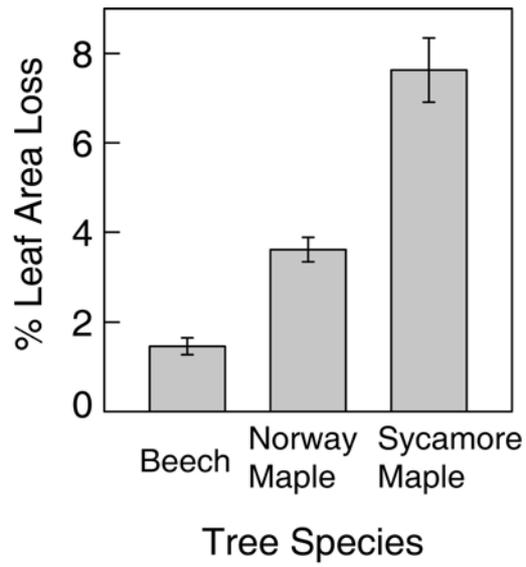


Fig. 5.1. Leaf area consumed per leaf by leaf-chewing insects on tree saplings in the Hainich National Park as mean percentages \pm one standard error (one-way ANOVA, $df = 2$, sum of squares = 0.1, mean of squares = 0.06, $F_{2,23} = 61.18$, $p < 0.001$ and Tukey HSD test, $p < 0.001$ for all combinations).

Table 5.1. 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 Nationalpark. † = removed during model simplification; not tested = no observations made for response variable. NumDF = numerator degrees of freedom , DenDF = denominator degrees of freedom.

Response Variable	Effect	Beech				Norway Maple				Sycamore Maple			
		NumDF	DenDF	F	p	NumDF	DenDF	F	p	NumDF	DenDF	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	-	-	-	†				

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, $F_{1,8} = 31.9$, $p < 0.001$, Fig. 5.2b). 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 5.1).

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 5.2c). 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 5.1).

Table 5.2. Number of specimens and relative abundance (% of total) of different insect feeding guilds, sampled or observed on forest plots in the Hainich National Park. ^aThe sum of the percentages falls below 100 % due to rounding.

