

GÖTTINGER ZENTRUM
FÜR BIODIVERSITÄTSFORSCHUNG UND ÖKOLOGIE
- GÖTTINGEN CENTRE FOR BIODIVERSITY AND ECOLOGY -

**Interacting effects of
forest edge, tree diversity and forest stratum
on the diversity of plants and arthropods in Germany's
largest deciduous forest**

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultäten der
Georg-August-Universität Göttingen

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Göttingen, März 2015

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Tag der mündlichen Prüfung: 27.04.2015

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CHAPTER 1

GENERAL INTRODUCTION



Introduction

Worldwide, forests are under pressure through global change. Since the climate of the Northern Hemisphere is predicted to become drier and warmer in the future (IPCC, 2007), current forest management schemes aim at converting mono-specific forest stands into structurally more diverse forests with a higher abundance and diversity of native deciduous tree species (Brang et al., 2008; Kolström et al., 2011; Pretzsch et al., 2013; Schmitz et al., 2014). The goal of this is not only to reduce the susceptibility of forests to climate change and pests („Insurance-Hypothesis“ (Yachi & Loreau, 1999)) but also to preserve overall biodiversity (Fritz, 2006). This last goal is embedded in the convention on biological diversity (Rio, 1992) (BMU, 2010). Yet, evidence for overall positive effects of increased tree diversity on biodiversity in temperate forests is scarce. Studies on tree diversity effects so far provide opposing results across study regions and taxa (Vehviläinen et al., 2007; Sobek et al., 2009a, 2009c; Schuldt et al., 2010; Scherber et al., 2014).

Another aspect of global change and a major threat to biodiversity is the increasing fragmentation of habitats (Fahrig, 2003). Once covering the major part of the land surface (Ellenberg & Leuschner, 2010), today forests constitute only one third of the total area of Germany (Schmitz et al., 2014) and primeval forests completely vanished. As a result, in Central Europe and globally forests are highly fragmented (Harper et al., 2005). Forest fragmentation is accompanied by an increase in forest edge zones. Edge effects can strongly alter environmental conditions and resource distribution in forest remnants and affect species invasion from the matrix (surrounding habitat), community composition and biotic interactions (Murcia, 1995; Ries et al., 2004). Thus, small fragments are exposed to the risk of not holding an “interior zone/habitat” anymore - to the detriment of species relying on inner forest conditions (Laurance & Yensen, 1991; Bender et al., 1998; Tschardtke et al., 2012).

Therefore, from a conservation perspective it is important to assess not only depth and strength that edge effects penetrate into forests, but also where they occur, where they do not occur and which species are affected (Ries & Sisk, 2010 and references therein). Edge effects are commonly believed to extend only a few meters into forests, generally not exceeding a depth of 50 m (Murcia, 1995). Hence, the majority of studies only assessed edge effects or edge vs. interior differences on small spatial scales (Duelli et al., 2002; Pohl et al., 2007; Wermelinger et al., 2007; Noreika & Kotze, 2012; Vodka & Cizek, 2013). However, evidence is increasing that edge effects can occur across large distances up to more than one kilometre. This has recently been shown for environmental factors, plants, invertebrates and vertebrates (Laurance, 2000; Ewers & Didham, 2008; Bergès et al., 2013; Hofmeister et al., 2013;

Pellissier et al., 2013). Patch contrast (difference in habitat quality between fragment and adjacent matrix) and the three-dimensional architecture (*sensu* plant structure) can influence the depth and strength that edge effects penetrate into fragments (Cadenasso et al., 2003; Ries & Sisk, 2004; Ries et al., 2004; Collinge, 2009). Patch contrast can have an impact on species invasion into forests since species are more likely to permeate into fragments with a low patch contrast (Cadenasso et al., 2003; Ries & Sisk, 2004; Noreika & Kotze, 2012). A remnant's architecture can influence factors such as wind and light penetration into the fragment, which in turn affect microclimatic conditions (e.g. temperature and humidity), understory plant growth, resource distribution and habitat heterogeneity (Ries et al., 2004). This can have far-reaching consequences on patch-dependent species and on the colonisation of remnants by edge and open-habitat species (Driscoll et al., 2013 and references therein).

Tree species composition shapes the (canopy) architecture of forests (Getzin et al., 2012; Seidel et al., 2013) and may therefore play an important role in this context. Tree species differ with respect to crown architecture, canopy cover, time of leaf budding, leaf litter quality and so forth. This can affect environmental and microclimatic conditions such as light availability on the forest floor, soil moisture and pH, litter layer depth and nutrient availability (Barbier et al., 2008; Wulf & Naaf, 2009; Jacob et al., 2010). Central European deciduous forests are typically dominated by the tree species *Fagus sylvatica* L. (Ellenberg & Leuschner, 2010), a shade tolerant, highly competitive autogenic ecosystem engineer, strongly shaping its environment by a dense, little light transmitting canopy, thick mats of acidic, slowly decomposing leaf litter and a species-poor herb layer (Guckland et al., 2009; Jacob et al., 2010; Mölder et al., 2014).

A mixture of different tree species may thus reduce litter depth and increase light availability, herb diversity, habitat heterogeneity and niche and resource diversity (Paillet et al., 2010; Vockenhuber et al., 2011). These factors have been shown to increase plant and invertebrate species richness in forests (Huston, 1994; Brändli et al., 2007; Sobek et al., 2009b; Vockenhuber et al., 2011; Lange et al., 2014) and may reduce the contrast between the variable conditions at the forest edge and the forest interior, thus enabling the permeation of species not explicitly adapted to inner forest conditions.

Results of Vockenhuber et al. (2011) indicate interacting effects of edge proximity and tree diversity on herb layer characteristics. However, their study was not designed for explicitly testing this hypothesis and to my knowledge there is no other study that did.

The way that species respond to edge proximity and tree diversity may depend on species specific requirements. Generalists and open habitat species are often positively affected by

forest edge zones (Rainio & Niemelä, 2003 and references therein) and may benefit from altered environmental conditions induced by a more diverse tree layer. Forest species are more likely to suffer from forest edge zones due to factors such as drier microclimate, heterogeneous environmental conditions and competition for resources with invading species but may on the other hand benefit from an increase in niche and resource diversity. The same may be true for species of different body size since this is linked to the sensitivity to environmental changes (Janzen & Schoener, 1968; Peters, 1986). Therefore, we test if the response of organisms to edge proximity and tree diversity depends on life history traits and habitat affinity.

Finally, forest canopy and understory have very different prerequisites regarding microclimate, habitat structure and composition of inhabiting species. Therefore, tree diversity and edge effects may differ across forest strata.

This thesis is the first to analyse the relative effects of forest edge, tree diversity and stratum, considering interactions among these potential predictors of changes in community structure of herb layer plants, ground-dwelling arthropods (ground beetles, rove beetles and spiders) and the total flying beetle fauna (captured with flight interception traps). In this context, the following main research questions were addressed:

1. Does tree diversity have overall positive effects on forest biodiversity across taxa?
2. Do tree diversity and forest edge interactively affect species richness and composition of arthropods and understory plants?
3. Do edge effects differ across forest strata?
4. Are tree diversity effects different across forest strata?
5. Are different functional groups (in terms of habitat specialisation and body size) of plants and invertebrates differently affected by edge proximity, tree diversity (and forest stratum)?

Study region

The study was conducted in the Hainich National Park. The Hainich region - a forested mountain range running 24 km from north to south (highest elevation at 494 m a.s.l.) - is located in northwestern Thuringia, Germany. It is based on limestone (Triassic Upper Muschelkalk), mainly covered by beech forest communities of calcareous soils. The main soil type is (stagnic) Luvisol with partial loess cover (Leuschner et al., 2009; Schmidt et

al., 2009). With a total area of 16.000 ha, this forest is the largest connected deciduous forest in Germany.

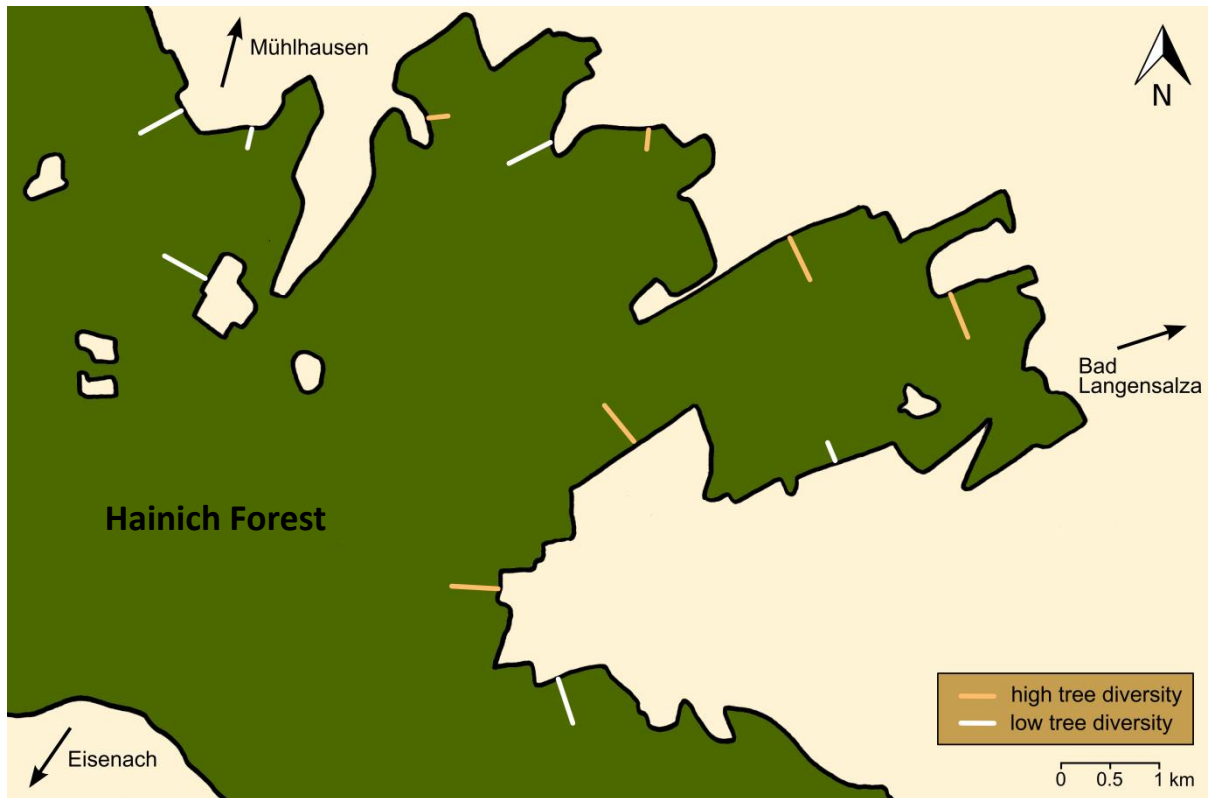


Figure 1 Distribution of the twelve transects within the forest of the Hainich National Park.

Its southern part, an area of 7.500 ha (Fig. 1 and 2), has been declared as national park in 1997. It is located between the cities of Mühlhausen, Bad Langensalza and Eisenach ($51^{\circ} 5' 0''$ N, $10^{\circ} 30' 24''$ E). The mean annual temperature of the region ranges between 7 and 8 °C, while the mean annual precipitation varies between 600 and 700 mm (Grossmann & Biehl, 2007). In 2011 the national park was included into the UNESCO World Heritage sites “Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany”. The main forest communities of the study area are *Hordelymo-Fagetum*, *Galio-Fagetum* and *Stellario-Carpinetum* (Mölder et al., 2006), with distinct differences in herb layer characteristics between spring (spring ephemerals) and summer (Fig. 3 and 4).

Historically, the forest has been used since the 12th century as irregular coppice with standards system (“Mittelwald”). From the middle of the 19th century on it was converted into high forest (“Hochwald”) and multiple aged forest system (“Plenterwald”). Since the study site became military restricted area in 1964, management was reduced to a minimum, allowing for a near natural development of the forest until today (Mölder et al., 2006).

An outstanding characteristic of this area is the mosaic of forest stands with contrasting tree diversity ranging from 1 to 14 tree species/ha (Fig. 2), which results from the past



Figure 2 Forest stands in the Hainich National Park with contrasting tree species diversity. Top: Beech dominated forest stand with low tree species richness; bottom: forest stand rich in tree species.



Figure 3 Characteristic plants occurring on the study sites: From top left to bottom right: *Campanula trachelium*, *Corydalis cava*, *Circaea lutetiana*, *Hepatica nobilis*, *Leucojum vernum*, *Stellaria holostea*, *Primula elatior*, *Senecio ovatus*.

management but with comparable climate and soil conditions (Mölder et al., 2006; Leuschner et al., 2009). This makes the Hainich National Park particularly suitable for the purpose of this project.

Transects ranging from the forest edge up to 500 m into the forest interior were established both in forest stands poor and rich in tree species. The target organisms were studied along each transect: herb layer plants with vegetation relevés, ground-dwelling arthropods with pitfall traps and the flying beetle fauna with flight interception traps. Forest stands with low tree species diversity were strongly dominated by beech (*Fagus sylvatica*). In contrast, beech dominance was reduced in forest stands with high tree species diversity (Fig. 2) and they



Figure 4 Characteristic plant species occurring on the study sites: From top left to bottom right: *Anemone nemorosa*, *Pulmonaria obscura*, *Melampyrum nemorosum*, *Daphne mezereum*, *Cardamine pratensis*, *Fragaria viridis*, *Anemone ranunculoides*.

contained a higher abundance and diversity of other deciduous tree species (*Quercus robur* L., *Quercus petraea* LIEBL., *Tilia* sp., *Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Fraxinus excelsior*, *Carpinus betulus* L., *Tilia cordata* MILL. and *T. platyphyllos* SCOP. Less abundant were *Prunus avium* L., *Betula pendula* ROTH, *Populus tremula* L., *Ulmus glabra* HUDS., *Salix caprea* L. and *Sorbus torminalis* (L.)). The matrix consisted of abandoned grassland.

In contrast to other studies conducted in the region within the framework of the research training group ‘Graduiertenkolleg 1086: The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests’ this study covers the whole forested area of the Hainich National Park (Fig. 1).

Chapter outline

Chapter 2: How forest edge–center transitions in the herb layer interact with beech dominance versus tree diversity

This chapter studies the effects of tree diversity and distance from the forest edge on herb layer vegetation. Higher tree diversity led to increased plant species richness of the herb layer in the forest interior. In the high tree diversity level plant species richness remained constant with increasing distance from the edge, whereas it strongly declined in the beech dominated forest stands poor in tree species. The dominance of forest specialist species within the plant community increased with distance from the forest edge and was much higher in the low tree species level. The fraction of forest generalists decreased from the forest edge towards the centre and was higher under increased tree diversity. The plant community composition in the high tree diversity level was different and more variable compared with the low tree diversity level. Furthermore, the variability of the community composition was stronger with increasing influence of the forest edge. Litter depth mediated by tree diversity was identified as most important predictor of plant species richness.

Chapter 3: Tree diversity and species’ traits moderate forest edge responses of ground-dwelling beetles and spiders

This study explores differences in tree diversity and edge response across different taxa of ground-dwelling arthropods (ground beetles, rove beetles and spiders) and different species’ traits (habitat specialisation and body size).

No general conclusion could be drawn for total species richness of the three taxa, since each taxon responded individually. Yet, dividing the species into habitat affinity groups (habitat

generalists (including open-habitat species) and forest species) and according to their body size into small and large species revealed general patterns across all taxa studied.

The species richness of forest species was hardly influenced by edge proximity. Species richness of habitat generalists strongly declined from the forest edge towards the forest interior. However, this effect was mitigated by increased tree diversity (not for spiders). Our results show that among all ground-dwelling arthropods, generalists and in particular small species benefitted from an increase in tree diversity, whereas the species richness of forest species was not affected. However, analysing the response of individual species showed that some forest species benefitted, whereas others suffered from increased tree diversity. We attribute our findings to changes in environmental conditions induced by tree diversity and edge proximity.

Chapter 4: Interacting effects of forest stratum, edge and tree diversity on beetles

In this chapter forest stratum was added as a third component to the study design and edge and tree diversity effects on beetles were compared between forest canopy and understory.

Edge effects extended up to 500 m into the forest interior and were not affected by tree diversity. However, edge effects were weaker in the canopy compared with the understory, which is likely to result from a higher, edge-like microclimatic variability and harshness in the canopy. The species richness of habitat generalists strongly declined from the forest edge towards the forest interior and drove the response of total beetle species richness. On the contrary, saproxylic and forest species only responded weakly. The richness of saproxylic and forest species peaked in the canopy, whereas habitat generalists and non-saproxylic species dominated the forest understory.

Pathways driving beetle richness differed across forest strata. In the canopy, tree diversity and dead wood amount were the decisive factors, whereas in the understory tree diversity effects were less strong and edge proximity and canopy openness were more important. In conclusion, tree diversity effects in the canopy were more direct, while effects in the understory were more indirect.

Conclusions

This thesis is the first to analyse the relative effects of forest edge, stratum and tree diversity in consideration of their interactions, thereby predicting plant and arthropod communities in forests.

The three studies show that increased tree diversity in general enhances biodiversity in forests. We thus conclude that converting mono-specific beech into mixed forest stands will contribute to preserving overall biodiversity of plants and arthropods as embedded in the convention on biological diversity 2020. Saproxyllic arthropods, a group containing many threatened species, may explicitly benefit from that. However, this study also showed that forest stands of contrasting tree diversity can house distinctly different communities of plants and arthropod and that some forest species may even suffer from increased tree diversity. This underlines the importance of not only increasing tree diversity as sole conservation goal, but also to preserve old-growth mono-beech forests as specified in the UNESCO World Heritage sites “Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany”. Across all groups studied the species richness of specialised species (forest and saproxyllic species) were least affected by edge effects.

Interactions of tree diversity and edge proximity seem to gain relevance from the canopy towards the forest floor. In concordance, species in the canopy are more directly and stronger affected by tree diversity, whereas tree diversity effects became weaker and more indirect in the understory by altering environmental conditions, such as habitat heterogeneity, litter depth and resource distribution, thereby enhancing the colonisation of species not explicitly adapted to inner forest conditions. Furthermore, more factors not linked to tree diversity seem important on the forest floor.

In conclusion, for gaining a deeper understanding of forest fragmentation the relative importance of edge, stratum and tree diversity, but also species’ life-history traits (e. g. body size) and habitat specialisation should be considered.

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CHAPTER 2

**HOW FOREST EDGE–CENTER TRANSITIONS IN THE
HERB LAYER INTERACT WITH BEECH DOMINANCE
VERSUS TREE DIVERSITY**



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First published online: January 19, 2016 in *Journal of Plant Ecology*



Abstract

Forest fragmentation and the associated augmentation of forest edge zones are increasing worldwide. Forest edges are characterized by altered plant species richness and community composition. As the tree layer and its species composition has been shown to influence herb layer composition, changes in tree species composition or richness may weaken or strengthen edge effects in forest ecosystems. We studied effects of the edge–center transition, tree species composition and their potential interaction on the understory vegetation in the Hainich National Park, Germany’s largest connected deciduous forest, allowing to cover large edge-center transects.

We established 12 transects in an area of 75 km² of continuous forest, 6 beech-dominated and 6 in multispecies forest stands. Each transect reached from the forest edge up to 500 m into the forest interior. Vegetation relevés were conducted in regular, logarithmic distances along each transect.

Herb species richness was influenced by an interaction of edge effects and tree diversity level. With increasing distance from the forest edge, herb species richness remained constant in multispecies forest stands but rapidly decreased in beech-dominated forest stands. Further, herb richness was higher in the interior of multispecies forest stands. Percent forest specialists increased and percent generalists decreased with distance from the edge and this contrasting pattern was much more pronounced in beech-dominated transects. By using structural equation modeling, we identified litter depth mediated by tree species composition as the most important driver of herb layer plant species richness.

Keywords

community composition, *Fagus sylvatica*, functional groups, habitat specialists and generalists, litter depth, tree diversity



Introduction

Forests are highly fragmented all over the world (Harper et al., 2005). One consequence of forest fragmentation is the rapid increase of area covered by forest edge zones (Fahrig 2003; Honnay et al., 2002). Forest edge zones may indirectly reduce the actual area of forests, as matrix effects have been shown to reach deep into the forest, thus altering the habitat conditions (Murcia 1995). As a result, small forest remnants may hold no ‘forest interior’ anymore, since edge zones do not represent suitable habitat for species that depend on inner forest conditions (Bender et al., 1998; Laurance & Yensen 1991; Tschardt et al., 2012). Consequently, from a conservation perspective, it is essential to evaluate the depth, strength and underlying mechanisms of edge effects in forest ecosystems, if the aim is to preserve species diversity in forests.

Forest herb species communities can be affected by edge effects since their composition is shaped by altered habitat conditions such as increased light availability, altered rates of herbivory, reduced soil moisture, fertilizer drift or increased atmospheric deposition (Burke & Nol 1998; Gonzalez et al., 2010; Honnay et al., 2002; Pellissier et al., 2013; Wuyts et al., 2013). Furthermore, conditions at the edge are more heterogeneous compared to the forest interior (Ewers & Didham 2006). Overall, plant species richness at forest edges is often higher than in the forest interior (Murcia 1995; Ries et al., 2004), since the edge can promote generalist, edge and open land species. In the 1990s, there was a consensus that the maximum distance at which forest plant communities are influenced by edge effects does not exceed ca. 50 m (Murcia 1995), whereas recent findings indicate that edge effects may reach several hundred meters into forest interiors (Bergès et al., 2013; Hofmeister et al., 2013; Pellissier et al., 2013; Vockenhuber et al., 2011). This emphasizes the need of taking larger spatial scales into account when evaluating the edge’s impact on forest plant communities.

Another important factor determining herbaceous plant species richness in Central European forests is tree species composition (Barbier et al., 2008; Wulf & Naaf 2009). Because tree species differ in traits such as growth height, leaf size, crown shape, canopy cover, time of leaf budding and leaf litter quality, tree species determine microclimatic conditions via light transmittance through the canopy, soil moisture, soil pH, litter depth and nutrient availability (Guckland et al., 2009; Jacob et al., 2010; Wulf & Naaf 2009).

The common beech *Fagus sylvatica* L., a shade tolerant, highly competitive autogenic ecosystem engineer species, strongly determines the environmental conditions in a beech forest, primarily due to low light availability (dense canopy structure) and a thick litter layer



(acidic, slowly decomposing leaf litter) (Härdtle et al., 2003; Jacob et al., 2010; Wulf & Naaf 2009). In Central Europe, most broadleaved forests are dominated by beech.

However, current ecological forest management schemes aim at establishing a higher abundance and diversity of other native deciduous tree species, thus reducing beech dominance (Barbier et al., 2008; Röhrig et al., 2006). This may result in an increasing species diversity of herb layer plants (Barbier et al., 2008; Vockenhuber et al., 2011) and proportion of generalist species (Mölder et al., 2006) due to indirect soil-mediated processes, but also due to increased habitat heterogeneity, light availability and altered herbivore pressure (Wirth et al., 2008). Yet, mechanisms are insufficiently understood (Barbier et al., 2008; Bengtsson et al., 2000) and analyses explicitly disentangling multiple mechanisms and pathways between tree diversity, herb layer diversity and herb layer species composition are still missing.

A habitat remnant's three-dimensional architecture (*sensu* plant structure) is shaped by its tree species composition (Seidel et al., 2013). It can determine the extent of edge effects (Murcia 1995; Pellissier et al., 2013; Ries et al., 2004), since it predicts factors such as light and wind penetration into a patch, in turn affecting abiotic factors (light availability, temperature, humidity) and thereby understory plant growth (Ries et al., 2004). Moreover, edge effects are stronger in habitat remnants with a high patch contrast (=quality contrast between two adjacent habitats or matrix and fragment) and matrix species are more likely to penetrate fragments with a low patch contrast (Cadenasso et al., 2003; Ries & Sisk 2004). Increased tree diversity in beech forests may reduce the contrast between heterogeneous conditions at the edge and conditions in the forest interior *inter alia* due to a higher light availability and habitat heterogeneity. This may lead to weaker edge effects compared with beech-dominated forest stands. Nevertheless, we are not aware of any study explicitly assessing interactions between tree diversity and edge effects. In this study, the following main hypotheses were tested:

1. Multispecies forest stands affect herb species richness positively.
2. Overall herb species richness, and especially species richness of generalist, edge and open land species, is higher at forest edges.
3. Edge effects on herb species richness are more pronounced in beech-dominated forest stands than in multispecies forest stands, which enable generalists, edge and open land species to permeate deeper into the forest.
4. Effects of tree layer and edge proximity on herb species richness are indirectly mediated by changes in soil pH, litter depth and light availability.



Material and Methods

The study region Hainich (forested mountain range running 24 km from north to south, highest elevation 494 m a.s.l.) is situated in northwestern Thuringia, Germany (51°5'0"N, 10°30'24"E). The bedrock is mainly limestone, covered by beech forest communities (Leuschner et al., 2009). With an area of 16,000 ha, this forest is the largest continuous stretch of deciduous forest in Germany. This enabled us to study edge effects on a large spatial scale. The study was conducted in Hainich's southern part (National Park and part of UNESCO World Heritage sites 'Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany').

The forest comprises areas with low tree species richness (dominated by *F. sylvatica* L.) and areas rich in tree species (containing up to 14 species per hectare); see Mölder et al., (2006) and Leuschner et al., (2009) for a detailed description of the study site.

Site selection

We laid out transects, reaching up to 500 m from the forest edge into the forest interior. Twenty-three forest stands were selected a priori using a map of the forest communities provided by the National Park administration. Twelve forest stands met the criteria of being either poor (c. 3 species) or rich (c. 6 species) in tree species, being of a similar age class and having a low variability of tree species richness within each stand. Six transects were situated in beech-dominated forest stands with a low tree species diversity (hereafter referred to as beech-dominated forest stands) and six in forest stands with a low beech dominance and a high tree species diversity (hereafter referred to as multispecies forest stands). Transects were distributed evenly along the edge of the whole Hainich forest, with a minimum distance of 750 m between transects.

Plots were established at different distances from the forest edge. As we expected the strongest changes to happen close to the edge (Didham & Lawton 1999), we chose the distances of 0, 4, 8, 32, 80, 200 and 500 m. However, the maximum distance of 500 m could not be reached on all transects, because tree species composition changed, stand age differed or the distance to the next edge was not large enough. Thus, 4 of the 12 transects only had a length of 200 m (2 transects in each tree diversity level). This yielded a total number of 80 plots for vegetation relevés (see below). The '0 m' point of the transects was set at the position where canopy tree trunks of the forest began.

The surrounding matrix consisted of (partially abandoned) grassland of different successional stages. Forest edges consisted of dense shrub belts characterized by blackthorn (*Prunus*

spinosa L. s. str.), whitethorn (*Crataegus laevigata* (Poir.) DC.) and saplings of ash (*Fraxinus excelsior* L.). Nomenclature of plants follows Wisskirchen and Haeupler (1998).

Tree layer measurements

On each plot, tree surveys were conducted in an area of 20 × 40 m (longer side parallel to forest edge), except for plots directly at the forest edge (distances 0, 4 and 8 from the forest edge), where only one tree relevé was placed (Supplementary Figure S1). This resulted in a total number of 56 tree relevés. All trees (diameter at breast height (DBH) ≥ 10 cm) and DBH were recorded. We assessed % beech (based on basal area), number of tree species (tree SR) and tree species diversity (Shannon–Wiener diversity index (H') based on basal area as it includes not only species richness but also the abundances of species (Magurran 2004)).

Vegetation measurements

Herb layer surveys were conducted on six subplots per plot. Subplots measured 1 × 3 m (longer side parallel to forest edge) and were arranged in a row running parallel to the forest edge (Supplementary Figure S1). Distance between relevés was ~1 m.

All flowering plant species up to 70 cm height and their cover (in percent) was recorded. For further analysis, the cover of every plant species was averaged over the six relevés per plot by taking the arithmetic mean. The survey was carried out twice to account for both spring ephemerals characteristic for deciduous forests and summer vegetation (Dierschke 1994), resulting in 960 relevés in total. The spring survey was done in April 2012, the summer survey in July/August 2012. Tree saplings were excluded from further analyses as they were not independent from the tree layer.

Measurement of environmental variables

Canopy openness was assessed using fish eye photographs (see Supplementary Appendix B for detailed procedure). Litter depth was measured in the center of each of the subplots using a tape measure. For the analyses, the six values were averaged for each plot.

Soil samples from the upper 30 cm of mineral soil were taken at plots of distances 0, 32, 80, 200 and 500 m using a soil corer. Twelve subsamples per plot were taken in a grid of 3 × 4 m around the center of each plot and pooled into a single sample. Since grids for the plots in 0, 4 and 8 m distance would have overlapped each other, only the plot at 0 m was sampled as a representative for the plots of 4 and 8 m distance. The soil samples were dried (40°C) and

sieved (2 mm mesh size). Soil pH was electronically measured in a suspension of 10 g soil and 25 ml 0.01 mol/l CaCl₂.

Data analysis

Tree diversity level, tree SR, H' trees and % beech were all highly correlated ($|\rho| > 0.6$; Supplementary Table S1). Therefore, only tree diversity level was used in the analyses. Spring and summer surveys were pooled. All analyses were performed using R, version 3.0.2 (R Core Team 2014).

Analysis of plant species richness.

We started with simple mixed-effects models (lme, 'nlme' package (Pinheiro and Bates 2000)) containing only the design variables distance (distance from the forest edge, continuous variable), tree diversity level (factor) and their two-way interaction as fixed effects. Distance was log-transformed. Transect was included as random effect. Plant species richness was transformed using $\frac{1}{4}$ powers as indicated by a Box–Cox transformation. Models were initially fitted using Restricted Maximum Likelihood ('REML') method and variance functions were used to account for heteroscedasticity or non-normality. We calculated corrected Akaike information criterion (AICc) per model. The model with the lowest AICc value was considered the best maximal model. This best maximal model was re-fitted using maximum likelihood. The minimal adequate model was arrived at using stepwise model selection based on AICc (stepAICc function, 'MASS' package, corrected for small sample sizes by C. Scherber (2009, <http://www.christoph-scherber.de/stepAICc.txt>)).

Analysis of plant community structure.

Plant species were subdivided into forest specialization groups according to Schmidt et al., (2011): (i) forest specialists (species predominantly occurring in closed forests), (ii) generalists (species occurring in forests as well as in open land), (iii) edge species (species preferring forest edges or clearings) and (iv) open land species (comprising species occurring partly in forests, but preferring open land and true open land species (joined into 'true open land species')). These four groups formed a multinomial response variable analyzed using multinomial models with distance (log) and tree diversity level as explanatory variables. The number of species in each of the four classes was used as a response matrix in these models. Multinomial models were calculated using the Mixcat package in R (Papageorgiou and Hinde 2012) with transect as a random effect. As Mixcat did not offer predict or plot methods, we re-



fitted these models without random effects using the multinom function in R for plotting ('nnet' package (Ripley 2013)). The significance of terms in the final model was assessed using sequential likelihood ratio tests.

Analysis of plant community composition.

Redundancy analyses (function rda, 'vegan' package (Oksanen et al., 2013)) were conducted to test the effect of tree diversity level (factorial variable) and distance on plant community composition. Distance was treated as a factor to enable a characterization of the plots at different distance classes. Prior to analyses, the community data matrix was Hellinger-transformed, thereby giving lower weight to rare species (Legendre and Gallagher 2001). We used a permutation test (function permutest, 'vegan' package (Oksanen et al., 2013)) with 999 permutations to assess statistical significance.

Analysis of additional covariate effects.

We additionally used structural equation modeling (SEM) to disentangle pathways between exogenous design variables (tree diversity level and distance from the forest edge), environmental variables (canopy openness, litter depth and soil pH) and herb layer plant species richness.

The model was fitted using the SEM function ('lavaan' package (Rosseel 2012)). The model was built on the hypothesis that (i) light availability, litter depth and pH are key factors predicting plant diversity in forests (Barbier et al., 2008; Brunet et al., 2010; van Oijen et al., 2005) and (ii) that these variables are influenced by both or at least one of the two design variables. Prior to model fitting, all variables were recoded to a common scale (range ~0–100). Distance from the forest edge was log-transformed. We used maximum likelihood estimation with robust standard errors and a Satorra–Bentler-scaled test statistic (estimator = Maximum Likelihood Estimation: 'MLM'). Model fit was assessed based on χ^2 values and associated P values, Root Mean Square Error of Approximation (RMSEA), Standardized Root Mean Square Residual (SRMR) and Confirmatory Fit Index (CFI of the model).

Results

Overall characteristics of the forest stands

Tree species richness in the plots ranged from one (only *F. sylvatica*) to nine. Shannon diversity (H') ranged from 0 to 1.81 and the percentage of beech based on relative basal area ranged from 0 to 100%. Forest stands poor in tree species were strongly dominated by *F. sylvatica* (% beech c. 83.5, H' trees c. 0.45), whereas in forest stands with a high tree diversity (% beech c. 26.5, H' trees c. 1.32), several other deciduous tree species occurred (Supplementary Table S2). Additional abundant tree species were *Quercus robur* L., *Quercus petraea* Liebl., *Tilia* sp., *Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *F. excelsior* and *Carpinus betulus* L. Less abundant were *Prunus avium* L., *Betula pendula* Roth, *Populus tremula* L., *Ulmus glabra* Huds., *Salix caprea* L. and *Sorbus torminalis* (L.). *Tilia cordata* Mill. and *T. platyphyllos* Scop. could not be reliably separated in the field and were thus only determined to genus level.

Herb layer characteristics

Totally, 124 plant species from 96 genera were recorded. They comprised 94 forb species (34 forest specialist species, 42 generalists, 7 edge species and 10 open land preferring species, 1 not specified), 15 graminoid species (10 forest specialists, 4 generalists, 1 not specified), 15 shrub species (3 forest specialists, 10 generalists, 2 not specified). Species number varied between 2 and 49 species per plot. In total, 88 species were found in the beech-dominated forest stands, whereas 109 species were found in multispecies forest stands.

The five most frequently occurring species on the plots were *Anemone nemorosa* L. (on 96% of plots), *Ranunculus ficaria* agg. (74%), *Hordelymus europaeus* (L.) Jessen ex Harz (64%), *Viola reichenbachiana* Boreau (63%) and *Stellaria holostea* L. (55%) (for complete species list, see Supplementary Table S3).

Plant species richness

Plant species richness of the herb layer was significantly affected by an interaction between tree diversity level and distance from the forest edge (Fig. 1, Table 1). In beech-dominated forest stands, species richness of the herb layer decreased by ca. 60% with increasing distance from the forest edge. 85% of the total decrease (13 species lost) occurred within the first 80 m from the forest edge. However, no edge effect was detected in stands rich in tree species—herb species richness remained almost constant with increasing distance from the edge.

Table 1 Results of linear mixed effects model testing the effects of tree diversity level and distance from the forest edge on species richness of herb layer plants. Plant species richness was power-transformed ($x^{0.25}$). Distance was log-transformed. All variables included in the minimal adequate model are shown. DF = degrees of freedom. Bold characters depict P -values < 0.05 .

	Explanatory	Estimate	SE	DF	t	P
Plant species richness	Intercept	2.16	0.08	66	25.45	<0.001
	distance	-0.07	0.02	66	-3.44	0.001
	tree diversity level	-0.04	0.12	10	-0.36	0.726
	distance x tree diversity level	0.06	0.03	66	2.14	0.036

Abbreviations: distance = distance from forest edge (m)

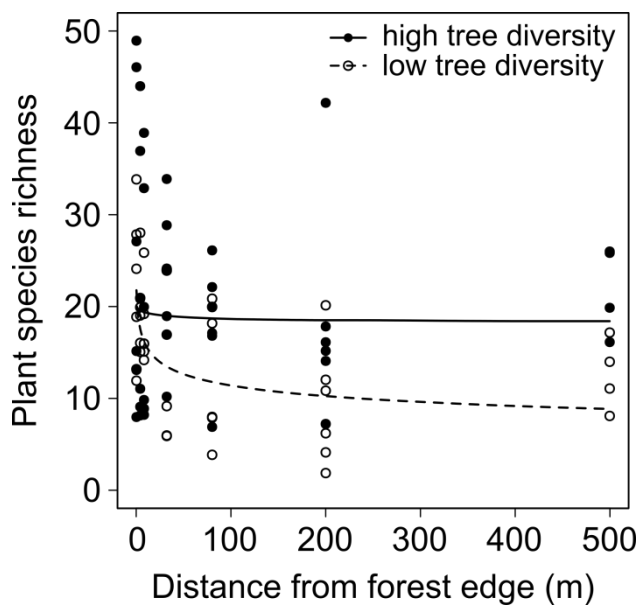


Figure 1 Interaction plot showing the relationship of herb layer plant species richness and distance from the forest edge (m) depending on tree diversity level. Lines show predictions from the lme model (Table 1). Plant species richness and distance from forest edge (m) were back-transformed for graphical presentation.

Plant community structure

The proportion of the forest specialization groups was significantly influenced by both tree diversity level and distance from the forest edge (Fig. 2, Table 2). The proportion of forest specialist species such as *Anemone ranunculoides* and *Galium odoratum* increased with increasing distance from the forest edge. At the same time, the proportion of generalists (e.g. *Fragaria vesca* and *Lilium martagon*) decreased. The strongest changes were observed within the first 80 m from the forest edge. The proportion of forest specialist species was higher beech-dominated compared multispecies forest stands, whereas the proportion of generalist species was reduced. So, the difference between forest specialists and generalists strongly decreased with increasing tree diversity.

Table 2 Result of sequential likelihood ratio tests of multinomial models testing the effect of distance from the forest edge and tree diversity level on the proportion of species of four different forest specialization groups. Distance was log-transformed. Resid. DF = Residual DF, Resid. Dev. = Residual deviance, LR stat. = Likelihood ratio statistic (difference of residual deviance). Bold characters depict *P*-values < 0.05.

No.	Explanatory	Resid. DF	Resid. Dev	Test	DF	LR stat.	<i>P</i>
1	1	237	2583.99	-	NA	NA	NA
2	distance	234	2554.83	1 vs 2	3	29.16	<0.001
3	distance + tree diversity level	231	2534.20	2 vs 3	3	20.63	<0.001

Abbreviations: distance = distance from forest edge (m)

In beech-dominated forest stands, forest specialists dominated the plant community from the edge on, whereas in multispecies forest stands they only became dominant with increasing distance from the edge.

The proportion of edge and open land species was very low compared with forest specialist and generalist species. Their proportion was highest in multispecies forest stands and within the first 32 m from the edge. Actual species numbers of the four forest specialization groups at the forest edge and in the forest interior are shown in Supplementary Table S4.

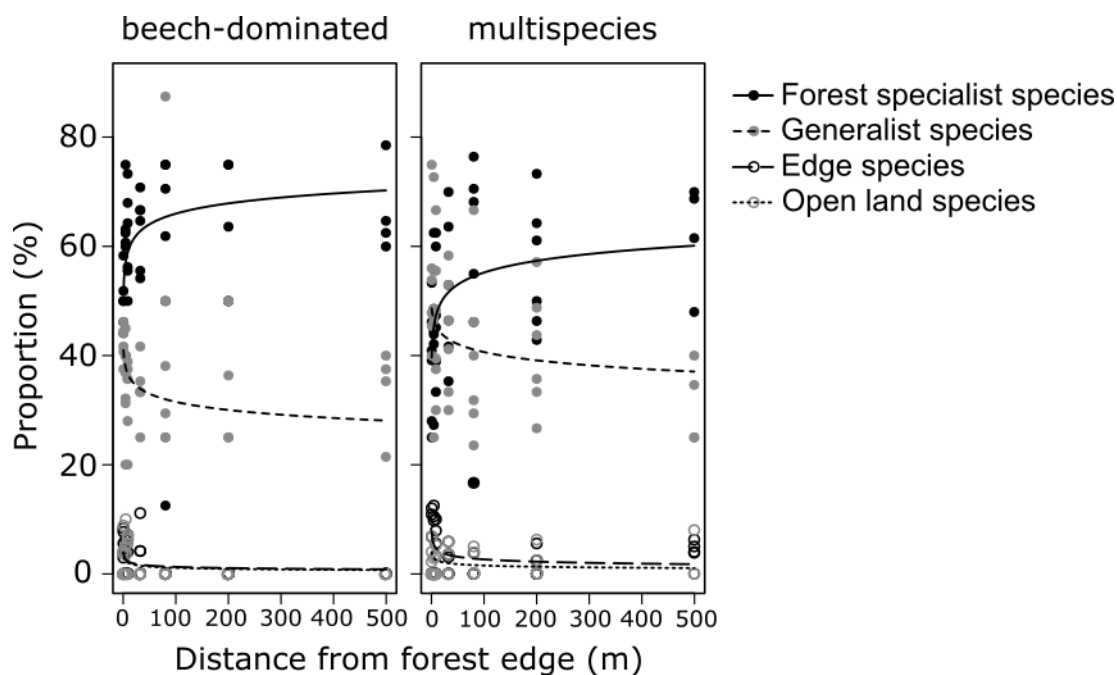


Figure 2 Proportional response of plant species belonging to four different forest specialization groups on distance from the forest edge (%) depending on tree diversity level. Lines show predictions from minimal adequate multinomial models (Table 2), but distance from forest edge (m) was back-transformed for graphical presentation.

Plant community composition

The partial RDAs (Fig. 3, Table 3) showed that tree diversity level and distance from the forest edge had a significant impact on the community composition of herb layer plants both

in spring and summer. No interaction could be detected. Variability in community composition was higher in multispecies forest stands and on plots closer to the forest edge (within the first 32–80 m). Species composition beyond 80 m distance became more and more distinct with increasing distance from the forest edge.

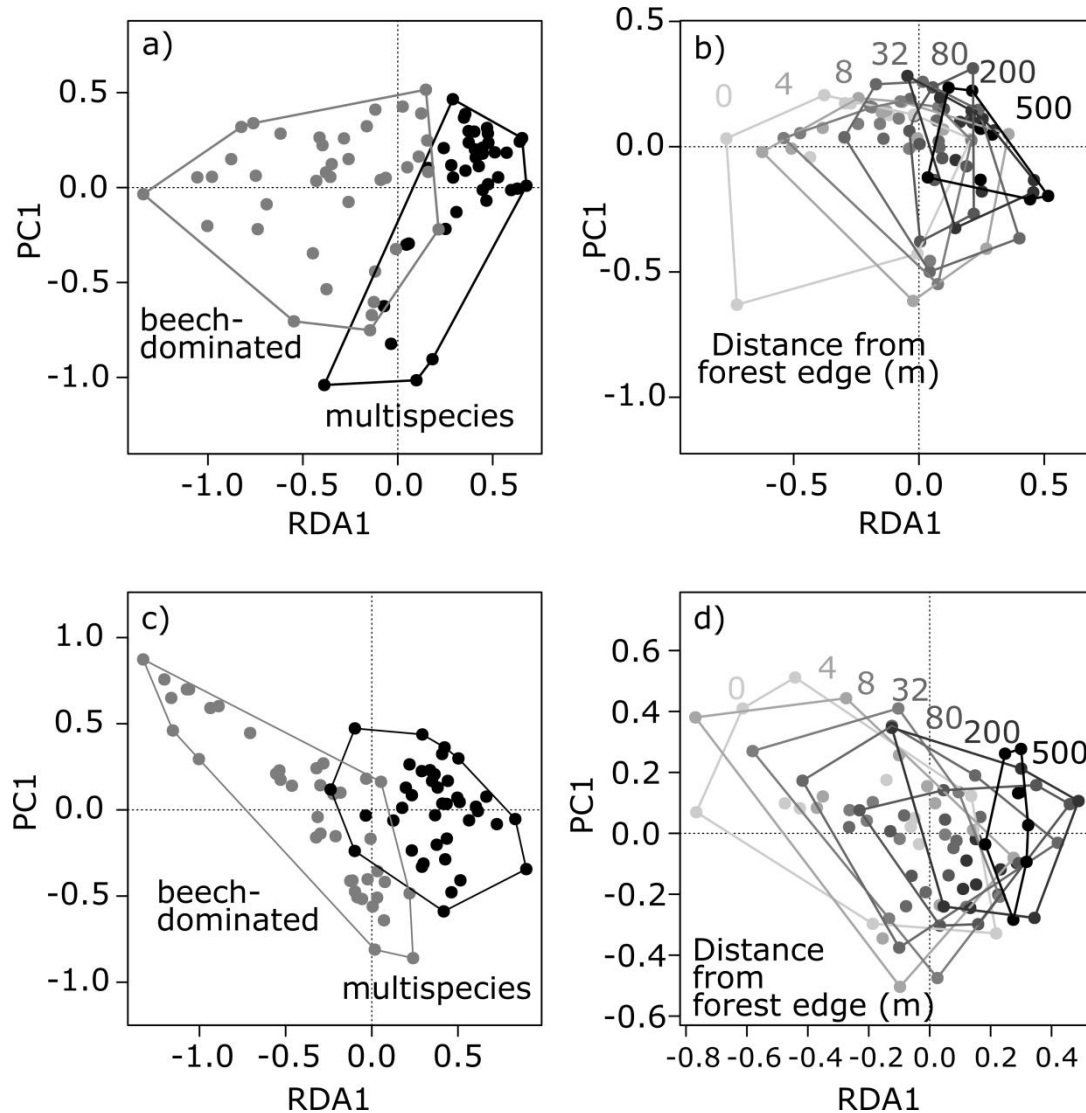


Figure 3 RDA ordination plots showing the effect of tree diversity level and distance from the forest edge (m) on plant species composition in spring and summer with minimum convex polygons: (a) tree diversity effect in spring (grey circles: multispecies forest stands, black circles: beech-dominated forest stands), (b) distance effect in spring, (c) tree diversity effect in summer (grey circles: multispecies forest stands, black circles: beech-dominated forest stands), (d) distance effect in summer (Table 3). Larger minimal convex polygons indicate a larger variability in community composition among plots. Note that the axes of the subplots originate from different models and are therefore not the same.