	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			2593	99.9 ^a

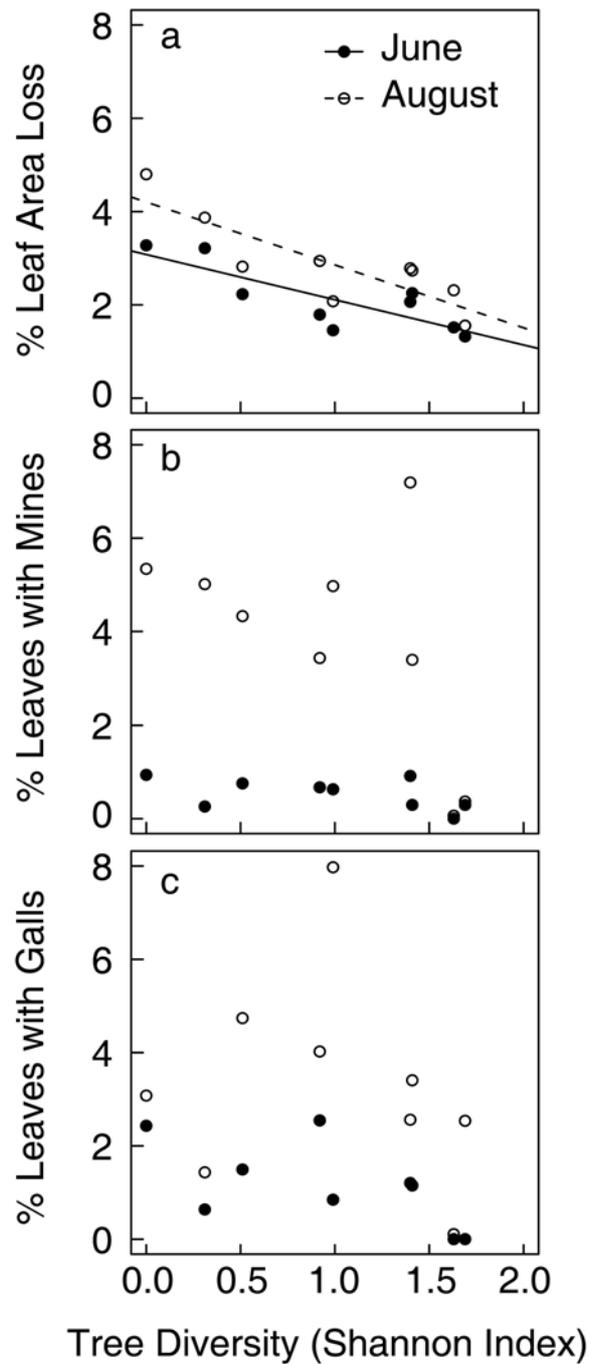


Fig. 5.2. Leaf damage of beech saplings (means per plot) across a tree diversity gradient ranging from monospecific beech to mixed forest stands in the Hainich National Park. (A) Percentage leaf area loss per leaf caused by leaf-chewing insects; (B) percentage of leaves infested with mines of *Stigmella* sp.; (C) percentage of leaves infested with galls of *Hartigiola annulipes* and *Mikiola fagi*. Closed points = June, open points = August.

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 (Appendix 5.1). 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 5.2). Parasitoids contributed 3.9 % and leaf-chewing insects amounted to 4.5 % of the total community (Table 5.2). 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. 5.3). In June, the percentage of predators increased with increasing tree diversity by 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. 5.3).

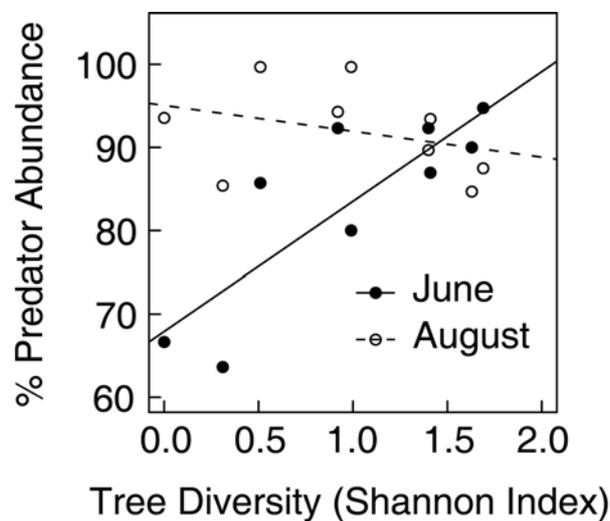


Fig. 5.3. Relative abundance of predators and parasitoids (per plot) on beech saplings across a tree diversity gradient ranging from monospecific beech to mixed forest stands in the Hainich National Park. Closed points = June, open points = August.

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 5.1), but related to sapling complexity (LME, $F_{1,5} = 7$, $p = 0.046$, Table 5.1).

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, Vehviläinen *et al.* 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 & 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 (Riihimäki *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 were 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 & Barkham 1975a, Jennings & Barkham 1975b, Cote *et al.* 2005), and particularly maple is a known food resource for snails and slugs (Pigot & 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 (Appendix 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 & 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 like 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.

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Appendix 5.1

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
%																		
<i>Acer campestre</i>	-		-	-	-	0.2	-	-	-	-	-	-	-	-	2	1.4	-	0.4
<i>Acer platanoides</i>	-	-	-	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
<i>Acer pseudoplatanus</i>	-	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
<i>Carpinus betulus</i>	-	-	-	-	-	-	-	-	-	-	-	1.1	3.4	-	9.2	1.8	10.8	1.8
<i>Fagus sylvatica</i>	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
<i>Fraxinus excelsior</i>	-	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
<i>Prunus avium</i>	-	3.1	-	-	-	-	-	-	-	-	-	-	-	-	1	5.9	-	2.2
<i>Quercus petraea</i>	-	-	-	-	14.8	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quercus robur</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.1	-	1.2	-
<i>Sorbus aucuparia</i>	-	3.1	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tilia cordata</i>	-	-	-	-	-	2.9	2.3	2.5	5.7	0.4	22	1.5	30.8	-	24.5	1.4	22.9	-
<i>Tilia platyphyllos</i>	-	-	2.8	0.6	-	-	1.5	1.5	5.2	-	11	0.4	3.4	-	42.9	0.7	41	-
<i>Ulmus glabra</i>	-	-	-	-	-	-	1.5	0.5	-	-	-	-	-	-	-	0.2	1.2	0.7

Appendix 5.3

Spearman rank correlations of biotic and abiotic plot characteristics with canopy tree diversity. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. ^CCanopy, ^UUnderstory, ^JJune, ^AAugust.