Table 3 Results of the RDA analyses testing the influence of tree diversity level and distance from the forest edge on the plant community composition in spring and summer. Bold characters depict P-values < 0.05.

		% variation	F	P
Partial RDA spring	tree diversity level	8.0	5.38	0.005
	distance	3.0	1.99	0.02
Partial RDA summer	tree diversity level	8.4	4.54	0.005
	distance	2.9	1.55	0.0499

Abbreviations: distance = distance from forest edge (m)

Additional covariate effects

The result of the SEM showed that the *a priori* hypothesis corresponded well with the observed covariance matrix ($\chi^2 = 1.395$; $P = 0.693$; degrees of freedom = 3; RMSEA = 0.000; SRMR = 0.016; CFI = 1.000, detailed statistical output given in Supplementary Table S5). Increased tree diversity increased soil pH and reduced litter depth, whereas canopy openness was only weakly affected. The pH decreased with distance from the forest edge and canopy openness was slightly reduced. Increased canopy openness and pH led to reduced litter depth. Increasing litter depth strongly reduced plant species richness, whereas canopy openness had no and pH only a weak positive effect (Fig. 4).

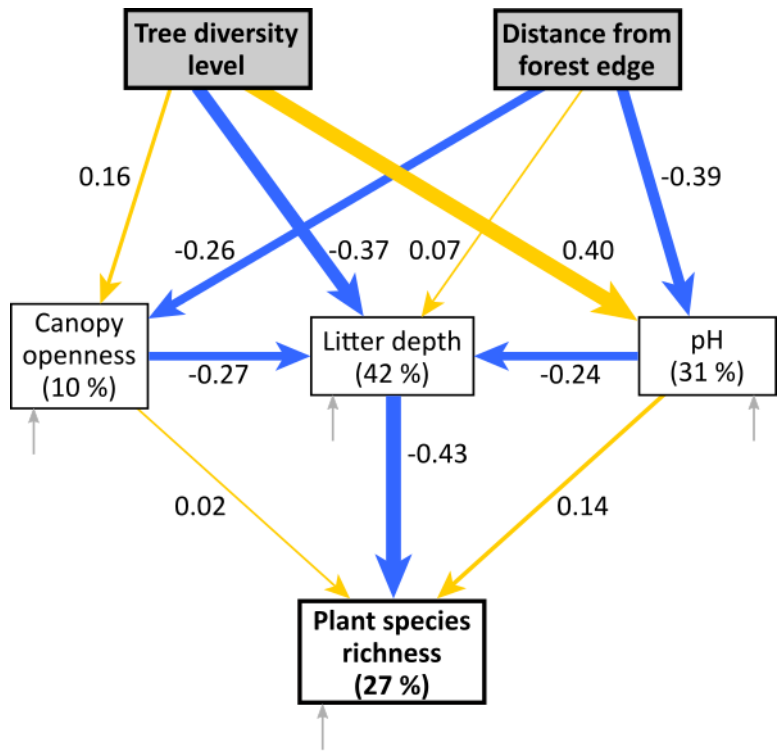


Figure 4 structural equation model showing the effects of tree diversity level, distance from the forest edge and other environmental variables on the plant species richness of the herb layer ($\chi^2 = 1.395$; $P = 0.693$). Reference level for tree diversity level was ‘beech-dominated’. Error terms are indicated by small grey errors. Numbers next to errors are standardized path coefficients. Blue arrows indicate a positive (+), orange arrows a negative (-) relationship. Arrow width shows effect strength. Error terms were omitted for clarity. Percentages are r^2 values. See Supplementary Table S5 for detailed results.



Discussion

Covering the whole forest area of the National Park, our study indicates that plant species richness of the herb stratum was affected by an interaction between edge–center transition and tree species composition. The proportion of forest specialists increased while the proportion of generalist decreased with distance from the edge in both beech-dominated and multispecies forest stands. In multispecies stands, the proportion of generalist, edge and open land species was generally increased. The floristic composition was determined independently by tree diversity level and edge proximity.

Effects of tree species composition

In line with Mölder et al. (2008) and Vockenhuber et al. (2011), we found a positive relationship between tree and herb species diversity. Reduced beech dominance and increased tree diversity influenced the herb layer indirectly by reducing litter depth—the most important predictor of herb layer species richness in our study system. Thick mats of leaf litter have been shown to reduce the diversity of ground vegetation due to its function as mechanical barrier which many species are not able to overcome (Kostel-Hughes et al., 2005; Xiong and Nilsson 1997 and references therein). Forest specialist species may be better adapted to thick, acidic litter layers since beech-dominated forests exhibit the natural potential vegetation of most parts of Central Europe (BfN 2000). Therefore, higher tree species diversity in beech forests may create environmental conditions suitable for a broader range of species such as generalist, edge and open land species. Beech dominance played a major role in our study, while in other studies with different tree compositions, contradictory results from positive to no effect of overstory diversity on herb layer species richness have been found (as summarized in Ampoorter et al., 2014; Barbier et al., 2008; Both et al., 2011).

Light availability did not influence plant species richness and was only weakly affected by tree species composition. This can be the case when a forests overall light regime is rather dark like it is typically the case in Germany's unmanaged forests. Under these conditions, soil parameters might gain importance (Schmidt et al., 2002). When light availability is higher, like in managed forests, the amount of light may become the decisive driver of herb species richness (Mölder et al., 2014).

Furthermore, the mix of many different tree species may have created a pattern of more heterogeneous environmental conditions compared with overall monotonous conditions in beech-dominated forest stands. According to the 'environmental heterogeneity hypothesis' (Huston 1994), this promotes plant species richness because here the individual habitat

requirements of more herb layer species are met. Furthermore, this explains the higher variability within the community composition of multispecies forest stands.

Edge effects

The proportion of open land, edge and generalist species and the variability within the community composition increased with increasing edge proximity while the proportion of forest specialist species declined. Honnay et al. (2002) observed a similar pattern. Changes in environmental conditions towards the edge such as reduced litter depth, increased pH and more light availability might have been the reason for this (Matlack 1994; Murcia 1995), since these factors are well known to increase overall herb layer species richness (Barbier et al., 2008; Brunet et al., 2010; van Oijen et al., 2005) and enhance plant invasion into forests (Honnay et al., 2002). Similar findings have been attributed to the drift of agrochemicals, higher input of base cations with throughfall deposition, higher decomposition rates of leaf litter, higher wind exposure and leaf litter originating from fewer trees at edges (Wirth et al., 2008). Overall, conditions at the forest edge are usually more heterogeneous than in forest interiors (Ewers & Didham 2006; Marchand & Houle 2006). In sum, these factors might have increased the range and proportion species which are not explicitly adapted to forest interior conditions (Schmidt 2011).

In both diversity levels, the strongest changes in the proportion of forest specialization groups were observed within the first 80 m from the forest edge, whereas changes were in total observed up to a distance of 500 m from the forest edge. This is in line with recent studies showing long distance edge influences on forest herb layer vegetation (Hofmeister et al., 2013; Pellissier et al., 2013). The same pattern was observed for the community composition, where a high variability occurs up to a distance of 80 m. Beyond that point, species composition becomes increasingly distinct indicating more stable environmental conditions within the forest interior in both tree diversity levels. In contrast, (Fraver 1994; Matlack 1994; Honnay et al., 2002) observed changes in community composition only up to a maximum distance of 23 m from the edge. Forest edges in this study were characterized by shrub belts (closed edges) potentially diminishing the strength of edge effects (Didham & Lawton 1999). Therefore, patterns found here may be more pronounced in forests with open edges.

Interacting effects of tree species composition and edge proximity

Species responses to habitat edges can be positive, negative or neutral, often mediated by changes of environmental conditions (Murcia 1995; Ries et al., 2004). In the present study,



the edge response of the herb species richness was dependent on tree diversity level (positive in beech-dominated and neutral in multispecies stands). As discussed above, forest edges are overall heterogeneous environments suitable for a broad range of species (Ewers & Didham 2006; Murcia 1995). Beech-dominated forests were characterized by overall monotonous conditions, a deep litter layer and low soil pH leading to a high fraction of forest specialist species. In contrast, multispecies forest stands were more heterogeneous with a thin litter layer and higher soil pH promoting a higher diversity of herb species. Therefore, we deduce our finding to a stronger environmental contrast between forest edge and center in beech-dominated forest than multispecies forest stands.

Observational versus experimental studies

In this study, we cannot completely separate tree diversity effects from effects of altered beech dominance (Baeten et al., 2013; Nadrowski et al., 2010). This problem could be avoided in experimentally planted forest stands (Bruehlheide et al., 2014; Scherer-Lorenzen 2014). However, most synthetic forest stands containing more than two-species mixtures have only been established during the last 20 years and differ from near-natural mature forests in many respects (Baeten et al., 2013; Leuschner et al., 2009). This makes drawing direct conclusions to ‘real world’ forests difficult. Therefore, at present, it is reasonable to take advantage of given natural tree diversity gradients in mature forests, that provide comparable stand conditions as it is the case in the Hainich National Park (Leuschner et al., 2009). Insights from both experimental and observational studies should be compared when assessing the functional role of tree species diversity in forests (Baeten et al., 2013; Leuschner et al., 2009).

Conclusion

Our results demonstrate that the edge response of herb layer plant species richness in forests can be shaped by tree species composition. The differences between forest interior and forest edge in environmental traits and habitat heterogeneity are greater in beech-dominated forests, presumably causing the greater edge–center differences. Multispecies forest stands did not only increase species richness in general but also enhanced the variability in community composition of the herb layer and the proportion of species not explicitly adapted to inner forest conditions. SEM revealed that tree diversity level determined herb species richness primarily via changes of the litter depth.

Pathways might be different in managed forests (Lange et al., 2014; Mölder et al., 2014). Therefore, future studies should be conducted both in managed and abandoned forests incorporating a larger range of forests with respect to tree species composition.

Funding

German Research Foundation within the framework of the Research Training Group (GRK 1086: ‘The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests’).

Acknowledgements

We thank Kris Verheyen and two anonymous reviewers for constructive comments on an earlier version of this paper. Thanks to Verena Rösch for her help in plant determination and improvement of the English. We would like to thank Margaritha Hottmann for helping with the fieldwork. Further, we are grateful to the Hainich National Park Administration for the permission to conduct the research and for supply of helpful information.

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Appendix

Appendix A

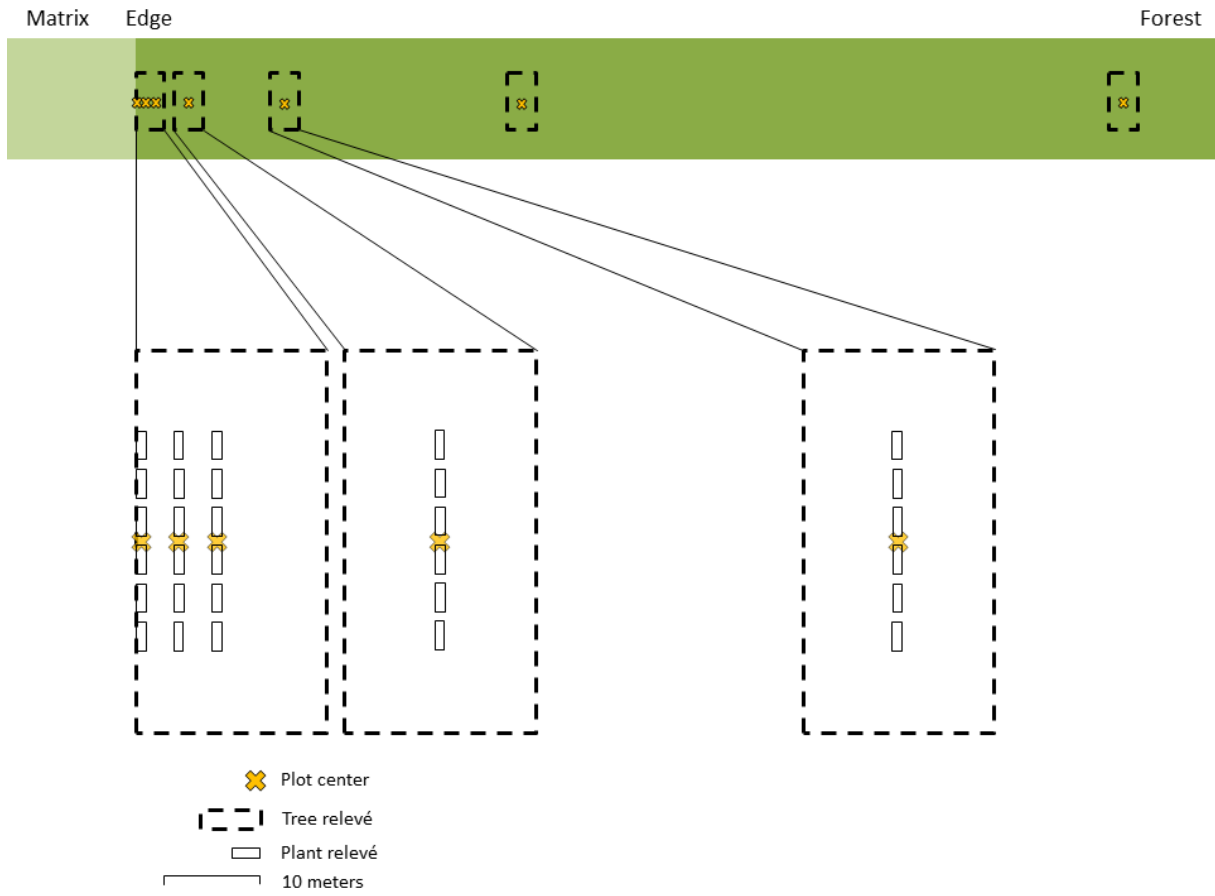


Figure S1 Location of plots along transects

Appendix B

Description of fish eye photograph processing

Canopy openness was assessed using fish eye photographs taken with a Nikon Coolpix 8400 camera plus Nikon FC-E9 fisheye converter and UR-E16 adapter ring (Nikon Corporation, Chiyoda, Tokyo, Japan). Photographs were processed using Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, California, USA) in the following way: 1. The image background was converted into an editable layer, 2. the ellipse selection tool was used to select an exactly circular area, excluding the black margin contained in each photograph, 3. in the layers menu, "layer mask" was selected and then "reveal selection" chosen; the formerly black area was thus removed and replaced by a transparent background. We then used Adobe Photoshop Lightroom 5.2 (Adobe Systems Inc.) and performed the following adjustments to all photographs: Contrast was set to -100, highlights were set to -73, whites were set to +7, black was set to -100 and clarity was set to 66. In the tone curve, lights were set to +96. SideLook 1.1.01 was then used to (automatically) estimate the optimal threshold for converting photographs into black-and-white pictures (Nobis and Hunziker 2005). Canopy openness was then calculated using Gap Light Analyzer 2.0 (Cary Institute of Ecosystem Studies, Millbrook, New York, USA).

Appendix C

Table S1: Spearman's rank correlation coefficients (ρ) of variables describing tree species composition. All correlations were highly significant ($P < 0.001$).

	Tree diversity level	Tree SR	H' tree
Tree SR	0.61	-	
H' tree	0.69	0.87	-
% beech	-0.77	-0.80	-0.83

Tree diversity level: factorial explanatory variable (beech-dominated vs. multispecies forest stands), H' tree: Shannon-Wiener diversity index (H') based on basal area, % beech (based on basal area)

Appendix D

Table S2 Summary statistics of variables describing tree diversity in low and high tree diversity stands calculated from a tree species survey on 20 x 40 m relevés around the plots. Values are means \pm standard error (SE). H' = Shannon-Wiener diversity index based on basal area (Magurran, 2004).

	beech-dominated	multispecies stands
Tree SR	3.11 \pm 0.37	6.32 \pm 0.3
% beech	83.49 \pm 3.81	26.5 \pm 4.03
H' tree	0.45 \pm 0.08	1.32 \pm 0.05

Tree diversity level: factorial explanatory variable (beech-dominated vs. multispecies forest stands), H' tree: Shannon-Wiener diversity index (H') based on basal area, % beech (based on basal area)

Appendix E

Table S3 List of plant species recorded (Classification of forest specialization types according to Schmidt *et al.* (2011): 1.1: mainly closed forests, 1.2 mainly forest edge or clearings, 2.1 forests as well as open land, 2.2 partly in forests, but mainly open land, O: openland, B: tree, K: herb, S: shrub. Nomenclature of plants following Wisskirchen and Haeupler (1998).

Species	Functional	Forest	Mean cover (%)	
	group	specialisation	spring	summer
<i>Acer campestre</i>	tree	B 2.1	0.080	0.148
<i>Acer platanoides</i>	tree	B 2.1	0.255	1.451
<i>Acer pseudoplatanus</i>	tree	B 2.1	1.301	2.647
<i>Aconitum lycoctonum</i>	forb	K 1.1	0.002	0.017
<i>Actea spicata</i>	forb	K 1.1	0.013	0.038
<i>Aegopodium podagraria</i>	forb	K 2.1	1.130	1.555
<i>Ajuga reptans</i>	forb	K 2.1	0.008	0.019
<i>Alliaria petiolata</i>	forb	K 2.1	0.663	0.055
<i>Allium olacerum</i>	forb	K 2.2	0.006	-
<i>Allium ursinum</i>	forb	K 1.1	5.737	-
<i>Allium vineale</i>	forb	K 2.2	0.008	-
<i>Anemone nemorosa</i>	forb	K 2.1	24.788	0.014
<i>Anemone ranunculoides</i>	forb	K 1.1	0.396	-
<i>Angelica sylvestris</i>	forb	K 2.1	0.004	0.015
<i>Anthriscus sylvestris</i>	forb	K 2.2	0.004	0.017
<i>Arctium nemorosum</i>	forb	K 1.2	0.090	0.216
<i>Arum maculatum</i>	forb	K 1.1	0.251	0.007
<i>Asarum europaeum</i>	forb	K 1.1	0.193	0.261
<i>Brachypodium pinnatum</i>	graminoid	K 2.1	-	0.001
<i>Brachypodium sylvaticum</i>	graminoid	K 1.1	0.138	0.533
<i>Bromus ramosus</i>	graminoid	K 1.1	0.002	0.044
<i>Calamagrostis epigejos</i>	graminoid	K 2.1	-	0.010
<i>Campanula patula</i>	forb	K O	0.004	0.006
<i>Campanula persicifolia</i>	forb	K 1.2	0.015	0.019
<i>Campanula rapunculoides</i>	forb	K 2.1	0.021	0.006
<i>Campanula trachelium</i>	forb	K 1.1	0.006	0.019
<i>Cardamine bulbifera</i>	forb	K 1.1	0.383	0.004
<i>Cardamine pratensis</i>	forb	K 2.1	0.002	0.003
<i>Carex remota</i>	graminoid	K 1.1	-	0.001
<i>Carex sp.</i>	graminoid	K -	0.002	-
<i>Carex sylvatica</i>	graminoid	K 1.1	0.284	0.401
<i>Carpinus betulus</i>	tree	B 1.1	0.323	0.460
<i>Chaerophyllum temulum</i>	forb	K 1.2	0.002	0.010
<i>Circaea lutetiana</i>	forb	K 1.1	-	0.152
<i>Colchicum autumnale</i>	forb	K 2.1	0.004	0.002
<i>Convallaria majalis</i>	forb	K 2.1	0.083	0.330
<i>Cornus sanguinea</i>	shrub	S 2.1	0.018	0.085
<i>Corydalis cava</i>	forb	K 1.1	0.383	-
<i>Corylus avellana</i>	shrub	S 2.1	-	0.004
<i>Crataegus laevigata</i>	shrub	S 2.1	0.260	0.318
<i>Dactylis polygama</i>	graminoid	K 1.1	0.525	0.563
<i>Dactylorhiza maculata</i>	forb	K 2.1	0.002	0.002
<i>Daphne mezereum</i>	shrub	S 1.1	0.004	0.015
<i>Deschampsia cespitosa</i>	graminoid	K 2.1	0.190	0.182
<i>Elymus caninus</i>	graminoid	K 1.1	0.033	0.044
<i>Epilobium montanum</i>	forb	K 2.1	-	0.002
<i>Epipactis helleborine</i>	forb	K 1.1	-	0.004
<i>Epipactis purpurata</i>	forb	K 1.1	-	0.002
<i>Euonymus europaea</i>	shrub	S 2.1	0.180	0.195
<i>Fagus sylvatica</i>	tree	B 1.1	3.546	4.451
<i>Festuca gigantea</i>	graminoid	K 1.1	-	0.067
<i>Filipendula ulmaria</i>	forb	K 2.1	-	0.039
<i>Fragaria vesca</i>	forb	K 2.1	0.036	0.074
<i>Fragaria viridis</i>	forb	K 2.2	0.019	0.056
<i>Fraxinus excelsior</i>	tree	B 2.1	0.544	1.535
<i>Gagea lutea</i>	forb	K 1.1	0.045	-
<i>Galeopsis tetrahit</i>	forb	K 2.1	-	0.019
<i>Galium aparine</i>	forb	K 2.1	0.010	0.028
<i>Galium odoratum</i>	forb	K 1.1	0.071	0.077
<i>Galium sylvaticum</i>	forb	K 1.1	0.098	0.197

<i>Geranium robertianum</i>	forb	K 2.1	0.050	0.104
<i>Geranium sylvaticum</i>	forb	K 2.1	0.002	0.004
<i>Geum urbanum</i>	forb	K 2.1	0.313	0.549
<i>Hedera helix</i>	shrub	S 1.1	0.289	0.372
<i>Hepatica nobilis</i>	forb	K 1.1	0.139	0.153
<i>Heracleum sphondylium</i>	forb	K 2.2	0.008	0.007
<i>Hieracium murorum</i>	forb	K 2.1	0.000	0.008
<i>Hordelymus europaeus</i>	graminoid	K 1.1	0.405	0.619
<i>Hypericum hirsutum</i>	forb	K 1.2	0.014	0.014
<i>Hypericum perforatum</i>	forb	K 2.2	0.002	-
<i>Impatiens parviflora</i>	forb	K 1.1	-	0.030
<i>Lamium album</i>	forb	K 2.2	0.002	0.010
<i>Lamium galeobdolon</i>	forb	K 1.1	0.551	0.727
<i>Lamium maculatum</i>	forb	K 2.1	0.048	0.030
<i>Lapsana communis</i>	forb	K 2.1	-	0.003
<i>Lathraea squamaria</i>	forb	K 1.1	0.008	-
<i>Lathyrus vernus</i>	forb	K 1.1	0.081	0.146
<i>Leucojum vernum</i>	forb	K 2.1	0.415	-
<i>Lilium martagon</i>	forb	K 2.1	0.032	0.033
<i>Listera ovata</i>	forb	K 2.1	0.044	0.004
<i>Lonicera xylosteum</i>	shrub	S 1.1	0.131	0.177
<i>Luzula sylvatica</i>	forb	K 2.1	0.003	0.010
<i>Lysimachia nummularia</i>	forb	K 2.1	-	0.010
<i>Maianthemum bifolium</i>	forb	K 1.1	0.004	0.012
<i>Melampyrum nemorosum</i>	forb	K 1.2	-	0.003
<i>Melica uniflora</i>	graminoid	K 1.1	0.129	0.364
<i>Mercurialis perennis</i>	forb	K 1.1	1.790	2.161
<i>Milium effusum</i>	graminoid	K 1.1	0.140	0.253
<i>Mycelis muralis</i>	forb	K 2.1	0.004	0.011
<i>Myosotis sp.</i>	forb	K -	0.002	0.010
<i>Neottia nidus-avis</i>	forb	K 1.1	-	0.006
<i>Oxalis acetosella</i>	forb	K 1.1	0.238	0.605
<i>Paris quadrifolia</i>	forb	K 1.1	0.021	0.040
<i>Phyteuma spicatum</i>	forb	K 2.1	0.044	0.019
<i>Picea sp.</i>	tree	B -	0.002	0.002
<i>Pimpinella major</i>	forb	K 2.1	0.004	0.004
<i>Pimpinella saxifraga</i>	forb	K 2.1	0.004	0.004
<i>Poa nemoralis</i>	graminoid	K 2.1	0.077	0.068
<i>Polygonatum multiflorum</i>	forb	K 1.1	0.197	0.273
<i>Polygonatum verticillatum</i>	forb	K 2.1	-	0.069
<i>Populus sp.</i>	tree	B 2.1	-	0.006
<i>Primula elatior</i>	forb	K 2.1	0.240	0.271
<i>Primula veris</i>	forb	K 2.1	0.016	0.016
<i>Prunella vulgaris</i>	forb	K 2.2	-	0.002
<i>Prunus avium</i>	tree	B 2.1	0.154	0.221
<i>Prunus spinosa</i>	shrub	S 2.1	0.035	0.167
<i>Pulmonaria obscura</i>	forb	K 1.1	0.091	0.158
<i>Quercus sp.</i>	tree	B 2.1	-	0.026
<i>Ranunculus auricomus</i>	forb	K 2.1	0.551	0.009
<i>Ranunculus ficaria</i>	forb	K 2.1	3.677	0.006
<i>Ranunculus lanuginosus</i>	forb	K 1.1	0.050	0.071
<i>Ribes alpinum</i>	shrub	S 2.1	0.174	0.154
<i>Ribes uva-crispa</i>	shrub	S 2.1	0.021	-
<i>Rosa sp.</i>	shrub	S -	0.033	0.049
<i>Rubus idaeus</i>	shrub	S 2.1	0.005	0.119
<i>Rubus sp.</i>	shrub	S -	0.035	0.077
<i>Rumex sanguineus</i>	forb	K 1.1	0.008	0.006
<i>Sambucus nigra</i>	shrub	S 2.1	0.116	0.153
<i>Sanicula europaea</i>	forb	K 1.1	0.040	0.083
<i>Senecio ovatus</i>	forb	K 1.2	0.117	0.340
<i>Sorbus aucuparia</i>	forb	K 2.1	0.007	0.003
<i>Sorbus torminalis</i>	tree	B 2.1	-	0.006
<i>Stachys sylvatica</i>	forb	K 1.1	0.022	0.127
<i>Stellaria holostea</i>	forb	K 1.1	1.416	1.674
<i>Stellaria media agg.</i>	forb	K 2.2	0.001	0.010
<i>Taraxacum sect. Ruderalia</i>	forb	K 2.1	0.038	0.016
<i>Tilia sp.</i>	tree	B 1.1	0.031	0.074
<i>Torilis japonica</i>	forb	K 1.2	-	0.004
<i>Ulmus glabra</i>	tree	B 1.1	0.002	0.014

<i>Urtica dioica</i>	forb	K 2.1	0.115	0.178
<i>Veronica chamaedrys</i>	forb	K 2.1	-	0.001
<i>Veronica montana</i>	forb	K 1.1	0.002	0.004
<i>Viburnum opulus</i>	shrub	S 2.1	-	0.041
<i>Vicia sepium</i>	forb	K 2.1	0.028	0.043
<i>Viola hirta</i>	forb	K 2.1	0.017	0.047
<i>Viola odorata</i>	forb	K 2.1	0.040	-
<i>Viola reichenbachiana</i>	forb	K 1.1	0.275	0.362

Appendix F

Table S4 Actual species numbers of the four forest specialization groups at forest edge (0 m) and in the forest interior (500 m) depended on the tree diversity level (values are mean values \pm standard error).

	<u>low tree diversity</u>		<u>high tree diversity</u>	
	Forest edge	Forest interior	Forest edge	Forest interior
Forest specialists	10.5 (\pm 1.52)	8.25 (\pm 1.6)	9.83 (\pm 2.71)	13.25 (\pm 1.11)
Generalists	9 (\pm 1.48)	4 (\pm 0.71)	12.5 (\pm 2.96)	7 (\pm 1.47)
Edge species	1 (\pm 0.26)	0 (\pm 0.00)	1.83 (\pm 0.87)	1 (\pm 0.00)
Open land species	0.83 (\pm 0.48)	0 (\pm 0.00)	1 (\pm 0.45)	0.5 (\pm 0.5)

Appendix G

Table S5 Results of the structural equation model (Fig. 4).

lhs	op	rhs	Estimate	SE	Z	P	Std.coef
Canopy openness	~	Tree diversity level	3,541	2,300	1,540	0,124	0,165
Canopy openness	~	logdist	-0,265	0,099	-2,666	0,008	-0,264
Litter depth	~	Tree diversity level	-14,370	3,534	-4,066	0,000	-0,374
Litter depth	~	logdist	0,127	0,182	0,699	0,485	0,071
Litter depth	~	Canopy openness	-0,487	0,189	-2,576	0,010	-0,272
Litter depth	~	pH	-0,349	0,152	-2,296	0,022	-0,236
pH	~	Tree diversity level	10,368	2,430	4,267	0,000	0,399
pH	~	logdist	-0,469	0,114	-4,126	0,000	-0,388
Plant SR	~	Litter depth	-0,449	0,123	-3,639	0,000	-0,430
Plant SR	~	pH	0,220	0,155	1,422	0,155	0,143
Plant SR	~	Canopy openness	0,041	0,167	0,246	0,806	0,022
Residual Covariances:							
Canopy openness	~~	Canopy openness	104,451	19,300	5,412	0,000	0,903
Litter depth	~~	Litter depth	212,888	35,450	6,005	0,000	0,576
pH	~~	pH	116,630	17,577	6,635	0,000	0,691
Plant SR	~~	Plant SR	294,015	42,579	6,905	0,000	0,730
Tree diversity level	~~	Tree diversity level	0,250	-	-	-	-
Tree diversity level	~~	logdist	0,000	-	-	-	-
logdist	~~	logdist	115,344	-	-	-	-
Intercepts							
Canopy openness	~1		55,863	4,974	11,230	0,000	5,194
Litter depth	~1		86,065	17,419	4,941	0,000	4,479
pH	~1		76,753	5,145	14,918	0,000	5,906
Plant SR	~1		38,961	13,563	2,873	0,004	1,941
Tree diversity level	~1		0,500	-	-	-	-
logdist	~1		41,438	-	-	-	-

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CHAPTER 3
TREE DIVERSITY AND SPECIES' TRAITS MODERATE
FOREST EDGE RESPONSES OF GROUND-DWELLING
BETTERLES AND SPIDERS



Abstract

Habitat fragmentation is among the major reasons for the worldwide biodiversity loss. The extent to which edge effects penetrate into forest fragments may depend on habitat structure. Here, we test for the first time the hypothesis that tree species richness can mitigate edge responses of arthropods.

We established 12 transects in Germany's largest deciduous forest extending from the edge up to 500 m into the forest interior (six in low and six in high tree diversity stands) and sampled ground-dwelling arthropods along each transect.

No consistent pattern was found for the total species richness of carabids, staphylinids and spiders. However, the response of all taxa to edge and tree diversity depended on habitat affinity and body size. In the low tree diversity level the number of habitat generalists declined strongly from the edge towards the forest interior. This effect was mitigated by increased tree diversity (except for spiders). Small-sized habitat generalists in particular were promoted by increased tree diversity. Forest species richness did not respond explicitly to edge proximity or tree diversity and size class was not important. However, some forest species suffered, whereas others benefited from increased tree diversity. In contrast, species specific responses of habitat generalists to diverse forests were in general positively.

We conclude that the role of forest edge effects can be modified by tree diversity and depends on species' traits such as body size and habitat specialisation, which need to be taken into account to understand and qualify the conservation value of habitat fragments.

Keywords

carabids, deciduous forest, edge effect, spiders, staphylinids, body size

Introduction

Edge effects are an important component of global forest fragmentation as influences from the matrix can substantially alter the characteristics of forest fragments. Thereby, forest edge zones are created with different conditions to the forest interior (Murcia, 1995). The occurrence of these forest edge zones can reduce the actual size of forest remnants, often to the detriment of forest specialist species (Bender et al., 1998; Tschardt et al., 2012). Therefore, carrying out investigations about the impact of edge effects on species communities is an important issue in conservation biology.

Species richness and diversity of secondary consumers are often highest at forest edges and decline towards the forests' core due to changes in environmental conditions, such as temperature, light availability or humidity (Murcia, 1995; Jokimäki et al., 1998; Ries et al., 2004). Thus, open-habitat, edge and generalist species are usually most abundant at forest edges (Molnár et al., 2001), whereas the species richness and abundance of forest species are more likely to be affected negatively or indifferent towards edge proximity.

In the past years, many studies have been published on edge responses of ground-dwelling forest arthropods such as spiders, carabids and staphylinids (Buse & Good, 1993; Baldissera et al., 2004; Koivula et al., 2004; Gallé & Torma, 2009). The extent to which edge effects penetrate into the forest found in these studies ranges from several meters (Pohl et al., 2007; Noreika & Kotze, 2012) up to distances of more than 1 km (Ewers & Didham, 2008). However, edge effect studies on large spatial scales are still scarce.

A habitat fragment's three-dimensional architecture (mainly in the sense of plant structure) has been suggested as an important factor predicting the extent of edge effects (Cadenasso et al., 2003; Murcia, 1995; Ries et al., 2004), as it can affect factors such as light and wind penetration into a patch that consequently change abiotic factors such as temperature or humidity and biotic factors like understorey plant growth (Ries et al., 2004). Moreover, architectural patch contrasts (=quality contrast between two adjacent habitats or matrix and fragment) can determine the strength of edge responses (Cadenasso et al., 2003; Ries & Sisk, 2004; Collinge, 2009; Noreika & Kotze, 2012) because species are more likely to penetrate from the matrix into fragments with a low patch contrast.

Tree species diversity can be an important determinant of forest architectural complexity (Getzin et al., 2012; Seidel et al., 2013). Environmental and microclimatic conditions may be altered due to species specific differences in canopy cover, growth height, litter quality and timing of leaf budding (Barbier et al., 2008; Wulf & Naaf, 2009). In Central Europe, broad-leaved forests poor in tree species are typically dominated by the common beech (*Fagus*

sylvatica L.) which has a dense, low light transmitting canopy that creates thick mats of acidic slowly decomposing leaf litter (Guckland et al., 2009; Jacob et al., 2010). Mixtures of different tree species can lead to higher light availability, reduced litter depth, increased herb diversity and higher environmental heterogeneity (Vockenhuber et al., 2011). The latter is a key factor for increased arthropod species richness, due to higher niche diversity and resource availability (Lange et al., 2014). These factors may contribute to lower patch contrasts between forest and surrounding grassland of forest stands rich in tree species compared with forest stands poor in tree species (= beech dominated) which should consequently lead to less strong edge responses. In particular, species that are not explicitly adapted to inner forest conditions (species predominantly occurring in open habitat or forest edges and habitat generalist species, hereafter referred to habitat generalists) may thus be enabled to permeate deeper into diverse forests.

Body size is related to several life history traits such as metabolic rate, home range, generation time, or space use (Peters, 1986; Woodward et al., 2005). Smaller species have been shown to be more susceptible to changes in environmental conditions such as moisture or temperature (Janzen & Schoener, 1968; Peters, 1986). According to Ribera et al. (2001) 'species in temporally stable, adverse, and spatially homogeneous environments have on average larger body sizes. As the opposite is likely to be the case in forest stands rich in tree species, we expect advantages for smaller species in those forest stands. This may apply in particular for small habitat generalists because the majority of these species are not explicitly adapted to forest conditions and thus may react especially sensitively to altered microclimatic parameters in forests.

As study organisms we chose carabids, rove beetles and spiders as they constitute an integral part of the forest soil macrofauna and because they are considered as good indicators of environmental change (Ekschmitt et al., 1997; Rainio & Niemelä, 2003; Pohl et al., 2007).

This study is the first to test potential interactions between tree diversity and edge effects and their impacts on ground-dwelling secondary consumers. Using a transect approach the study was conducted in Hainich National Park, Germany's largest deciduous forest.

The following main hypotheses were tested:

1. Tree diversity: Increased tree diversity has a positive impact on the total species richness of ground-dwelling arthropods. Habitat generalists, especially small species, may increase in species richness due to changes in environmental conditions such as a more open canopy accompanied by increased tree diversity. No general trend is expected for forest species, but we expect differences in species level responses.

2. Edge effects: Arthropod total species richness is highest at the forest edge and declines nonlinearly towards the forest interior. This pattern is expected to be driven by habitat generalists, while the decline of small species might be stronger compared to large species. The number of forest species may increase with distance from the forest edge towards forest interior.
3. Interrelations: Edge effects are stronger in beech dominated forests, because of a higher contrast in environmental conditions (and habitat heterogeneity) between forest edge and interior. Habitat generalists, especially small species, may show higher abundances and species richness in diverse forests, thus reducing the decline of total species richness from the forest edge into the forest interior.

Material and Methods

Study site

The study was conducted in the Hainich National Park, which forms part of Germany's largest connected deciduous forest. The study area is situated in the northwest of the Federal state of Thuringia in the centre of Germany (51° 5' 0" N, 10° 30' 24" E).

Most of the national park's area (75 km²) is covered by beech forest communities on calcareous soils. It used to be a military training area in the time of the German Democratic Republic (GDR), which allowed for a near-natural development of the forest for the last c. 50 years. The national park's core zone has been designated as a UNESCO World Heritage site ("Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany") in 2011. An outstanding characteristic of this area are forest stands differing in tree species richness, ranging from one species (*Fagus sylvatica* L.) to 14 deciduous tree species per hectare (Mölder et al., 2006). This makes it particularly suitable for the purpose of this study. See Mölder et al. (2006) for a detailed description of the study site.

Site selection

A transect survey was conducted with transects distributed over the whole forested area of the Hainich National Park. They extended from the forest edge up to 500 m into the forest interior.

We selected a total pool of 23 forest stands from a map of forest communities provided by the national park administration. As tree diversity and percentage of beech were highly correlated (results not shown), transects with a proportion of beech < 75 % were defined as "high tree diversity level" and transects with a proportion of beech > 75 % as "low tree

diversity level". From the original selection of 23 potential forest stands, we selected 12 stands of defined species richness, comparable age class and low variability of tree diversity within each stand. Overall, we ended up with 12 transects (one for each forest stand) with a minimum distance of 750 m between transects (six in low, six in high tree diversity stands). Tree diversity and species richness were higher in high diversity forest stands compared with low diversity stands (Table 1).

As we expected the strongest changes in species richness, abundance and community composition of the observed taxa to occur close to the edges (Didham & Lawton, 1999), we placed sampling plots at distances of 0, 4, 8, 32, 80, 200 and 500 m from the forest edge within each transect. Additionally, one plot was placed outside the shrub belt of the forest edge. However, the maximum distance of 500 m could not be reached on all transects, because tree species composition changed, stand age differed or the distance to the next edge was not large enough. Thus, four of the 12 transects only had a length of 200 m (two transects in each tree diversity level). This resulted in a total of 92 plots. The "0 m" point of each transect was set where the tree trunks began.

The forest edges were characterised by dense shrub belts mainly consisting of blackthorn (*Prunus spinosa* L. s. str.), whitethorn (*Crataegus laevigata* (Poir.) DC.) and saplings of ash (*Fraxinus excelsior* L.). The whole forest area was surrounded by abandoned grassland of different successional stages.

Sampling methods

We sampled ground-dwelling invertebrates along all transects using funnel traps (Duelli et al., 1999). Traps were sunk into PVC tubes (10 cm diameter) and filled with a saturated salt water solution and a detergent. Additionally, traps were equipped with a wire mesh (1 cm mesh size) inserted to prevent small mammals from falling into the traps. Each trap was covered with a plastic cover.

At each plot, two traps were placed at a distance of 5 m from each other (parallel to the forest edge). Sampling was performed for a total period of two consecutive years in four sampling periods of two weeks each (late May, middle of July and early September 2011, middle of April 2012). Specimens caught were then transferred into ethanol (70 % vol.). Only ground beetles, rove beetles and spiders were selected as these were the main arthropod groups sampled. Only adult specimens were determined to species level and used for analysis.

Traits

Ground beetles, rove beetles and spiders were divided into four functional groups. First, they were classified according to habitat preference: (1) *forest species*, i.e. species predominantly occurring in forests; (2) *habitat generalists*, i.e. species occurring both in forests and elsewhere. We joined open habitat and habitat generalist species (i.e. all species not predominantly occurring in forests) in the group “habitat generalists” since the actual habitat generalists constituted the largest fraction of this group and all species (including the open-habitat species) were captured either inside the forest or directly at the forest edge. The classification was based on published literature (Appendix S1).

Secondly, all species within each habitat preference group of a given taxon were further subdivided into small and large bodied species. This resulted in four categories (“forest small”, “forest large”, “habitat generalist small”, “habitat generalist large”). To classify organisms into body size classes, the mean body length of each species was determined based on published literature (Appendix S1). In case of sexual dimorphism, the mean body length of both sexes was used. For each taxon and habitat preference group (e. g. spiders, forest species) we determined the specific median body size. Species larger than the median were defined as large, whereas species smaller than the median were defined as small.

Vegetation measurements

Overall plant species richness and vegetation cover of the herb layer was recorded on six botanical subplots of each of the plots inside the forest, except for the plot outside the forest. For a detailed description of the survey procedures see Appendix S2.

Tree layer measurements

In an area of 20 x 40 m, we conducted tree surveys on each of the 80 plots that were located inside the forest, except for the plots of 0, 4 and 8 m where only one tree relevé was placed. This yielded a total number of 56 tree relevés, where all trees (DBH \geq 10 cm) were recorded. Tree species richness and diversity on the plots was estimated using the number of tree species as well as the Shannon-Wiener diversity index (H') based on basal area as it includes both species richness and abundances of species (Magurran, 2004) (Tree species richness: 1 - 9, H' : 0 - 1.81 % beech (basal area): 0 - 100 %).

The most abundant tree species was the common beech (*Fagus sylvatica* L.), which strongly dominated forest stands poor in tree species. Other abundant tree species on diverse plots were *Quercus robur* L., *Quercus petraea* LIEBL., *Tilia* sp., *Acer campestre* L., *Acer platanoides*

L., *Acer pseudoplatanus* L., *Fraxinus excelsior* and *Carpinus betulus* L.. Less abundant were *Prunus avium* L., *Betula pendula* ROTH, *Populus tremula* L., *Ulmus glabra* HUDS., *Salix caprea* L. and *Sorbus torminalis* (L.). Lime was only determined to genus level as *Tilia cordata* MILL. and *T. platyphyllos* SCOP. could not be reliably separated in the field.

Measurement of environmental variables

Canopy openness was used as an indirect measure of light availability on the plots inside the forest. It was calculated using fish-eye photographs (see Appendix S3 for details).

Soil samples from the first upper 30 cm of the mineral soil were taken using a soil corer (Pürckhauer) in order to analyse pH. 12 subsamples were taken in a grid of 3 x 4 m around the plot centre at the distances 0, 32, 80, 200 and 500 m. Subsamples were joined in one sample, dried at 40 °C and sieved (2 mm mesh size). The pH was electronically measured (suspension of 10 g soil and 25 ml 0.01 mol/l CaCl₂).