	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	0.6
% 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

Appendix 5.3

Feeding guilds and classification of the insect community sampled/observed on forest plots in the Hainich National Park.

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

6

Discussion & Conclusion

Discussion & Conclusion

To test and unravel biodiversity-functioning relationships, currently two competing approaches exist: biodiversity experiments (e.g. Jena Experiment, Cedar Creek, BIODDEPTH, BIOTREE) and real-world observations (e.g. Research Training Group 1086, Biodiversity Exploratories). The goal behind both approaches is to evaluate how plant species loss affects ecosystem functioning. Whereas biodiversity experiments might be a useful tool for investigating biodiversity-functioning relationships for assessments of productivity in grassland habitats (Schmid 2002), their explanatory value for forest ecosystems is debatable. Major concerns of applicability and comparability to real-world forest systems include the small plot size, plot history, age structure, canopy architecture and planting patterns (Leuschner *et al.* in press). Especially if faunal responses to plant diversity are investigated, it is questionable if the fauna residing on experimental sites is comparable to the native fauna of naturally grown vegetation, which has developed over a long time span and undergone various successional stages. Moreover, not only the residing fauna in biodiversity experiments might be artificial, the assemblage of plant species in biodiversity experiments is strongly biased and does not necessarily correspond to the environmental conditions of real-world systems (Leps 2004), especially if multiple site comparisons are lacking. In contrast, observational studies are often criticised because they lack control and manipulation of possible confounding variables, such as soil fertility etc., which limits strong conclusions on how plant diversity *per se* affects higher trophic levels and ecosystem functioning. Nevertheless, this limitation can be overcome by integrating researchers of multiple disciplines into large-scale observational projects, thereby ensuring consolidation of measurements which should comprise as many biotic and abiotic parameters as possible.

In the multidisciplinary observational study on hand, species richness of beetles and true bugs responded to the semi-natural tree diversity gradient in accordance to our main hypothesis that insect species richness increases with increased tree diversity. However, species richness of cavity-nesting bees and wasps did not directly respond to tree diversity *per se* and only increased with enhanced bee and wasp abundance, but differences were present across forest strata. Considering the fact that different taxa depend on different resources, it is not surprising that tree diversity does not affect all taxa directly and alike. Beetles and in particular, true bugs, are often closely associated with certain plant and tree species (Wachmann *et al.* 2004), and should thus be more susceptible to changes in tree and plant diversity. In contrast, bees might depend on a high variety and density of flowering resources

(Höhn *et al.* submitted) simply not present in temperate forest habitats, whereas wasp diversity and abundance might also be controlled by the availability of larval food (e.g. aphids, lepidopteran caterpillars, spiders) and light intensity (Klein *et al.* 2006).

We could demonstrate for beetles and true bugs, that species turnover (β -diversity) in space and time contributed most to overall γ -diversity, accounting for about 90 % of the observed total species richness. It was particularly striking that turnover between trees, even between conspecific beech individuals, was high if a sufficient number of tree replicates was analysed. Besides stand-level heterogeneity mediated by tree diversity, between-tree heterogeneity, e. g. different microhabitat conditions (microclimate, water-run off, sun exposure etc.) might play an important role for the diversity and distribution of insect species within temperate deciduous forest stands (Winter & Möller 2008).

Additionally we could show that leaf area loss of beech saplings was directly related to tree diversity and decreased in the more species rich stands as hypothesised, while relative abundance of predators increased, but no effect was found for other tree species or the abundance of galls and mines. Here, mechanisms of resource concentration (Tahvanainen & Root 1972, Root 1973,) and natural enemy abundance (Root 1973, Russell 1989) most likely play a role for biocontrol of insect herbivores, and our results demonstrate that multitrophic interactions in real-world forest ecosystems are complex and vary vastly across the studied taxa. Further studies, for example focusing on certain herbivore species and using phytometers, might help to disentangle the core mechanisms of the observed biodiversity-functioning relationships.