In addition, litter layer thickness (measured from the estimated mean top of the litter layer to the boundary of the humus layer) was recorded on all plots (except of the plot outside the shrub belt) using a tape measure. Litter depth was measured in the centre of each of the six botanical subplots. The mean of the six subplots was calculated for further analyses.

The total volume of lying and standing dead wood with a length > 1 m was recorded on every tree relevé plot. Threshold diameter for dead wood pieces was 7 cm, if the thicker end lay inside of the plot. Dead wood volume was then calculated following Meyer (1999).

Based on the method of the Second Swiss National Forest Inventory (Brassel & Lischke, 2001) adjusted to the tree relevé plot size, we assessed the structural diversity of the plots. The method consisted of the assessment of several parameters such as stage of development, stand structure, coverage of shrub layer and presence of standing dead trees. Each parameter received a certain value from which the structural diversity could be calculated. Using the method of Brassel & Lischke (2001), theoretical values for structural diversity can range from 3 (low diversity) to 56 (high diversity). Actual values of this survey ranged from 11 to 31.

Since a part of the pitfall traps was destroyed by wild boars (*Sus scrofa* L.), we excluded the sampling periods of July and September from further analyses. From the remaining sampling periods, only one of the two traps per plot and sampling period was selected. In case one trap was destroyed and one was intact, the undamaged one was chosen. In case both traps were intact we chose the sample containing more individuals. For each taxon, the mean species

abundances calculated from the two sampling occasions. Values were then rounded (values < 1 were rounded to 1).

Statistical analyses

Spearman's rank correlation showed that the tree diversity describing parameters tree diversity level, tree species richness and H' trees and proportion of beech (based on relative basal area) were highly correlated. Therefore, only tree diversity level was included as factorial explanatory variable in the following statistical models. All analyses were conducted using R, version 3.0.2 (R Development Core Team 2013).

The main models did not include environmental parameters as explanatory variables because they were not independent of the design variables "tree diversity level" and "distance from forest edge" (Table 1). Additional effects of environmental parameters on the three taxa were analysed with Spearman's rank correlation tests.

Total species richness of each taxon was analysed using generalized linear mixed models fit by penalized quasi-likelihood (glmmPQL, "nlme" package (Venables & Ripley, 2002)) and poisson (carabids) or negative binomial errors (spiders, rove beetles). Explanatory variables were tree diversity level and distance from forest edge (distance). Distance was log-transformed to account for increasing distance between plots within one transect. Prior to running the glmmPQL's we fitted four generalized linear models (without random effects) either with poisson or negative binomial model errors and either untransformed or log-transformed distance. Then Akaike's Information Criterion, corrected for small sample sizes (AICc), was calculated for each of the models (AICc, "MuMIn" package (Burnham & Anderson, 2002)). The model with the lowest AICc value was considered the best maximal model. The best maximal model was then re-fitted using glmmPQL with transect as random factor to account for unmeasured transect-specific environmental effects. In addition, we weighted data points according to the number of sampling periods from which each sample mean had originated (...weights=NoOfSamples...). We started off with the full models containing interactions between explanatory variables. Model simplification was conducted manually by removing non-significant effects starting with the interactions.

To test if habitat specialisation and body size class had an impact on the response of species richness on tree diversity level and distance from forest edge, we fitted an additional generalized linear mixed model separately for each taxon. This model contained "forest.size" (levels: forest species_large, forest species_small, habitat generalist_large, habitat

generalist_mall) as an additional explanatory variable and allowed for interactions between all three explanatory variables. The remaining procedure was the same as described above.

Finally, we fitted multinomial models (multinom function, nnet library, (Ripley, 2013)) to assess the species-level responses of each taxon to tree diversity level and distance from the forest edge. As response variable we used a matrix containing the abundances of each species (including only species with a total abundance of > 10 individuals). No transformation of explanatory variables was performed as multinomial models are inherently nonlinear (Scherber et al., 2014). Models were automatically simplified using stepwise model selection based on AICc (stepAICc function, “MASS” package, corrected for small sample sizes by C. Scherber (2009, <http://wwwuser.gwdg.de/~cscherb1/stepAICc.txt>)). Multinomial models were fitted without random effects, as additional models (fit using the bayesx function in R, package “R2BayesX”) showed higher AIC values, indicating that model fits were not improved by the incorporation of random effects.

Results

In total we recorded 12298 specimens from 335 species. Ground beetles were the most abundant group (5481 individuals). 20 of 43 ground beetle species were forest species, 23 were habitat generalists (all species that do not predominantly occur in forests). The most abundant species were *Pterostichus oblongopunctatus* F. (19.8 %), *Pterostichus burmeisteri* HEER (17.57 %) and *Abax parallelepipedus* PILL. & MITTER. (15.14 %). Rove beetles comprised 3686 individuals from 94 species (25 forest species, 69 habitat generalists). The by far most dominant species was *Philonthus decorus* GRAV. (66.77 %), followed by *Liogluta microptera* THOMS. (4.94 %) and *Aleochara ruficornis* GRAV. (2.33 %). We found 3131 spider specimens from 98 species (49 forest species, 45 habitat generalists). The most abundant species were *Trochosa terricola* THORELL (10.0 %), *Inermocoelotes inermis* L. KOCH (9.01 %) and *Diplocephalus picinus* BLACKWALL (7.7 %).

Overall species richness

Total species richness responded differently to edge proximity and tree diversity level, depending on taxon (Fig. 1, Table S1). Total species richness of ground beetles was not affected by any of the two design variables. Contrarily, total species richness of rove beetles was significantly influenced by an interaction between both factors. While species richness remained constant in the high diversity level with increasing distance from the forest edge, it rapidly declined in the low tree diversity level. 70 % of this decline was observed within a

distance 80 m from the edge. Total species richness of rove beetles was higher in the forest interior of the high tree diversity level compared with the forest interior of the low tree diversity level. Spider total species richness significantly decreased with increasing distance from the forest edge (60 % of total decline within first 80 m), but was not affected by tree diversity.

Response of small vs. large and forest vs. habitat generalist species

When habitat specialisation categories and body size class (incorporated in the explanatory variable “forestsized”) were included into the models, all three taxa responded differently to edge proximity and tree diversity, depending on body size and habitat specialisation type. The two beetle taxa were significantly influenced by a three-way interaction of all explanatory variables, whereas spider species richness was influenced by two-way interactions between “forestsized” and tree diversity level as well as a two-way interaction between “forestsized” and distance from the forest edge (Fig. 2, Table S2).

In general, forest species reacted slightly positively (carabids) or not at all (staphylinids and spiders) to increasing distance from the forest edge. Carabid forest species richness slightly increased in the high tree diversity level, whereas staphylinid and spider forest species richness tended to decrease. In contrast to that, the habitat generalists species richness of all three taxa rapidly decreased with increasing distance from the forest edge in the low tree diversity level (strongest changes within the first 80 m from the edge). Overall, this decline was dampened (or even reversed as found for small habitat generalist staphylinids) in the high tree diversity level and the number of habitat generalists increased in the high tree diversity level. The relative increase in species number in the forest interior of the high tree diversity level was particularly pronounced for small habitat generalists.

Species-level responses

Edge proximity and tree diversity had a significant impact on the species-level relative abundance of ground beetles, rove beetles and spiders (Fig. 3).

In general, forest stands poor in tree species were dominated by only a few species, whereas in the high tree diversity level more species had higher abundances and the community was more heterogeneous. Also, the response to the edge differed with tree diversity level.

Environmental variables

Most of the environmental parameters such as litter layer thickness, pH and herb layer characteristics differed with edge proximity and tree diversity level (Table 1).

All environmental parameters measured had an influence on the focal taxa, whereas the correlations differed between the three taxa, but also between the species richness of the functional groups (Table 2).

Table 1 Summary statistics of parameters characterising the forest stands at the forest edge (distance from forest edge 0 m) and the forest interior (distance from forest edge 500 m) in the high and in the low tree diversity level. Values are means \pm standard error (SE). H' = Shannon-Wiener diversity index based on basal area (Magurran, 2004).

	low tree diversity		high tree diversity	
	Edge	Interior	Edge	Interior
pH	5.52 \pm 0.38	4.16 \pm 0.09	6.25 \pm 0.44	5.51 \pm 0.69
Litter layer thickness (cm)	2.28 \pm 0.70	3.19 \pm 0.33	1.32 \pm 0.28	1.9 \pm 0.44
Canopy Openness (%)	12.36 \pm 1.61	10.78 \pm 0.71	12.28 \pm 1.03	11.05 \pm 0.44
Dead wood volume (m ³)	0.46 \pm 0.24	0.29 \pm 0.19	2.5 \pm 0.93	2.23 \pm 1.32
Forest structural diversity	26.5 \pm 1.57	18.25 \pm 1.31	23 \pm 2.42	20.5 \pm 1.04
Herb layer overall plant SR	32.50 \pm 5.10	18.25 \pm 2.02	28.50 \pm 6.09	29.50 \pm 3.66
Herb layer plant cover (spring)	30.72 \pm 6.59	49.33 \pm 12.15	34.11 \pm 8.65	61.67 \pm 9.97
Herb layer plant cover (summer)	34.29 \pm 9.33	18.33 \pm 4.75	28.78 \pm 7.90	32.92 \pm 6.23
No. tree species	4.83 \pm 1.19	1.75 \pm 0.48	7.33 \pm 0.84	6.5 \pm 0.50
% beech area	60.48 \pm 12.07	97.66 \pm 1.48	7.91 \pm 2.37	34.32 \pm 13.99
H' tree area	0.91 \pm 0.22	0.1 \pm 0.06	1.47 \pm 0.1	1.35 \pm 0.11

Abbreviations: SR = species richness

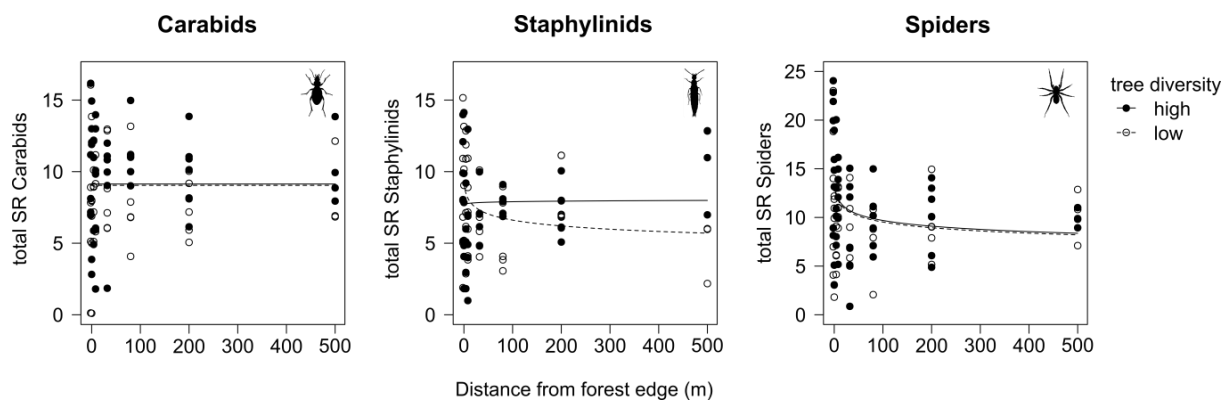


Figure 1 Effects of distance from the forest edge and tree diversity level on the total species richness of ground beetles, rove beetles and spiders. Curves represent predictions from the glmmPQL model (Table S4). Distance from the forest edge (m) was back-transformed for graphical illustration. Note the different scales on the y-axis.

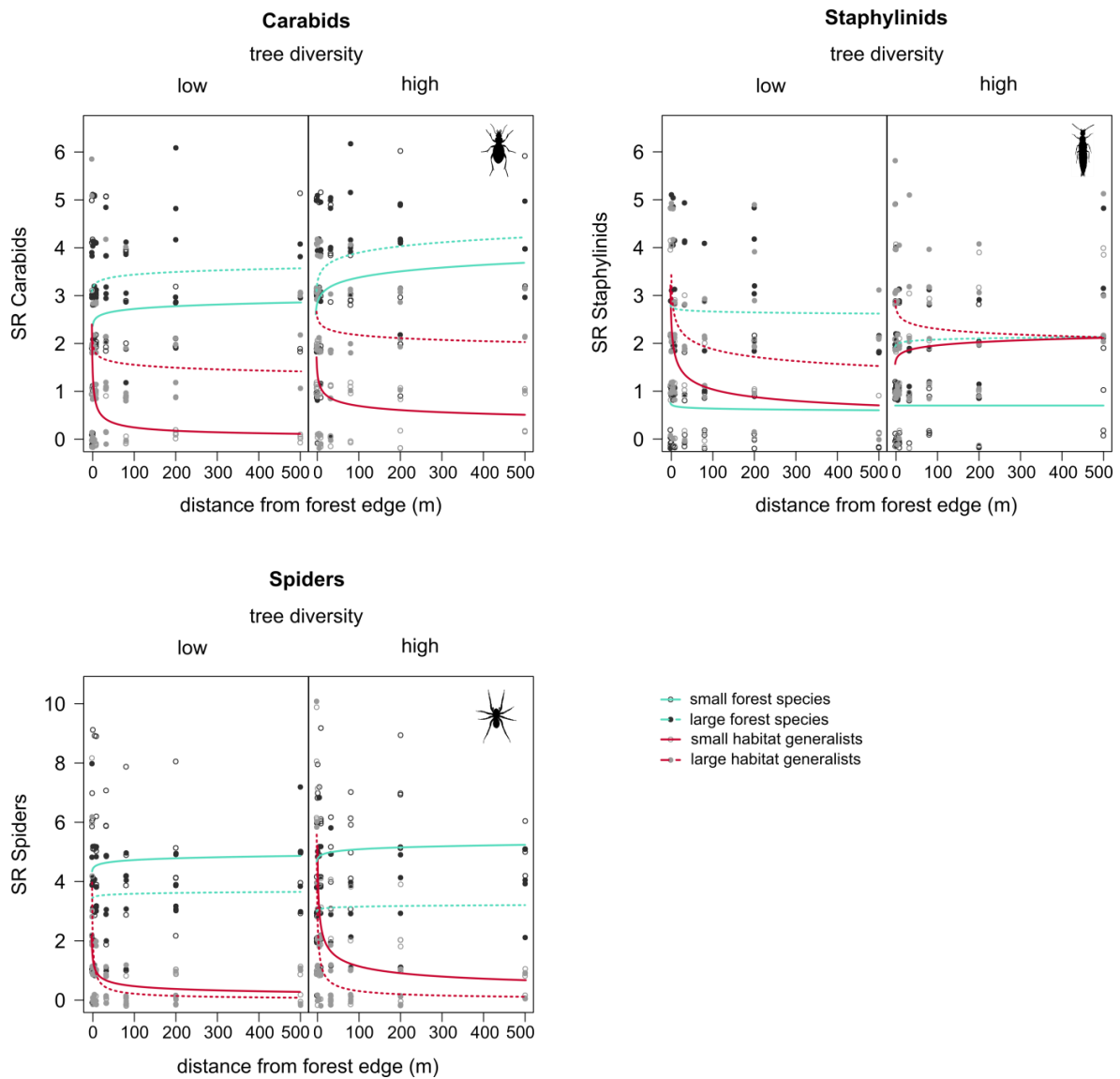


Figure 2 Effects of the explanatory variables distance from the forest edge (m), tree diversity level and forest size on species richness of carabids, staphylinids and spiders. Curves show predictions from the glmmPQL models (Table S5). Distance from the forest edge was backtransformed for graphical presentation.

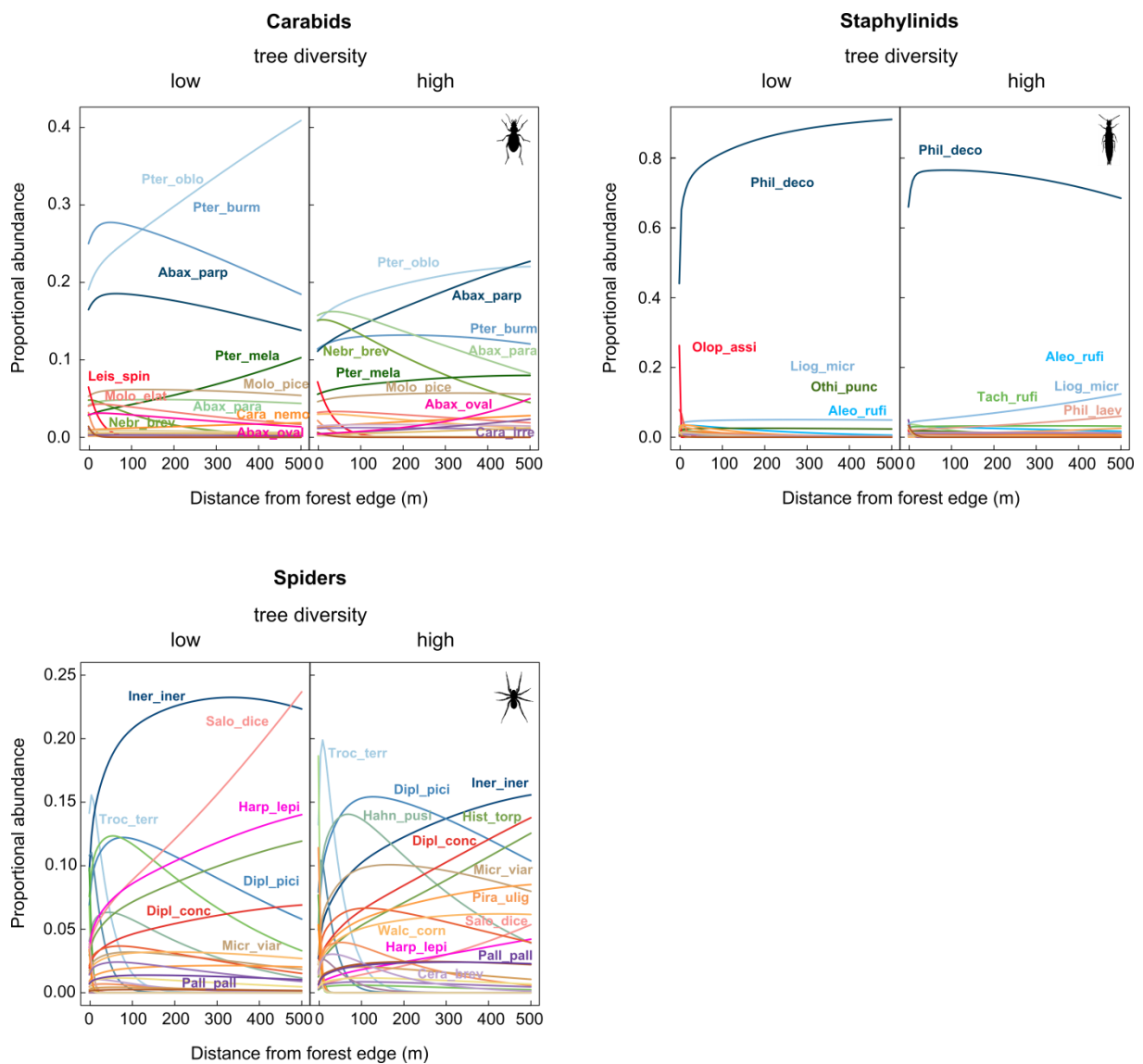


Figure 3 Relative abundance of single species to distance from the forest edge (m) and tree diversity level found for carabids, staphylinids and spiders. Curves show predictions from the minimal adequate multinomial models of the three taxa. Note different scales on the y-axes. Complete species names are listed in Table S6.

Table 2 Spearman's rank correlation coefficient (rho) between environmental parameters characterising the forest and total species richness (SR), SR of small forest species, SR of large forest species, SR of small habitat generalists and SR of large habitat generalists of ground beetles, rove beetles and spiders.

	total SR	SR small forest species	SR large forest species	SR small habitat generalists	SR large habitat generalists
Ground beetles					
pH	-0.02	-0.11	-0.10	0.15	0.04
Litter layer thickness (cm)	-0.18	-0.20	0.15	-0.33**	-0.13
Canopy Openness (%)	0.42**	0.37**	0.04	0.37**	0.40**
Dead wood volume (m ³)	0.16	0.14	0.14	0.03	0.14
Forest structural diversity	0.13	0.01	0.11	0.22*	0.16
Herb layer overall plant SR	0.15	0.07	-0.12	0.27*	0.16
Herb layer plant cover (spring)	0.17	0.14	0.21	-0.02	0.07
Herb layer plant cover (summer)	0.27	0.16	0.08	0.29**	0.16
Rove beetles					
pH	-0.08	-0.03	-0.28*	0.11	-0.02
Litter layer thickness (cm)	0.11	0.16	0.38**	-0.09	-0.14
Canopy Openness (%)	0.00	-0.26*	-0.05	0.04	0.25*
Dead wood volume (m ³)	0.21	-0.10	-0.06	0.30**	0.27*
Forest structural diversity	0.29**	0.15	0.16	0.25*	0.20
Herb layer overall plant SR	0.03	-0.08	-0.04	0.04	0.14
Herb layer plant cover (spring)	0.10	0.04	0.13	-0.02	0.07
Herb layer plant cover (summer)	0.04	-0.10	0.09	-0.10	0.21
Spiders					
pH	0.11	0.06	-0.23*	0.32**	0.42**
Litter layer thickness (cm)	-0.04	0.01	0.27*	-0.34**	-0.29**
Canopy Openness (%)	0.36**	0.35**	0.10	0.28*	0.20
Dead wood volume (m ³)	-0.09	-0.02	-0.08	-0.08	-0.12
Forest structural diversity	0.27*	0.31**	0.11	0.04	0.10
Herb layer overall plant SR	0.09	0.01	0.02	0.15	0.23*
Herb layer plant cover (spring)	0.17	0.13	0.24*	0.01	0.10
Herb layer plant cover (summer)	0.30**	0.23	0.12	0.19	0.29**

**= p-value <0.01; *= p-value <0.05; Abbreviations: SR = species richness

Discussion

This study has clearly shown that responses of ground-dwelling arthropods to edge proximity and tree diversity depended on taxon, body size and habitat specialisation. While carabid species richness was unaffected by edge or tree diversity, staphylinids and spiders showed opposing patterns. The same was true for species of different sizes and forest specialisation classes: Responses to forest edge and tree diversity were strongly modified by whether organisms were small or large and whether they preferred forest habitats or not. The richness of habitat generalists strongly declined with increasing distance from the forest edge. However, this effect was mitigated by increased tree diversity level, and small habitat generalists even increased in the interior of species-rich stands. The response of forest species

was less unidirectional. This pattern was further reflected in a wide variety of single species responses.