We conclude that in diverse real-world forest ecosystems, a variety of biodiversity-functioning relationships are effective. A loss of tree species would result in changes of the residing insect community, leading to a shift and eventually loss of functional responses. Simple beech stands alone are insufficient in conserving forest biodiversity and the related ecosystem functions. Forest management has to ensure that a variety of deciduous tree species is afforested and conserved, thereby maintaining habitat heterogeneity. It remains tantalising if the patterns observed in our study can be reproduced and approved in temperate tree diversity experiments, and we suggest an integrative approach of real-world observations and diversity experiments as best-practice for future research.

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Summary

Throughout the last decade, linking biodiversity with ecosystem functioning and services, such as pollination and biocontrol of pest species, has gained major attention in ecological research. In particular biodiversity loss due to human land use and disturbance has been determined as a major threat, eventually leading to a decline in ecosystem services and functions.

The major proportion of global biodiversity can be found in forest ecosystems, and especially in tropical regions pristine forest habitats become more and more scarce. In temperate regions the situation is hardly any better: even though in Germany 30 % of land surface is covered by forest, the proportion of old-growth natural forest equals zero. Hence it is of immediate importance to identify the contribution of the remaining semi-natural forests to biodiversity and ecosystem functioning.

Investigations in tropical rainforests have shown that insects in the forest canopy contribute highly to global biodiversity, but data on canopy fauna in temperate deciduous forests are scarce. Even though plant diversity in agricultural or experimental grassland habitats has often been related to insect diversity, no information is available whether the same relationship exists in forest habitats. In the study on hand, we related diversity and function of canopy and understory insect communities to a natural tree diversity gradient ranging from simple beech to mixed deciduous forest stands. The scope of our investigation was to analyse effects of canopy tree diversity on insect species richness, community structure and multitrophic interactions across various spatiotemporal scales in a real-world ecosystem, based on two major hypotheses: (1) insect diversity increases with increased canopy tree diversity, (2) herbivory decreases with increased canopy tree diversity.

The study was conducted using 12 forest plots in the Hainich National Park, Germany's largest remaining semi-natural deciduous forest. A variety of methods was applied to sample the resident insect fauna, such as flight-interception traps, beating samples, and trap nests for cavity-nesting hymenopterans. Furthermore, herbivory of tree saplings was estimated (leaf area loss, abundance of galls and mines). This approach ensured that a variety of taxa (beetles, true bugs, bees, wasps and their natural enemies) and functions (herbivory, predation, parasitism) was included in the analyses.

Total species richness (γ -diversity) of beetles and true bugs increased across the tree diversity gradient as hypothesised, and the same pattern was found for most functional groups (e.g forest specialists, predators etc.). Species richness of cavity-nesting bees and wasps did not

respond to tree diversity. For beetles and true bugs, species turnover (β -diversity) in space and time contributed most (~90 %) to overall γ -diversity. Turnover between tree individuals was high if a sufficient number of tree replicates was analysed, even among trees of the same species in simple beech stands. Besides stand-level heterogeneity, between-tree heterogeneity apparently plays a major role in determining insect species richness in deciduous forests. Furthermore, the forest stands showed a distinct stratification of bee and wasp abundance, community composition, and parasitism rates. Enhanced resource availability (e.g. nesting sites, host and prey abundance) might be one reason why increased tree diversity also controls species richness, but not function of higher trophic levels. Concerning herbivory damage on tree saplings in the forest understory, leaf area loss was generally higher in maple compared to beech saplings, but only beech showed a decline in damage across the tree diversity gradient. No pattern was 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. Rather than tree diversity *per se*, the identity and abundance of the sampled tree species in most cases was a better predictor for the observed responses, and effects can be explained by mechanism of resource concentration and abundance of natural enemies (enemies hypothesis).