Up to date, the majority of studies on tree compositional effects considered different types of forest stands such as pure coniferous vs. mixed or different successional stages (Riihimäki et al., 2005; Fuller et al., 2008; Do & Joo, 2013), but actual tree diversity was scarcely addressed. Thus, our study is likely the first to show clear effects of tree diversity on edge effects in ground-dwelling arthropods. Hence, our finding that edge effects can be mediated by (tree) biodiversity is a novel insight, so far not found in previous studies.

However, results from the present study may not always easily translate to other forest systems (Nadrowski et al., 2010; Schuldt et al., 2011; Bruelheide et al., 2014), as our forest stands were dominated by beech acting as ecosystem engineer (Lawton, 1994; Mölder et al., 2014).

Total species richness

Many previous studies reported that species richness of ground-dwelling arthropods is highest at forest edges (Jokimäki et al., 1998; Horváth et al., 2002; Gallé & Fehér, 2006; Elek & Tóthmérész, 2010), as communities from different habitats may merge. However, in the present study the total species richness response differed among taxa. Spider total species richness decreased with increasing distance from the edge, whereas carabids did not respond. As hypothesized, the edge response of staphylinid species richness depended on tree diversity, being neutral in high diversity stands and declining towards the centre in low tree diversity stands. This resulted in a higher rove beetle species richness in the forest interior of the high tree diversity stands. Spider and carabid total species richness were not affected by tree diversity. According to this, comparable previous studies showed taxon dependent responses to alterations in tree species composition (Riihimäki et al., 2005; Schuldt et al., 2008; Sobek et al., 2009a, 2009b, 2009c; Scherber et al., 2014).

It appears that the response of the total species richness of the focal taxa was driven by the response of habitat generalists, with the exception of carabids where the negative response of habitat generalists and the weak positive response of forest species compensated each other and may have been the reason of an overall indifferent response.

Forest specialisation, edge effects and tree diversity

In concordance with previous studies, the richness of habitat generalists species across taxa was highest at the forest edge and declined strongly towards the interior (Niemelä et al., 1993;

Horváth et al., 2002), whereas forest species richness was less sensitive (Heliölä et al., 2001; Koivula et al., 2004).

We found that habitat generalists species were positively affected by higher tree diversity and thus permeated deeper into diverse than into beech dominated forests. Furthermore, edge responses were mitigated by high tree diversity (found for carabids and staphylinids but not for spiders). This benefit from high tree diversity was particularly pronounced for small habitat generalists.

We believe that our findings can be attributed to changes of environmental parameters and habitat heterogeneity. Explanations for the observed patterns might be similar for all focal taxa, although beetles and spiders in particular have different life histories, but exploit similar resources (Alaruikka et al., 2002).

The overall positive response of habitat generalists to edge proximity may be ascribed to edges being more dynamic and heterogeneous habitats meeting the requirements of different kinds of species (Didham et al., 1998; Ewers & Didham, 2006; Marchand & Houle, 2006).

Increased tree diversity can also have profound effects on environmental parameters such as soil pH (Barbier et al., 2008; Guckland et al., 2009). Here, reduced litter thickness and increased canopy openness appear as the most important environmental factors for the increased richness of species explicitly preferring forests which is in line with other studies (Fuller et al., 2008; Guillemain et al., 1997; Molnár et al., 2001; but see Ziesche & Roth, 2008). Forest species showed contrasting responses to several environmental parameters, which might indicate an affinity to thick litter layers and moist, cool microclimatic conditions (Bultman & Uetz, 1982; Pohl et al., 2008). However, overall, forest species responded less to altered environmental parameters compared with habitat generalists and only responded very weakly to increased tree diversity.

Tree assemblages consisting of more different tree species cause a pattern of patchily distributed resources, thus increasing habitat heterogeneity and niche differentiation (Beatty, 2003; Sobek et al., 2009a, 2009b). Habitat heterogeneity is generally regarded as driver of species diversity ("environmental heterogeneity hypothesis" (Huston, 1994); "enemies hypothesis" (Russell, 1989)), because heterogeneous habitats meet the requirements of a broader range of species. Small scale effects have been shown for forest's carabid, staphylinid and spider assemblages (Fuller et al., 2008 and references therein; Pohl et al., 2007; Ziesche & Roth, 2008). As demonstrated here, generalist species being more tolerant for changes of environmental conditions may benefit more from spatial heterogeneity than specialist species

being less tolerant (McIver et al., 1992; Ye et al., 2014). Furthermore, this may favour the invasion of species not exclusively residing in forest habitats.

Body size, edge effects and tree diversity

Large habitat generalists were not affected negatively, but the relative increase of species richness with increased tree diversity was particularly accentuated for small habitat generalists. In the course of evolution, it has been hypothesized that terrestrial species increase in size under stable and monotonous conditions (Brown & Maurer, 1986; Ribera et al., 2001). Consequently, a shift of arthropod assemblages towards smaller and less specialised species in more heterogeneous habitats has been reported (Šustek, 1987; Blake et al., 1994; Brändle et al., 2000; Gibbs & Stanton, 2001; Alaruikka et al., 2002; Magura et al., 2006). Matching our results for the two beetle taxa Blake (1996) found carabid forest species to be larger than habitat generalists (results not shown).

Small species have been shown to be more susceptible to changes in environmental conditions such as moisture or temperature than large species (Janzen & Schoener, 1968; Peters, 1986). Therefore, microclimatic conditions in the beech dominated forest stands might have been particularly unhostile for small species not explicitly adapted to forests. Thus, this group might benefit more from conditions in the high diversity forests being more open and heterogeneous compared with large species. In line with our results, Tyler (2008) explained less small carabid species in beech forest Podzol sites with a negative effect of increased litter depth and litter structure influences the distribution of small and large bodied rove beetles differently.

Moreover, small and large species have been shown to forage on different spatial scales (Peters, 1986; Woodward et al., 2005). Thus, forage efficiency might have been promoted by higher tree diversity due to lower spatial resistance (reduced litter depth) and increased prey abundance. Furthermore, Blackburn & Gaston (1994) argued that species of different body size than the original species are more likely to invade a habitat, which would in this case be smaller-bodied species. Body size had no substantial impact on the edge or the tree diversity response of the forest species.

However, large spiders and rove beetles tended to react slightly negatively to increased tree diversity, which can be related to more heterogeneous and less stable environmental conditions (Blake et al., 1994; Alaruikka et al., 2002; Niemelä et al., 2002).

Species specific responses

The dominance structure of the observed arthropod communities clearly changed with increased tree diversity and distance from the forest edge. Overall, more species reached higher relative abundances in the high tree diversity level, whereas the low tree diversity level was dominated by few forest species. The results found for the habitat generalist species richness are reflected in the species specific responses, as certain species not predominantly occurring in forests increased more in abundance in the high tree diversity level, such as the red-listed lycosid species *Pirata uliginosus* (Thorell 1856) or the staphylinid species *Philonthus laevicollis* (Lacordaire 1835). Among all taxa some forest species were favoured whereas others suffered from high tree diversity. Species with a high conservation value benefitting from high tree diversity were *Abax parallelus* (Duftschmid 1812), a species preferring species rich oak-hornbeam forests (Assmann, 1995; Müller-Kroehling, 2013), and the red-listed *Carabus irregularis* (Fabricius 1792), a species of ravine forests (Müller-Kroehling, 2008). In contrast, the red-listed linyphiid species *Saloca diceros* (O. P.-Cambridge 1871) and the red-listed *Pterostichus burmeisteri* (Heer 1838), a typical species of beech forests (Müller-Kroehling, 2009), preferred beech dominated forests. These individual responses may explain the overall weak responses of forest species richness. This underlines the qualitative gain of information when modelling the response of whole arthropod communities rather than exclusively analysing community level responses (Scherber et al., 2014). The relative abundance of forest species might have declined not only due to changes in environmental conditions unfavourable for these species but also because of competition with invading species from the matrix (Pohl et al., 2008).

Conclusions

We have shown that tree diversity modified edge effects in Germany's largest deciduous forest, presumably due to alterations of environmental parameters and habitat heterogeneity. However, as the environmental parameters analysed were not independent, we emphasize the need of more experimental studies investigating the effects of certain environmental parameters independently.

We showed that both eco-evolutionary background and the life history trait body size could be used to predict the response of the three taxa to tree diversity and edge proximity. Habitat generalists and among these particularly small species benefited most from increased tree diversity, whereas forest species only responded weakly. This pattern resembles results found in disturbed forests and small forest fragments (Deichsel, 2006) indicating similar underlying

mechanisms. We conclude that increased tree diversity, by creating more open and heterogeneous environmental conditions, mitigated the edge-interior contrast and thus enabled the invasion of more species not exclusively residing in forests.

According to Rainio & Niemelä (2003), the response of a good indicator species group to habitat alteration should reflect the response of other species. Our results demonstrate that total species richness is not an appropriate proxy for species responses to habitat alterations, but that the same functional groups of different taxa might resemble each other more and allow for more causal overall conclusions. This is in particular of interest in the case of rove beetles, the responses of which to habitat fragmentation are still largely unknown (Pohl et al., 2007, 2008).

The weak impairment of forest species richness by edge proximity might be due to the near natural, dense shrub belt surrounding the national park's forests. This would further underline the importance of natural forest edges for maintaining forest species diversity.

In our study, the dominance structure of the arthropod communities was altered by tree diversity and edge proximity. Some red-listed species clearly relied on beech-dominated forests, whereas others were promoted by increased tree diversity. This highlights the importance of maintaining not only old growth beech forests (like the UNESCO World Heritage sites "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany") but also near natural forests rich in tree species as a conservation goal.

Our study highlights the importance of taking into account tree diversity, but also life history traits of species when addressing edge effects in forests.

Acknowledgements

This study was financed by the German Research Foundation (DFG) in the framework of the research training group 'Graduiertenkolleg 1086: The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests'. Thanks to Urs Kormann and Pierre Gras for helpful comments on the statistics and Dominik Seidel for inventing study region specific formulae for the calculation of original tree heights of standing dead wood. Furthermore, we thank the Hainich National Park administration for collaboration and valuable information.

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Appendix

S1

Data bases:

www.carabids.org

<http://wiki.spinnen-forum.de>

<http://www.araneae.unibe.ch>

Literature:

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S2

Vegetation measurements:

Vegetation surveys of the herb layer were conducted comprising six botanical subplots per plot. They had a size of 1 x 3 m (longer side parallel to forest edge) and were arranged in a row running parallel to the forest edge. Distance between relevés was approximately 1 m.

All flowering plant species up to 70 cm height and their cover (in percent) were recorded. For further analysis the cover of every plant species was averaged over the six relevés per plot by taking the arithmetic mean. The survey was carried out twice to account for both spring ephemerals characteristic for deciduous forests and summer vegetation, resulting in 960 relevés in total. The spring survey was done in April 2012, the summer survey in July/August 2012.

References:

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S3

Assessment of canopy openness:

Canopy openness was assessed using fish eye photographs taken with a Nikon Coolpix 8400 camera plus Nikon FC-E9 fisheye converter and UR-E16 adapter ring (Nikon Corporation, Chiyoda, Tokyo, Japan). Using Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, California, USA) the photographs were processed in three steps: 1. The image background was converted into an editable layer, 2. the ellipse selection tool was used to select an exactly circular area, excluding the black margin contained in each photograph, 3. in the layers menu, "layer mask" was selected and then "reveal selection" chosen; the formerly black area was thus removed and replaced by a transparent background. Thereafter we used Adobe Photoshop Lightroom 5.2 (Adobe Systems Inc.) and performed adjustments to all photographs in the following way: Contrast was set to -100, highlights were set to -73, whites were set to +7, black was set to -100 and clarity was set to 66. In the tone curve, lights were set to +96. Using SideLook 1.1.01 we (automatically) estimated the optimal threshold for converting photographs into black-and-white pictures (Nobis & Hunziker, 2005). We then calculated canopy openness with Gap Light Analyzer 2.0 (Cary Institute of Ecosystem Studies, Millbrook, New York, USA).

References:

Nobis, M., & Hunziker, U. (2005) Automatic thresholding for hemispherical canopy-photographs based on edge detection. *Agricultural and Forest Meteorology*, **128**, 3-4, 243–250.

Table S4 Results of the generalised linear mixed models testing the effects of tree diversity level (reference level = treediversityhigh) and distance from the forest edge on the total species richness of carabids, staphylinids and spiders. Distance from the forest edge was log-transformed. Only the results of simplified models are shown, if simplification was necessary. DF = degrees of freedom. Bold characters depict P-values < 0.05.

Explanatory	Estimate	SE	DF	<i>t</i>	<i>p</i>
<u>total SR Carabids</u>					
Intercept	2.21	0.07	79	31.67	<0.001
<u>total SR Staphylinids</u>					
Intercept	2.32	0.12	76	19.49	<0.001
treediversityhigh	-0.31	0.17	10	-1.82	0.099
distance	-0.09	0.03	76	-2.95	0.004
treediversityhigh x distance	0.10	0.04	76	2.28	0.025
<u>total SR Spiders</u>					
Intercept	2.68	0.08	79	35.23	<0.001
distance	-0.09	0.02	79	-4.64	<0.001

Abbreviations: distance = distance from forest edge (m)

Table S5 Results of the generalized linear mixed models testing the effects of tree diversity level, distance from the forest edge, body size class and habitat preference on species richness of carabids, staphylinids and spiders. Distance from the forest edge was log-transformed. Only the results of simplified models are shown, if simplification was necessary. Reference level of the explanatory variable tree diversity level (treediversity) was treediversityhigh. and Forest specialisation and body size class were included in one explanatory variable (forestsize, reference level = forestsize_forestLarge). DF = degrees of freedom. Bold characters depict P-values < 0.05.

Explanatory	Estimate	SE	DF	<i>t</i>	<i>p</i>
SR Carabids					
Intercept	1,13	0,15	342	7,65	<0,001
treediversityhigh	0,00	0,20	10	0,01	0,989
distance	0,02	0,03	342	0,74	0,457
forestsize_forestSmall	-0,27	0,18	342	-1,47	0,142
forestsize_othersLarge	-0,42	0,20	342	-2,13	0,034
forestsize_othersSmall	-0,25	0,21	342	-1,17	0,241
treediversityhigh x forestsize_forestSmall	0,10	0,25	342	0,39	0,699
treediversityhigh x forestsize_othersLarge	0,27	0,26	342	1,03	0,306
treediversityhigh x forestsize_othersSmall	-0,34	0,30	342	-1,13	0,259
treediversityhigh x distance	0,03	0,04	342	0,60	0,546
distance x forestsize_forestSmall	0,01	0,05	342	0,14	0,886
distance x forestsize_othersLarge	-0,08	0,05	342	-1,51	0,132
distance x forestsize_othersSmall	-0,51	0,09	342	-5,94	<0,001
treediversityhigh x distance x forestsize_forestSmall	0,00	0,06	342	-0,02	0,986
treediversityhigh x distance x forestsize_othersLarge	-0,01	0,07	342	-0,17	0,868
treediversityhigh x distance x forestsize_othersSmall	0,27	0,11	342	2,48	0,014
SR Staphylinids					
Intercept	1,03	0,17	334	6,09	<0,001
treediversityhigh	-0,37	0,25	10	-1,45	0,177
distance	-0,01	0,04	334	-0,24	0,813
forestsize_forestSmall	-1,31	0,34	334	-3,81	<0,001
forestsize_othersLarge	0,20	0,22	334	0,94	0,350
forestsize_othersSmall	0,14	0,23	334	0,61	0,541
treediversityhigh x forestsize_forestSmall	0,30	0,49	334	0,61	0,542
treediversityhigh x forestsize_othersLarge	0,20	0,32	334	0,62	0,538
treediversityhigh x forestsize_othersSmall	-0,35	0,35	334	-1,00	0,318
treediversityhigh x distance	0,03	0,06	334	0,40	0,689
distance x forestsize_forestSmall	-0,02	0,10	334	-0,26	0,796
distance x forestsize_othersLarge	-0,12	0,06	334	-1,90	0,058
distance x forestsize_othersSmall	-0,23	0,07	334	-3,26	0,001
treediversityhigh x distance x forestsize_forestSmall	0,01	0,14	334	0,07	0,946
treediversityhigh x distance x forestsize_othersLarge	0,06	0,09	334	0,61	0,544
treediversityhigh x distance x forestsize_othersSmall	0,27	0,10	334	2,65	0,009
SR Spiders					
Intercept	1,23	0,14	346	8,88	<0,001
treediversityhigh	-0,13	0,14	10	-0,92	0,381
distance	0,01	0,03	346	0,35	0,729
forestsize_forestSmall	0,24	0,17	346	1,43	0,153
forestsize_othersLarge	0,15	0,21	346	0,70	0,484
forestsize_othersSmall	-0,46	0,23	346	-2,02	0,045
treediversityhigh x forestsize_forestSmall	0,20	0,16	346	1,31	0,192
treediversityhigh x forestsize_othersLarge	0,47	0,23	346	2,08	0,038
treediversityhigh x forestsize_othersSmall	1,01	0,22	346	4,51	<0,001
distance x forestsize_forestSmall	0,01	0,04	346	0,19	0,850
distance x forestsize_othersLarge	-0,64	0,07	346	-8,57	<0,001
distance x forestsize_othersSmall	-0,34	0,06	346	-5,91	<0,001

Abbreviations: distance = distance from forest edge (m)

Table S6 List of carabid, staphylinid and spider species recorded along the 12 transects. The explanatory variable “forestsize” consists first of the habitat specialisation category and second of the body size class. Classification into trait groups was conducted following data bases, literature and expert knowledge listed in S1. Forest species = species predominantly occurring in forests; Habitat generalists = species occurring in forests and elsewhere

Species	Abbreviation	"forestsize"
<u>Carabids</u>		
<i>Abax carinatus</i>	Abax_cari	forest species_large
<i>Abax parallelepipedus</i>	Abax_parp	forest species_large
<i>Abax parallelus</i>	Abax_para	forest species_large
<i>Carabus coriaceus</i>	Cara_cori	forest species_large
<i>Carabus granulatus</i>	Cara_gran	forest species_large
<i>Carabus irregularis</i>	Cara_irre	forest species_large
<i>Cychrus caraboides</i>	Cych_cara	forest species_large
<i>Molops elatus</i>	Molo_elat	forest species_large
<i>Pterostichus burmeisteri</i>	Pter_burm	forest species_large
<i>Pterostichus madidus</i>	Pter_madi	forest species_large
<i>Abax ovalis</i>	Abax_oval	forest species_small
<i>Harpalus latus</i>	Harp_latu	forest species_small
<i>Lebia chlorocephala</i>	Lebi_chlo	forest species_small
<i>Leistus rufomarginatus</i>	Leis_rufo	forest species_small
<i>Molops piceus</i>	Molo_pice	forest species_small
<i>Notiophilus biguttatus</i>	Noti_bigu	forest species_small
<i>Platynus assimilis</i>	Plat_assi	forest species_small
<i>Pterostichus oblongopunctatus</i>	Pter_oblo	forest species_small
<i>Stomis pumicatus</i>	Stom_pumi	forest species_small
<i>Trichotichnus nitens</i>	Tric_nite	forest species_small
<i>Amara eurynota</i>	Amar_eury	habitat generalist_large
<i>Amara ovata</i>	Amar_ovat	habitat generalist_large
<i>Calathus fuscipes</i>	Cala_fusc	habitat generalist_large
<i>Carabus nemoralis</i>	Cara_nemo	habitat generalist_large
<i>Harpalus rufipes</i>	Harp_rufi	habitat generalist_large
<i>Leistus spinibarbis</i>	Leis_spin	habitat generalist_large
<i>Poecilus cupreus</i>	Poec_cupr	habitat generalist_large
<i>Pterostichus macer</i>	Pter_mace	habitat generalist_large
<i>Pterostichus melanarius</i>	Pter_mela	habitat generalist_large
<i>Pterostichus niger</i>	Pter_nige	habitat generalist_large
<i>Zabrus tenebrioides</i>	Zabr_tene	habitat generalist_large
<i>Anchomenus dorsalis</i>	Anch_dors	habitat generalist_small
<i>Badister bullatus</i>	Badi_bull	habitat generalist_small
<i>Bembidion guttula</i>	Bemb_gutt	habitat generalist_small
<i>Bembidion lampros</i>	Bemb_lamp	habitat generalist_small
<i>Brachinus explodens</i>	Brac_expl	habitat generalist_small
<i>Clivina fossor</i>	Cliv_foss	habitat generalist_small
<i>Loricera pilicornis</i>	Lori_pili	habitat generalist_small
<i>Nebria brevicollis</i>	Nebr_brev	habitat generalist_small
<i>Ophonus azureus</i>	Opho_azur	habitat generalist_small
<i>Pterostichus ovoideus</i>	Pter_ovo	habitat generalist_small
<i>Pterostichus vernalis</i>	Pter_vern	habitat generalist_small
<i>Trechus quadristriatus</i>	Trec_quad	habitat generalist_small
<u>Staphylinids</u>		
<i>Dinothenarus fossor</i>	Dino_foss	forest species_large
<i>Domene scabricollis</i>	Dome_scab	forest species_large
<i>Euryporus picipes</i>	Eury_pici	forest species_large
<i>Othius punctulatus</i>	Othi_punc	forest species_large
<i>Philonthus decorus</i>	Phil_deco	forest species_large
<i>Quedius fumatus</i>	Qued_fuma	forest species_large
<i>Quedius lateralis</i>	Qued_late	forest species_large

<i>Quedius paradisianus</i>	Qued_para	forest species_large
<i>Staphylinus erythropterus</i>	Stap_eryt	forest species_large
<i>Xantholinus tricolor</i>	Xant_tric	forest species_large
<i>Mycetoporus eppelsheimianus</i>	Myce_eppe	forest species_NA
<i>Siagonium humerale</i>	Siag_hume	forest species_NA
<i>Stenus ludyi</i>	Sten_ludy	forest species_NA
<i>Anotylus mutator</i>	Anot_muta	forest species_small
<i>Anthobium atrocephalum</i>	Anth_atro	forest species_small
<i>Atheta britanniae</i>	Athe_brit	forest species_small
<i>Atheta putrida</i>	Athe_putr	forest species_small
<i>Enalodroma hepatica</i>	Enal_hepa	forest species_small
<i>Eusphalerum semicoleoptratum</i>	Eusp_semi	forest species_small
<i>Habrocerus capillaricornis</i>	Habr_capi	forest species_small
<i>Leptusa ruficollis</i>	Lept_rufi	forest species_small
<i>Othius subuliformis</i>	Othi_subu	forest species_small
<i>Oxypoda annularis</i>	Oxyp_annu	forest species_small
<i>Oxypoda rufa</i>	Oxyp_rufa	forest species_small
<i>Quedius microps</i>	Qued_micr	forest species_small
<i>Aleochara curtula</i>	Aleo_curt	habitat generalist_large
<i>Aleochara ruficornis</i>	Aleo_rufi	habitat generalist_large
<i>Bolitobius castaneus</i>	Boli_cast	habitat generalist_large
<i>Gabrius osseticus</i>	Gabr_osse	habitat generalist_large
<i>Ischnosoma longicorne</i>	Isch_long	habitat generalist_large
<i>Lathrobium brunnipes</i>	Lath_brun	habitat generalist_large
<i>Lathrobium fulvipenne</i>	Lath_fulv	habitat generalist_large
<i>Lathrobium longulum</i>	Lath_long	habitat generalist_large
<i>Liogluta pagana</i>	Liog_paga	habitat generalist_large
<i>Ocypus fuscatus</i>	Ocyp_fusc	habitat generalist_large
<i>Ocypus nitens</i>	Ocyp_nite	habitat generalist_large
<i>Othius angustus</i>	Othi_angu	habitat generalist_large
<i>Oxypoda acuminata</i>	Oxyp_acum	habitat generalist_large
<i>Paederus brevipennis</i>	Paed_brev	habitat generalist_large
<i>Parabolitobius formosus</i>	Para_form	habitat generalist_large
<i>Pella humeralis</i>	Pell_hume	habitat generalist_large
<i>Pella limbata</i>	Pell_limb	habitat generalist_large
<i>Philonthus addendus</i>	Phil_adde	habitat generalist_large
<i>Philonthus cognatus</i>	Phil_cogn	habitat generalist_large
<i>Platydracus latebricola</i>	Plat_late	habitat generalist_large
<i>Quedius curtipennis</i>	Qued_curt	habitat generalist_large
<i>Quedius fuliginosus</i>	Qued_fuli	habitat generalist_large
<i>Quedius nitipennis</i>	Qued_niti	habitat generalist_large
<i>Rugilus rufipes</i>	Rugi_rufi	habitat generalist_large
<i>Staphylinus caesareus</i>	Stap_caes	habitat generalist_large
<i>Stenus clavicornis</i>	Sten_clav	habitat generalist_large
<i>Tachinus rufipes</i>	Tach_rufi	habitat generalist_large
<i>Tasgius melanarius</i>	Tasg_mela	habitat generalist_large
<i>Xantholinus laevigatus</i>	Xant_laev	habitat generalist_large
<i>Xantholinus linearis</i>	Xant_line	habitat generalist_large
<i>Eusphalerum primulae</i>	Eusp_prim	habitat generalist_NA
<i>Philonthus laevicollis</i>	Phil_laev	habitat generalist_NA
<i>Platystethus nitens</i>	Plat_nite	habitat generalist_NA
<i>Rhopalotella validiuscula</i>	Rhop_vali	habitat generalist_NA
<i>Stenus ochropus</i>	Sten_ochr	habitat generalist_NA
<i>Tasgius winkleri</i>	Tasg_wink	habitat generalist_NA
<i>Xantholinus elegans</i>	Xant_eleg	habitat generalist_NA
<i>Amischa analis</i>	Amis_anal	habitat generalist_small
<i>Amischa bifoveolata</i>	Amis_bifo	habitat generalist_small
<i>Anotylus insecatus</i>	Anot_inse	habitat generalist_small
<i>Anthophagus angusticollis</i>	Anth_angu	habitat generalist_small
<i>Atheta fungi</i>	Athe_fung	habitat generalist_small
<i>Carpelimus elongatulus</i>	Carp_elon	habitat generalist_small
<i>Cypha tarsalis</i>	Cyph_tars	habitat generalist_small

<i>Dinaraea angustula</i>	Dina_angu	habitat generalist_small
<i>Drusilla canaliculata</i>	Drus_cana	habitat generalist_small
<i>Eusphalerum tenenbaumi</i>	Eusp_tene	habitat generalist_small
<i>Geostiba circellaris</i>	Geos_circ	habitat generalist_small
<i>Ilyobates bennetti</i>	Ilyo_benn	habitat generalist_small
<i>Ischnosoma splendidum</i>	Isch_sple	habitat generalist_small
<i>Lesteva longoelytrata</i>	Lest_long	habitat generalist_small
<i>Liogluta granigera</i>	Liog_gran	habitat generalist_small
<i>Liogluta longiuscula</i>	Liog_long	habitat generalist_small
<i>Liogluta microptera</i>	Liog_micr	habitat generalist_small
<i>Mycetoporus lepidus</i>	Myce_lepi	habitat generalist_small
<i>Ocalea picata</i>	Ocal_pica	habitat generalist_small
<i>Oligota pumilio</i>	Olig_pumi	habitat generalist_small
<i>Olophrum assimile</i>	Olop_assi	habitat generalist_small
<i>Omalius caesum</i>	Omali_caes	habitat generalist_small
<i>Omalius rivulare</i>	Omali_rivu	habitat generalist_small
<i>Oxypoda brevicornis</i>	Oxyp_brev	habitat generalist_small
<i>Oxypoda opaca</i>	Oxyp_opac	habitat generalist_small
<i>Plataraea brunnea</i>	Plat_brun	habitat generalist_small
<i>Rugilus orbiculatus</i>	Rugi_orbi	habitat generalist_small
<i>Sepedophilus immaculatus</i>	Sepe_imma	habitat generalist_small
<i>Sepedophilus pedicularius</i>	Sepe_pedi	habitat generalist_small
<i>Sunius melanocephalus</i>	Suni_mela	habitat generalist_small
<i>Tachinus laticollis</i>	Tach_lati	habitat generalist_small
<i>Tachyporus nitidulus</i>	Tach_niti	habitat generalist_small

Spiders

<i>Agroeca brunnea</i>	Agro_brun	forest species_large
<i>Amaurobius fenestralis</i>	Amau_fene	forest species_large
<i>Anyphaena accentuata</i>	Anyp_acce	forest species_large
<i>Apostenus fuscus</i>	Apos_fusc	forest species_large
<i>Centromerus sylvaticus</i>	Cent_sylv	forest species_large
<i>Ceratinella scabrosa</i>	Cera_scab	forest species_large
<i>Clubiona terrestris</i>	Club_terr	forest species_large
<i>Coelotes atropos</i>	Coel_atro	forest species_large
<i>Haplodrassus silvestris</i>	Hapl_silv	forest species_large
<i>Haplodrassus umbratilis</i>	Hapl_umbr	forest species_large
<i>Harpactea lepida</i>	Harp_lepi	forest species_large
<i>Histopona torpida</i>	Hist_torp	forest species_large
<i>Inermocoelotes inermis</i>	Iner_iner	forest species_large
<i>Linyphia hortensis</i>	Liny_hort	forest species_large
<i>Macrargus rufus</i>	Macr_rufu	forest species_large
<i>Nigma walckenaeri</i>	Nigm_walc	forest species_large
<i>Ozyptila praticola</i>	Ozyp_prat	forest species_large
<i>Pardosa alacris</i>	Pard_alac	forest species_large
<i>Pardosa lugubris</i>	Pard_lugu	forest species_large
<i>Pardosa saltans</i>	Pard_salt	forest species_large
<i>Robertus lividus</i>	Robe_livi	forest species_large
<i>Tegenaria silvestris</i>	Tege_silv	forest species_large
<i>Xysticus luctuosus</i>	Xyst_luct	forest species_large
<i>Zelotes apricorum</i>	Zelo_apri	forest species_large
<i>Zelotes subterraneus</i>	Zelo_subt	forest species_large
<i>Agneta ramosa</i>	Agyn_ramo	forest species_small
<i>Centromerus sellarius</i>	Cent_sell	forest species_small
<i>Diplostyla concolor</i>	Dipl_conc	forest species_small
<i>Diplocephalus latifrons</i>	Dipl_lati	forest species_small
<i>Diplocephalus picinus</i>	Dipl_pici	forest species_small
<i>Formiphantes lephthyphantiformis</i>	Form_leph	forest species_small
<i>Gonatium rubellum</i>	Gona_rube	forest species_small
<i>Hahnia pusilla</i>	Hahn_pusi	forest species_small
<i>Maso sundevalli</i>	Maso_sund	forest species_small

<i>Micrargus herbigradus</i>	Micr_herb	forest species_small
<i>Microneta viaria</i>	Micr_viar	forest species_small
<i>Neon reticulatus</i>	Neon_reti	forest species_small
<i>Neriere peltata</i>	Neri_pelt	forest species_small
<i>Saloca diceros</i>	Salo_dice	forest species_small
<i>Tapinocyba insecta</i>	Tapi_inse	forest species_small
<i>Tenuiphantes alacris</i>	Tenu_alac	forest species_small
<i>Tenuiphantes cristatus</i>	Tenu_cris	forest species_small
<i>Tenuiphantes flavipes</i>	Tenu_flav	forest species_small
<i>Tenuiphantes tenebricola</i>	Tenu_tene	forest species_small
<i>Tenuiphantes tenuis</i>	Tenu_tenu	forest species_small
<i>Walckenaeria corniculans</i>	Walc_corn	forest species_small
<i>Walckenaeria cucullata</i>	Walc_cucu	forest species_small
<i>Walckenaeria cuspidata</i>	Walc_cusp	forest species_small
<i>Walckenaeria obtusa</i>	Walc_obtu	forest species_small
<i>Alopecosa cuneata</i>	Alop_cune	habitat generalist_large
<i>Alopecosa pulverulenta</i>	Alop_pulv	habitat generalist_large
<i>Clubiona reclusa</i>	Club_recl	habitat generalist_large
<i>Drassodes lapidosus</i>	Dras_lapi	habitat generalist_large
<i>Drassyllus praeficus</i>	Dras_prae	habitat generalist_large
<i>Haplodrassus signifer</i>	Hapl_sign	habitat generalist_large
<i>Metellina mengei</i>	Mete_meng	habitat generalist_large
<i>Micaria pulicaria</i>	Mica_puli	habitat generalist_large
<i>Neriere clathrata</i>	Neri_clat	habitat generalist_large
<i>Pardosa amentata</i>	Pard_amen	habitat generalist_large
<i>Pardosa palustris</i>	Pard_palu	habitat generalist_large
<i>Pardosa pullata</i>	Pard_pull	habitat generalist_large
<i>Piratula hygrophila</i>	Pira_hygr	habitat generalist_large
<i>Trachyzelotes pedestris</i>	Trac_pede	habitat generalist_large
<i>Trochosa ruricola</i>	Troc_ruri	habitat generalist_large
<i>Trochosa terricola</i>	Troc_terr	habitat generalist_large
<i>Xysticus acerbus</i>	Xyst_acer	habitat generalist_large
<i>Xysticus bifasciatus</i>	Xyst_bifa	habitat generalist_large
<i>Xysticus cristatus</i>	Xyst_cris	habitat generalist_large
<i>Xysticus kochi</i>	Xyst_koch	habitat generalist_large
<i>Zelotes latreillei</i>	Zelo_latr	habitat generalist_large
<i>Zora spinimana</i>	Zora_spin	habitat generalist_large
<i>Aulonia albimana</i>	Aulo_albi	habitat generalist_small
<i>Bathyphantes parvulus</i>	Bath_parv	habitat generalist_small
<i>Centromerita bicolor</i>	Cent_bico	habitat generalist_small
<i>Ceratinella brevipes</i>	Cera_brev	habitat generalist_small
<i>Dicymbium nigrum brevisetosum</i>	Dicy_nigr	habitat generalist_small
<i>Drassyllus pusillus</i>	Dras_pusi	habitat generalist_small
<i>Erigonella hiemalis</i>	Erig_hiem	habitat generalist_small
<i>Meioneta saxatilis</i>	Meio_saxa	habitat generalist_small
<i>Ozyptila simplex</i>	Ozyp_simp	habitat generalist_small
<i>Ozyptila trux</i>	Ozyp_trux	habitat generalist_small
<i>Pachygnatha degeeri</i>	Pach_dege	habitat generalist_small
<i>Pachygnatha listeri</i>	Pach_list	habitat generalist_small
<i>Palliduphantes pallidus</i>	Pall_pall	habitat generalist_small
<i>Pardosa prativaga</i>	Pard_prat	habitat generalist_small
<i>Phrurolithus festivus</i>	Phru_fest	habitat generalist_small
<i>Phrurolithus minimus</i>	Phru_mini	habitat generalist_small
<i>Piratula latitans</i>	Pira_lati	habitat generalist_small
<i>Pirata uliginosus</i>	Pira_ulig	habitat generalist_small
<i>Porrhomma microphthalmum</i>	Porr_micr	habitat generalist_small
<i>Walckenaeria acuminata</i>	Walc_acum	habitat generalist_small
<i>Walckenaeria antica</i>	Walc_anti	habitat generalist_small
<i>Walckenaeria atrotibialis</i>	Walc_atro	habitat generalist_small
<i>Walckenaeria dysderoides</i>	Walc_dysd	habitat generalist_small
<i>Clubiona cf. similis</i>	Club_simi	NA
<i>Enoplognatha sp.</i>	Enop_sp.	NA

<i>Liocranum sp.</i>	Lioc_sp.	NA
<i>Scotophaeus sp.</i>	Scot_sp.	NA

CHAPTER 4

INTERACTING EFFECTS OF FOREST STRATUM, EDGE AND TREE DIVERSITY ON BEETLES



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Published in *Forest Ecology and Management*, **361**, 421-431

Abstract

Edge effects are an important component of forest fragmentation, altering microclimatic conditions and species composition within forest remnants. Yet, major factors affecting strength and extent to which edge effects might penetrate into fragments have remained elusive. Here, we study for the first time how tree diversity and forest stratum alter edge effects and how these factors affect beetle communities. We sampled beetles over 7 months using 92 flight interception traps in the canopy and near the ground in the Hainich National Park; Germany's largest connected deciduous forest. Traps were exposed along 10 transects (0–500 m) from the forest edge into the forest interior, comparing transects with high or low abundance of beech (low or high tree diversity).

Tree diversity had no influence on the range or strength of edge effects. In the understory, edge effects extended up to maximal transect length of 500 m into the forest interior. Edge effects were weaker in the canopy than in the understory, likely because of higher, edge-like microclimatic variability and harshness in the canopy. The edge response of beetle species richness was driven by habitat generalists while forest and saproxylic species responded less strongly.

The richness of forest and saproxylic beetles peaked in the canopy, whereas habitat generalists and non-saproxylic beetles strongly dominated the understory. Pathways driving beetle species richness differed across forest strata. Structural equation modelling showed that tree diversity (+, positive effect) and overall dead wood volume (+) were the most important factors driving beetle species richness in the canopy. In contrast, tree diversity effects (+) were less strong and canopy openness (+) and distance from the forest edge (-) were more important in the understory.

Keywords

canopy, *Fagus sylvatica*, forest species, habitat generalists, saproxylic beetles, understory

Introduction

Forest fragmentation is increasing worldwide and is a major driver of biodiversity loss (Didham et al., 1996). Invertebrates in forest fragments are affected by fragment size, fragment shape, habitat connectivity and edge effects (Didham, 1997). Edges can cause alterations in microclimatic conditions and induce changes in invertebrate species richness and community composition (Murcia, 1995). How far and how strong edge effects on invertebrates penetrate into forests is variable. The depth of edge effects can range from a few meters (Noreika & Kotze, 2012; Vodka & Cizek, 2013) up to more than 1 km as shown by Ewers & Didham (2008). However, the majority of studies only examine edge effects on small spatial scales, thereby potentially missing out long range effects. Patch contrast (the difference in habitat quality between fragment and adjacent matrix) and a fragment's three-dimensional architecture (plant structure) can determine the depth and strength of edge effects in forest fragments (Cadenasso et al., 2003; Collinge, 2009; Ries & Sisk, 2004; Ries et al., 2004). In this context, tree species composition might play an important role by determining a forest's (canopy) architecture (Getzin et al., 2012; Seidel et al., 2013) and thereby light availability, microclimatic conditions, resource distribution and habitat heterogeneity. Current forest management schemes aim at converting monospecific forest stands into structurally more diverse forests with a higher abundance and diversity of native deciduous tree species (Pretzsch et al., 2013; Schmitz et al., 2014). In Central Europe, deciduous forests are commonly dominated by *Fagus sylvatica* L., creating (rather) homogeneous conditions by a dense canopy, a thick acidic litter layer and a species-poor herb layer (Mölder et al., 2008). Due to species specific differences in traits such as canopy cover, growth height or nutrient quality of the leaf litter (Barbier et al., 2008; Wulf & Naaf, 2009) an increase in tree species richness (and reduced beech dominance) should therefore lead to increased light availability, habitat heterogeneity and niche and resource diversity (Paillet et al., 2010) - factors positively affecting invertebrate species richness (Huston, 1994; Lange et al., 2014; Wermelinger et al., 2007). This may not only increase the number of forest specialists (Sobek et al., 2009b), but also reduce the contrast between the forest interior and the more variable forest edge habitat and thus increase the permeation of species not explicitly adapted to inner forest conditions. Most studies on edge effects in forests only sample the forest understory. This is not sufficient for drawing conclusions about the entire system since forests are complex, highly structured habitats (Horchler and Morawetz, 2008). A forest's understory and its canopy can considerably differ with respect to habitat structure (as well as structural diversity) and microclimate (Tal et al., 2008). Furthermore, arthropod diversity and community composition

have been shown to differ markedly across forest strata (Bouget et al., 2011; Gruppe et al., 2008).

Microclimatic conditions in the forest canopy may be less affected by forest edge proximity since it is an “edge-like” heterogeneous habitat itself (Didham & Ewers, 2014). In contrast to the understory, forest canopies are exposed to a high microclimatic variability throughout the day. While dry and warm conditions are characteristic features during the day, humidity increases as temperature drops during the night (Parker, 1995; Tal et al., 2008). In line with Didham & Ewers (2014) and Tal et al. (2008) found this microclimatic stratification to collapse at the forest edge as microclimatic variability at the ground increased, and they stated that this may in turn affect arthropod community composition. Consequently, we expect weaker edge effects on arthropods in the canopy and possibly different causal pathways between forest understory and canopy. Yet, surprisingly, studies comparing edge effects across forest strata are scarce.

Not only may edge effects differ across strata but tree diversity effects may differ as well. Tree diversity in beech dominated forests has been shown to increase the diversity of several invertebrate taxa (Cesarz et al., 2007; Sobek et al., 2009a,b). However, it has hardly been tested if tree diversity effects differ across forest strata (but see Sobek et al., 2009c). As described above, forest canopy and understory differ with respect to arthropod community composition, abiotic conditions and micro-habitats. Therefore, we hypothesize that pathways determining arthropod communities in the canopy and understory are different.

Furthermore, we expect differences between ecological groups of beetles due to differences in habitat requirements. Saproxylic beetles may particularly benefit from increased tree diversity in the forest canopy, because many species not only require sufficient amounts of dead wood but also sunny habitats (Müller et al., 2008; Schmidl & Bussler, 2008), and a higher tree diversity is likely to increase the amount of dead wood. In particular, Gamfeldt et al. (2013) showed that the probability of dead wood occurrence remained constant from 1 to 4 and increased from 4 to 10 tree species mixtures.

Studies on forest beetles often examine saproxylic beetles only (Bouget et al., 2011; Gossner et al., 2013a,b). However, saproxylic beetles represent only a part of the entire beetle community in forests. Therefore, we compare different ecological groups of all captured beetles. The study was conducted in Hainich National Park, which forms part of Germany’s largest continuous broad-leaved forest. This area is especially suitable for testing our research questions since it consists of forest sites with a natural tree diversity gradient under comparable site conditions (Leuschner et al., 2009). We compared edge and tree diversity

effects on beetles in both canopy and understory on a large spatial scale. In particular, we hypothesize:

1. Edge effects are stronger in forest stands with a low tree diversity (high patch contrast) compared with forest stands rich in tree species.
2. Edge effects are weaker in the canopy than in the understory.
3. Effects of tree diversity differ across forest strata.
4. Different functional groups of beetles are differently affected by edge proximity, tree diversity and forest stratum.

Methods

Study area and study design

The study region, the Hainich National Park, is situated between the cities of Bad Langensalza, Mühlhausen and Eisenach in the federal state of Thuringia in Central Germany (51°5 0"N, 10°30'24"E). The area is characterised by 75 km² of beech forests on calcareous soils with the dominant forest communities Hordelymo-Fagetum, Galio-Fagetum and Stellario-Carpinetum. The parent material is Triassic limestone (Upper Muschelkalk) with a loess cover. The area has been a military restricted area and the forest has hardly been managed for 33 years before it became National Park in 1997 (Mölder et al., 2006, 2008). This allowed for a near-natural development of the forest. In 2011, the core zone has been declared as UNESCO World Heritage site (“Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany”).

Due to past management, the National Park’s forest consists of a mosaic of forest stands with contrasting tree diversity (ranging from 1 to 14 tree species/ha) but with comparable climate and soil conditions (Leuschner et al., 2009; Mölder et al., 2006), making it particularly suitable for our research questions.

We laid out transects extending from the forest edge into the forest interior. Transects were evenly distributed over the whole forested area of the National Park. A pool of 23 potentially suitable transects were selected a priori using maps of forest types provided by the National Park’s administration. 10 of these transects fulfilled the criteria of being either poor (c. 3 species) or rich (c. 6.5 species) in tree species, having a similar age class and a low variability of tree diversity within each stand and were permitted for this study by the National Park’s administration. Five transects were located in beech dominated forest stands with a low tree diversity and five transects were in forest stands with a high tree diversity. Minimum distance between transects was 750 m.

We expected the strongest changes in beetle communities close to the forest edge (Didham & Lawton, 1999). Therefore, we established plots at the distances of 0, 32, 80, 200 and 500 m from the edge. In four of ten cases the maximum distance of 500 m from the edge could not be implemented because tree species composition changed, stand age differed or the distance to the next edge was not large enough. The “0 m” point of the transects was set at the position where canopy tree trunks of the original forest began.