In conclusion, our study gives new insights into the effects of tree diversity on insect species richness and multitrophic interactions. Although planted experiments are of great value for determining fundamental mechanisms behind observed effects, these effects might not occur or run differently in undisturbed, semi-naturally established forests, since planted experiments are insufficient in imitating the age structure and spatial heterogeneity of natural forests. By studying one of Europe's largest semi-natural deciduous forests we could demonstrate that complex biodiversity-functioning relationships are effective in real-world forest ecosystems, and that temporal and spatial species turnover is the key to understanding biodiversity patterns. It became evident that simple beech stands alone are unsatisfactory in conserving the full set of regional insect species richness. We suggest that sustainable forest management should aim at maintaining a diverse mix of structurally different tree species and individuals, thereby enhancing habitat heterogeneity and providing resources for a diverse and highly functional insect community.

Zusammenfassung

Während des letzten Jahrzehnts ist der Zusammenhang zwischen Biodiversität und Ökosystemfunktionen bzw. -dienstleistungen, wie z. B. Bestäubung oder biologische Schädlingskontrolle, ins Zentrum ökologischer Forschung gerückt. Vor allem Verlust von Biodiversität durch anthropogen bedingte Störung und Landnutzung wurde als Gefahr determiniert, wodurch ein Rückgang an Ökosystemfunktionen und -dienstleistungen zu erwarten ist. Der größte Anteil der globalen Biodiversität findet sich in Waldökosystemen, und besonders in den Tropen nimmt der Anteil an ursprünglichen Waldhabitaten immer mehr ab. Auch in der temperaten Zone ist die Situation kaum besser: Obwohl in Deutschland 30 % der Landesfläche von Wald bedeckt sind, beträgt der Urwaldanteil an diesen Waldflächen gleich Null. Daher ist es von großer Bedeutung, den Beitrag der noch verbleibenden naturnahen Wälder für den Erhalt von Biodiversität und den damit einhergehenden Ökosystemfunktionen zu bestimmen. Untersuchungen in tropischen Regenwäldern haben gezeigt, dass Insekten im Kronenraum den größten Teil der globalen Biodiversität stellen, für temperate Laubwälder liegen jedoch kaum Daten vor. Obwohl Pflanzendiversität in der Agrarlandschaft oder in experimentellen Graslandhabitaten häufig mit erhöhter Insektendiversität in Verbindung gebracht werden konnte, gibt es kaum Hinweise ob der gleiche Effekt auch in Waldhabitaten gilt. In der vorliegenden Arbeit wurde die Diversität und Funktion von Insektengemeinschaften entlang eines natürlichen Baumartendiversitätsgradienten untersucht, unter Berücksichtigung von Buchenreinbeständen bis hin zu hochdiversen Laubmischwäldern. Ziel der Arbeit war eine Analyse des Effekts von Baumartendiversität auf den Artenreichtum, die Gemeinschaftsstruktur und multitrophische Interaktion von Insekten entlang verschiedener räumlich-zeitlicher Skalen in einem real existierenden (nicht experimentellen) Ökosystem. Dabei wurden folgende Leithypothesen verfolgt: (1) Insektendiversität ist mit steigender Baumartenvielfalt erhöht, (2) Herbivorieschäden werden bei zunehmender Baumartenvielfalt verringert.

Für die Untersuchung wurden 12 Waldflächen im Nationalpark Hainich, Deutschlands größtem noch verbleibenden zusammenhängenden Laubwaldgebiet, genutzt. Verschiedene Methoden kamen zum Fang der Insektenfauna zum Einsatz, z. B. Kreuzfensterfallen, Klopfproben und Nisthilfen für Bienen und Wespen. Desweiteren wurde der Herbivorieschaden von Baumjungwuchs geschätzt (Verlust an Blattfläche, Vorhandensein von Gallen und Minen). Durch diesen Ansatz konnte gewährleistet werden, dass eine Vielfalt von Taxa (Käfer, Wanzen, Bienen, Wespen und deren natürliche Feinde) und Funktionen

(Herbivorie, Prädation, Parasitismus) in die Analyse mit einbezogen werden konnte. Der Gesamtartenreichtum (γ -Diversität) der Käfer und Wanzen nahm mit steigender Baumartenvielfalt zu, und das gleiche Muster konnte auch in den meisten funktionellen Gruppen gefunden werden (z. B. Waldspezialisten, Prädatoren, etc.). Der Artenreichtum von Bienen und Wespen reagierte jedoch nicht auf die erhöhte Baumartenvielfalt. Bezüglich Käfern und Wanzen spielte vor allem der räumlich und zeitliche Arten turnover (β -Diversität) eine Rolle und trug am meisten (~90 %) zur allgemeinen γ -Diversität bei. Der Turnover zwischen Baumindividuen war stets hoch, wenn eine ausreichend hohe Anzahl an Bäumen berücksichtigt wurde, auch zwischen Bäumen der gleichen Art in Buchenreinbeständen. Neben Heterogenität auf Bestandesebene spielt also auch Heterogenität zwischen Einzelbäumen eine Rolle für den Artenreichtum von Insekten in temperaten Laubwäldern. Darüberhinaus zeigten die untersuchten Bestände auch eine distinkte Stratifizierung von Bienen- und Wespenabundanz, Gemeinschaftszusammensetzung und Parasitierungsrate. Gesteigerte Ressourcenverfügbarkeit (z. B. Nistmöglichkeiten, Wirts- und Beuteabundanz), vor allem im Kronenraum ist ein möglicher Grund warum Baumartenvielfalt sich ausserdem positiv auf den Artenreichtum höher trophischer Ebenen (Parasitoide) auswirkt. Eine gesteigerte Funktion (Parasitierungsrate) konnte mit dem Anstieg der Baumartenvielfalt jedoch nicht in Zusammenhang gebracht werden. Bezüglich des Herbivorieschadens an Baumjungwuchs in der Krautschicht konnte festgestellt werden, dass der Blattflächenverlust zwar generell bei Ahorn am höchsten war, jedoch nur bei Buchensämlingen mit steigender Baumartenvielfalt tatsächlich auch geringer wurde. Es wurde kein bestimmtes Muster für das Vorkommen von Gallen und Minen gefunden. Die relative Abundanz von Prädatoren auf Buchensämlingen zeigt ein saisonal bedingtes Muster und stieg im Juni in gemischten Beständen an, was eine erhöhte biologische Schädlingskontrolle bewirkt haben könnte. Nicht Baumartenvielfalt allein, sondern die Artenidentität und Abundanz der beprobten Baumsämlinge war häufig besser geeignet, um die beobachteten Effekte zu erklären, welche vermutlich sich vermutlich auf Ressourcenkonzentration und die Abundanz von natürlichen Feinden zurückführen lassen.

Zusammenfassend lässt sich feststellen, dass die vorliegende Arbeit neue Einsichten bezüglich des Effekts von Baumartenvielfalt auf den Artenreichtum und multitrophischen Interaktionen von Insektengemeinschaften zulässt. Auch wenn angepflanzte Experimente einen großen Wert für die Bestimmung fundamentaler Mechanismen bestimmter Effekte besitzen, kann es dennoch sein dass diese Effekte in naturnahen Wäldern anders, oder im Extremfall gar nicht, in Erscheinung treten, da Anpflanzungen die Altersstruktur und räumliche Heterogenität eines

natürlich gewachsenen Waldes nur unzulänglich wiedergeben. Durch die Untersuchung eines der größten zusammenhängenden Laubwaldgebiete Europas konnten wir zeigen, dass in realen Waldökosystem komplexe Biodiversitäts-Ökosystemfunktionsbeziehungen eine Rolle spielen, und das räumlicher und zeitlicher Artenturnover der Schlüssel zum Verständnis von Diversitätsmustern ist. Es konnte deutlich gemacht werden, dass Buchenreinbestände nur unzulänglich in der Lage sind, den vollen regionalen Artenreichtum von Insekten zu erhalten. Wir schlagen vor, dass nachhaltige Waldnutzung darauf abzielen sollte, dass ein diverser Mix an strukturell verschiedenen Baumarten und –individuen erhalten bleibt, wodurch die Habitatheterogenität erhöht wird, um mehr Ressourcen für eine artenreiche und hochfunktionelle Insektenlebensgemeinschaft zur Verfügung steht.

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“Most children have a bug period, and I never grew out of mine!”

Curriculum Vitae

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Education

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Publications

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