Forest edges were characterised by dense shrub belts consisting of blackthorn (*Prunus spinosa*), whitethorn (*Crataegus laevigata*) and saplings of ash (*Fraxinus excelsior*). The surrounding habitats comprised (mostly abandoned) grasslands of different successional stages.

Tree survey

Around each of the 41 plots we conducted a tree survey (tree relevé sized 20 x 40 m, longer side parallel to forest edge). Each tree (DBH \geq 10 cm) and its diameter at breast height (DBH) were recorded. We assessed tree species richness (SR), % beech (based on basal area) and the Shannon–Wiener diversity index (H') based on basal area (Magurran, 2004). As *Tilia cordata* and *Tilia platyphyllos* could not be reliably separated in the field, lime was only determined to genus level.

Beetle sampling and processing

At each of the plots, two cross-window flight interception traps (Fig. 1) were installed which resulted in a total of 92 traps. One trap was placed in the understory 1 m above the ground and another one in the forest canopy. Traps were positioned in the vertical centre ((tree crown base + tree height)/2) and horizontal outer part of beech tree crowns (Kowalski et al., 2011). Trap height ranged from app. 20 to 28 m. Traps in the low diversity stands were bordering only other beech trees. In high diversity plots neighbouring trees were two different deciduous tree species other than beech. Each trap consisted of two translucent polycarbonate sheets (40 x 60 cm) fixed to two funnels made of tarpaulin, one at the top and one at the bottom of the traps and leading to collecting jars filled with ethylene–glycol (diluted with



Figure 1 Flight interception trap used to sample beetles along transects extending from forest edges to the interior, across two vertical strata.

water 1:1). In the beginning of April the traps were installed for a period of seven months and were emptied monthly until the beginning of November 2012.

Beetles were transferred into 70% ethanol and determined to species level. The nomenclature follows de Jong (2013). The abundance of each species per trap was pooled over the seven months of sampling. Ecological traits for each species were identified based on literature (Böhme, 2001, 2004; GAC, 2008; Gossner et al., 2013a; Koch, 1989a, 1989b, 1992; Köhler, 2000; Weigel & Apfel, 2011). Beetles were grouped (1) according to their forest specialisation (variable name ForestSpec) into forest species (predominantly occurring in forests) and habitat generalists (occurring in forests and elsewhere) and (2) according to their dependence on dead wood as saproxylic and non-saproxylic species (variable name SaproxylicSpec).

Measurement of environmental parameters

Canopy openness was assessed on each plot using fish-eye photography (see Appendix A for a detailed procedure). Dead wood volume was recorded on each of the tree relevé plots. All standing and lying pieces of dead wood (length ≥ 1 m, diameter ≥ 7 cm) were registered if the thicker end lay inside the plot. The total dead wood volume was then calculated following Meyer (1999).

Data analysis

To account for the hierarchical study design (transect, sampling point, stratum), we used mixed-effects models to assess the effects of tree diversity, distance from the forest edge, stratum, forest specialisation and dead wood dependence on beetle species richness. Tree diversity level, tree species richness, Shannon index and beech proportion were highly correlated (Table 1), and we decided to use only tree diversity level as variable in the following analyses. Multinomial models were used to analyse single species responses and beetle community composition. Finally, interrelations between the design variables, environmental variables and beetle species richness were analysed using structural equation modelling. All analyses were conducted using R (R Core Team, 2014).

Table 1 Spearman's rank correlation coefficients (ρ) of parameters describing tree species composition. All correlations were highly significant ($P < 0.001$).

	Tree diversity level	No. tree species	H' tree area	% beech area
Tree diversity level	-			
No. tree species	0.77	-		
H' tree area	0.80	-0.91	-	
% beech area	-0.78	-0.90	-0.91	-

Analysis of total beetle species richness

Mixed-effects models for total beetle species richness (SR) included the fixed-effects terms distance from the forest edge (“distance”, continuous), tree diversity level (“treediversity”, categorical, levels: low and high) and stratum (“stratum”, categorical, levels: canopy and understory). As distances along transects followed a power law, “distance” was log-transformed. Transect and location along transect (e.g. at 32 m distance) were included as random effects as location was nested within transect (...random = ~1|transect/location,...). The lowest hierarchical level (individual traps) was not explicitly included in the random-effects part of the model as this would have saturated our models with random effects.

Initial models contained three-way interactions among explanatory variables and were fitted using restricted maximum likelihood-method (REML) and variance functions to ensure homoscedasticity and normality of errors. We then calculated AICc (Akaike’s Information Criterion, corrected for small sample sizes, “MuMIn” package (Burnham and Anderson, 2002)) for each model and selected the one with lowest AICc as the maximal model with optimal random part. This model was re-fitted using maximum likelihood. We then performed stepwise model simplification based on AICc (stepAICc function, “MASS” package, corrected for small sample sizes by C. Scherber (2009, <http://www.christoph-scherber.de/stepAICc.txt>)).

In additional models, we tested if forest specialisation and dead wood dependence influenced the response of beetle species richness to the design variables. For this, we fitted two further mixed-effects models and included either “ForestSpec” (levels: forest species, habitat generalists) or “SaproxylicSpec” (levels: saproxylic species, non-saproxylic species) as explanatory variables into the basic mixed-effects model (see above). Moreover, position of the flight interception traps (canopy or understory) was added to the random effects (...random= ~1|transect/location/position,...). All following procedures were as described above.

Community composition

To analyse the effect of distance from the forest edge, tree diversity level and stratum on beetle community composition, we used multinomial models (multinom function, “nnet” library (Ripley, 2013; Scherber et al., 2014)) including three-way-interactions between explanatory variables. Although multinomial models are inherently nonlinear, we log-transformed distance from the forest edge because it improved the model fit (compared using AICc). The response variable was a matrix containing the abundances of each species

(including only species with a total abundance ≥ 20). We removed rare species as they contribute negligible information about treatment effects (Warton et al., 2014). Model simplification was conducted automatically using stepwise model selection based on AICc (see above). Significance of terms in final models was assessed using the Anova() function in the car library (Fox & Weisberg, 2011), setting MaxNWts = 2000 and error.df = 86. Note that multinomial models did not include random effects as these did not improve model fit.

Additional covariate effects

In order to analyse causal pathways between tree diversity level (exogenous design variable), distance from the forest edge (exogenous design variable) and additional observed variables characterising forest stands, structural equation models were fitted using the lavaan function (“lavaan” package (Rosseel, 2012)) in R. Variables were standardized to a common scale (range approx. 0–10) prior to model fitting. Distance from the forest edge was logtransformed. To account for non-normal distribution of the response variable beetle SR, we used a maximum likelihood estimation with robust standard errors (Huber–White) and a scaled test statistic (equal to the Yuan–Bentler) that can be applied to complete and incomplete data (estimator = “MLR”).

To account for potentially different pathways in the canopy and the understory, we set up multi-group models using “stratum” as grouping variable.

Canopy openness and dead wood volume were included as additional explanatory variables. We built the model based on the hypotheses that (1) light availability and dead wood amount are the key factors predicting forest beetle biodiversity (Müller et al., 2008; Paillet et al., 2010; Ranius & Jansson, 2000) and that (2) these factors are influenced by both or at least one of the two design variables.

Model fit was assessed using the Chi²-value and associated p-values, RMSEA, SRNR, CFI and AICc (Akaike’s Information Criterion, corrected for small sample sizes (“MuMIn” package (Burnham and Anderson, 2002)) of the model.

Results

Overall characteristics of the forest stands

Forest stands poor in tree species (mean tree SR: 3.00 ± 0.34 , mean beech %: 81.37 ± 4.48 , mean H' trees: 0.44 ± 0.08) contrasted with forest stands with a high tree diversity (mean tree SR: 6.43 ± 0.33 , mean beech %: 25.46 ± 4.27 , mean H' trees: 1.37 ± 0.05) which were characterised by various other deciduous tree species such as *Quercus robur*, *Quercus petraea*, *Tilia* sp., *Acer campestre*, *Acer platanooides*, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Carpinus betulus*. Additionally, *Prunus avium*, *Betula pendula*, *Populus tremula*, *Ulmus glabra*, *Salix caprea* and *Sorbus torminalis* occurred.

Beetle taxa

In total, we recorded 13,204 beetle specimens from 76 families and 536 species. They comprised 228 forest species and 290 habitat generalists (defined here as species not predominantly occurring in forests). 227 species (42.4% of all species) were saproxylic. Species richness and abundance per trap varied from 25 to 94 species and 63 to 458 individuals. 61 species (of which 79% were saproxylic) had a high conservation value since they were either red-listed or protected by German law.

The five most abundant species were *Corticicara gibbosa* (Latridiidae; 13.2% of all individuals), *Meligethes aeneus* (Nitidulidae; 10.8%), *Athous vittatus* (Elateridae; 9.1%), *Epuraea melanocephala* (Nitidulidae; 4.4%) and *Trixagus meyerbohmi* (Throscidae; 3.2%) (see Appendix Table B1 for a complete species list). The most species rich families were Staphylinidae (111 species, 20.7% of all species), Curculionidae (39 species, 7.3%), Carabidae (31 species, 5.8%), Cerambycidae (12 species, 2.2%) and Elateridae (21 species, 3.9%). The most abundant families were Latridiidae (2310 individuals, 17.5%), Nitidulidae (2213, 16.8%), Elateridae (1966, 14.9%), Curculionidae (1010, 7.65%) and Staphylinidae (915, 6.9%).

Total beetle species richness

In the understory, total species richness of beetles (Fig. 2, Table 2 (model a)) declined strongly from the edge towards the forest interior while this effect was mitigated in the canopy. Tree diversity had a strong positive impact on total beetle species richness both in the canopy and the understory.

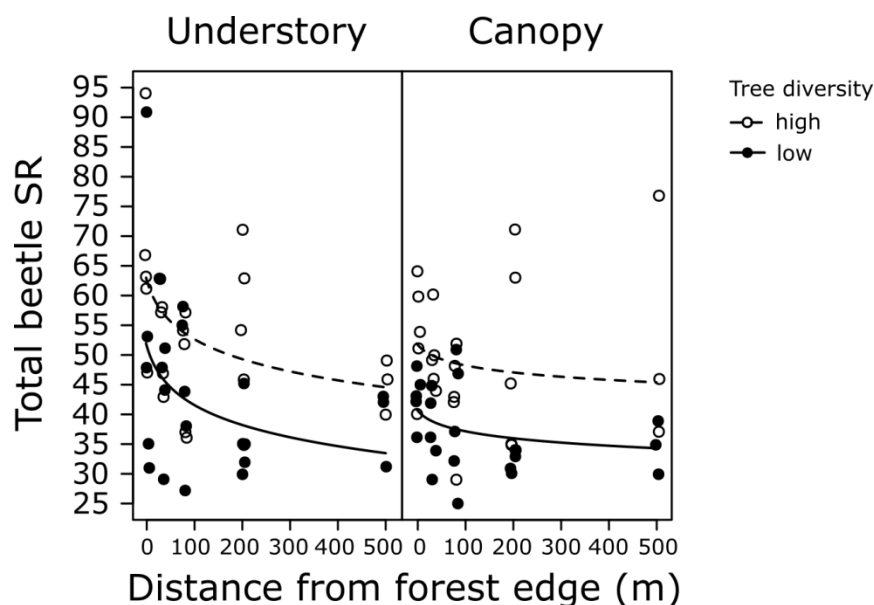


Fig. 2. Effect of distance from the forest edge, tree diversity and stratum on total beetle species richness. Lines represent predictions from a mixed-effects model (Table 2 (model a)). Distance from forest edge was back-transformed to the original scale for graphical illustration.

Table 2 Results of mixed-effects models for predicting a) total beetle species richness, b) species richness of forest and non-forest species and c) saproxylic species and non-saproxylic species. Reference level of stratum was canopy, of treediversity low tree diversity, of ForestSpec forest, of SaproxylicSpec saproxylic. Distance from the forest edge was log-transformed.

lme analysis		Estimate	SE	DF	<i>t</i>	<i>P</i>
a) Effect of design variables on total beetle species richness	Intercept	46,425	7,126	44	6,515	0,000
	Logdist	-1,942	1,412	35	-1,375	0,178
	Treediversity	11,097	3,952	8	2,808	0,023
	Stratum	21,456	8,905	44	2,410	0,020
	Logdist:Stratum	-3,565	1,883	44	-1,894	0,065
b) Effect of design variables and forest specialisation on beetle species richness	Intercept	18,524	4,381	88	4,228	0,000
	Logdist	-0,794	0,868	35	-0,915	0,366
	Treediversity	5,570	1,940	8	2,872	0,021
	Stratum	-0,084	5,718	44	-0,015	0,988
	ForestSpec	8,748	4,858	88	1,801	0,075
	Logdist:Stratum	-0,389	1,176	44	-0,331	0,742
	Logdist:ForestSpec	-0,223	0,979	88	-0,228	0,820
	Stratum:ForestSpec	21,742	6,870	88	3,165	0,002
c	-2,811	1,384	88	-2,031	0,045	
c) Effect of design variables and saproxylic specialisation on beetle species richness	Intercept	17,136	4,143	89	4,136	0,000
	Logdist	-0,016	0,813	35	-0,019	0,985
	Treediversity	5,572	1,933	8	2,883	0,020
	Stratum	4,080	4,689	44	0,870	0,389
	SaproxylicSpec	10,934	3,771	89	2,899	0,005
	Logdist:Stratum	-1,821	0,956	44	-1,906	0,063
	Logdist:SaproxylicSpec	-1,694	0,742	89	-2,283	0,025
Stratum:SaproxylicSpec	13,853	1,552	89	8,928	0,000	

“:” indicates interactions; Logdist = log-transformed distance from forest edge; ForestSpec = Forest specialisation; SaproxylicSpec= Saproxylic specialisation

Forest species vs. habitat generalists

Comparing forest species and habitat generalists (Fig. 3a, Table 2 (model b)) showed that the richness of forest species was higher in the canopy compared with the understory. Tree diversity had a positive effect on both habitat specialisation groups. The overall edge response of all groups was weak, except for habitat generalists whose species richness strongly increased towards the edge in the understory.

Saproxylic vs. non-saproxylic species

In the understory, the beetle community was strongly dominated by non-saproxylic beetles (Fig. 3b, Table 2 (model c)). This was not the case in the canopy, where the richness of saproxylic species strongly increased while the richness of non-saproxylic species decreased compared with the understory. Tree diversity affected both groups positively. The edge response of both groups was much weaker in the canopy compared with the understory and saproxylic species responded weaker than non-saproxylic species in the understory and not at all in the canopy.

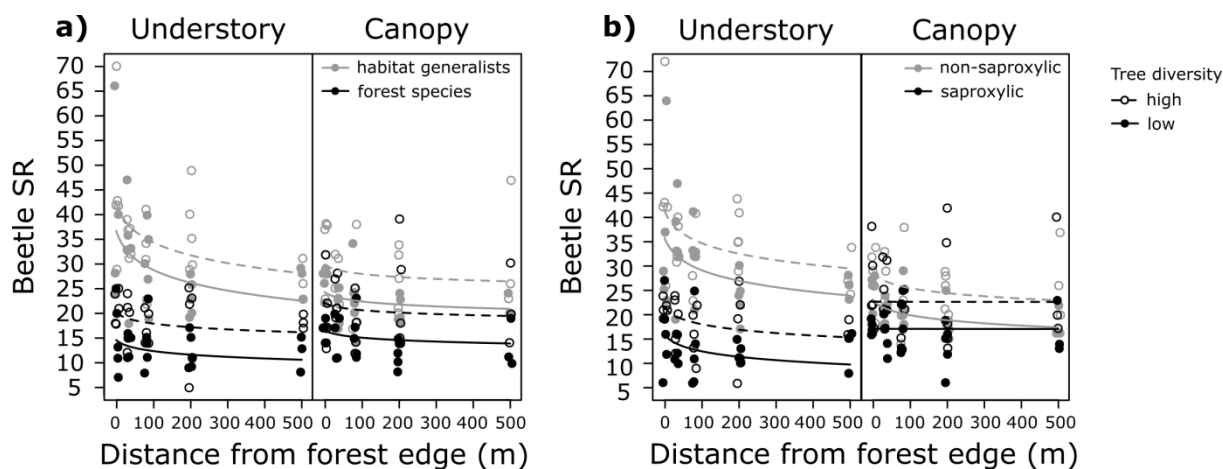


Figure 3 Effect of distance from the forest edge, tree diversity, stratum and (a) forest specialisation, (b) dead wood dependence on beetle species richness. Lines represent predictions from mixed-effects models (Table 2 (models b and c)). Distance from forest edge was back-transformed to the original scale for graphical illustration.

Effects on community composition

Multinomial models showed that beetle community composition was driven by a two-way-interaction of distance from the forest edge and tree diversity and by a two-way-interaction of distance from the forest edge and stratum (Fig. 4, Table 3).

Table 3 Results of the minimal adequate multinomial model testing the effect of tree diversity level, distance from the forest edge and stratum on beetle community composition. LR = Likelihood ratio statistic.

	LR	Chisq	DF	P
Logdist	-497053	1	1	
Treediversity	275329	1	<0.001	
Stratum	527244	1	<0.001	
Logdist:Treediversity	12000986	1	<0.001	
Logdist:Stratum	12196642	1	<0.001	

“:” indicates interactions; Logdist = log-transformed distance from forest edge

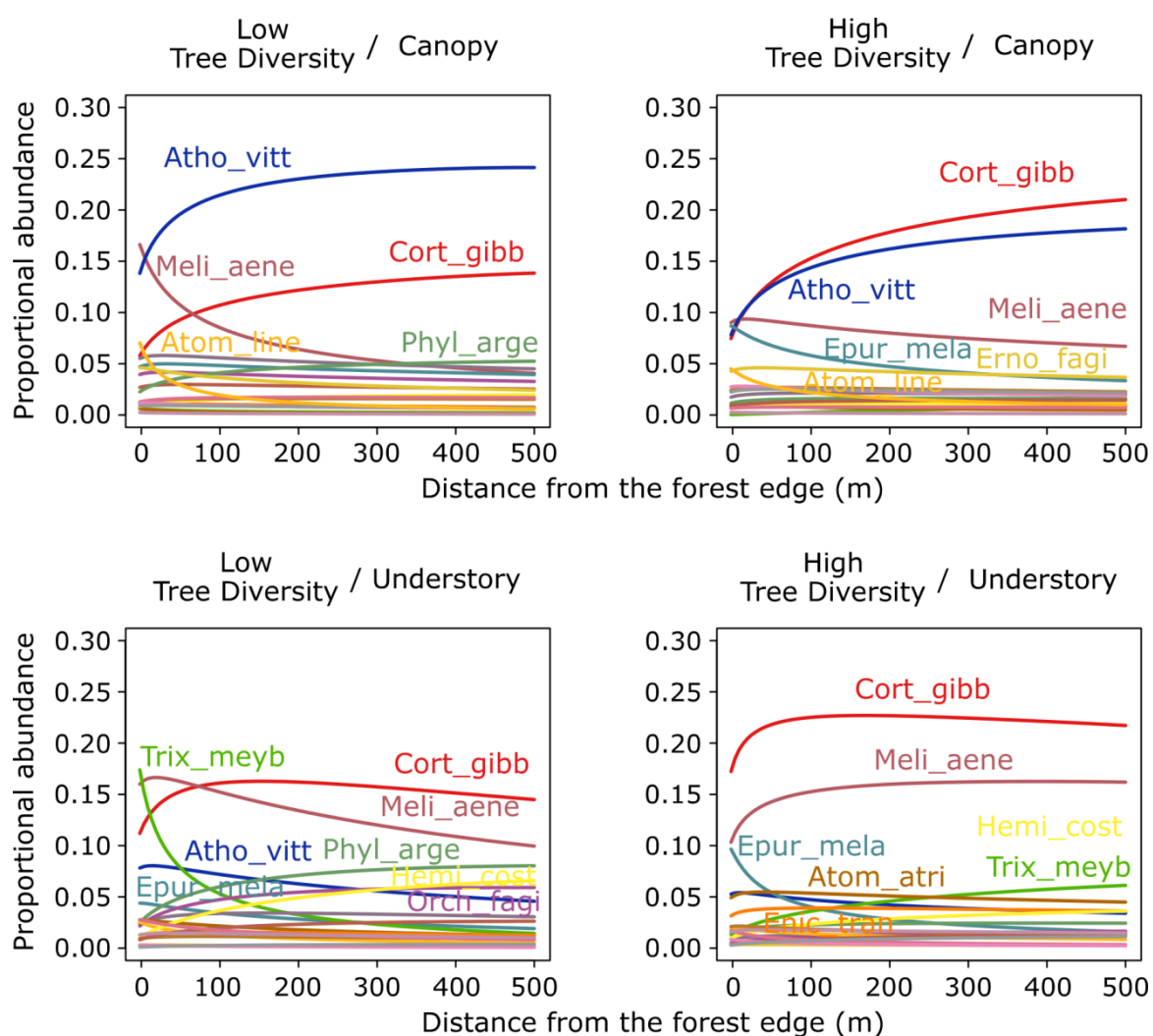


Figure 4 Effect of distance from forest edge, tree diversity and stratum on beetle community composition and relative abundance of single beetle species. Curves show predictions from a minimal adequate multinomial model. For full species names, see Appendix Table B1.

Causal pathways

Structural equation modelling (Fig. 5, $\chi^2 = 1.469$; $P = 0.832$, detailed statistical output in Appendix Table C1) revealed that our a priori hypothesis corresponded well with the observed covariance matrix. It explained 43% of the variance in beetle SR in the canopy and 37% in the understory. We found a strong positive effect of tree diversity on dead wood volume. Canopy openness was only weakly affected by tree diversity. Increasing distance from the forest edge had almost no effect on dead wood volume and a slightly negative effect on canopy openness.

Beetle species richness of the canopy was positively affected by tree diversity and dead wood volume. Additionally, canopy openness had a moderately positive effect. Increased distance from the forest edge had a weakly negative influence on beetle species richness of the canopy. On the contrary, in the understory, the negative impact of distance from the forest edge on beetle species was much stronger. The positive effect of tree diversity on beetle SR was attenuated compared with the canopy. Moreover, the positive effect of canopy openness was stronger compared with the canopy but the effect of dead wood volume was hardly existent. Including additional environmental variables into the model reduced model fit (based on AICc).

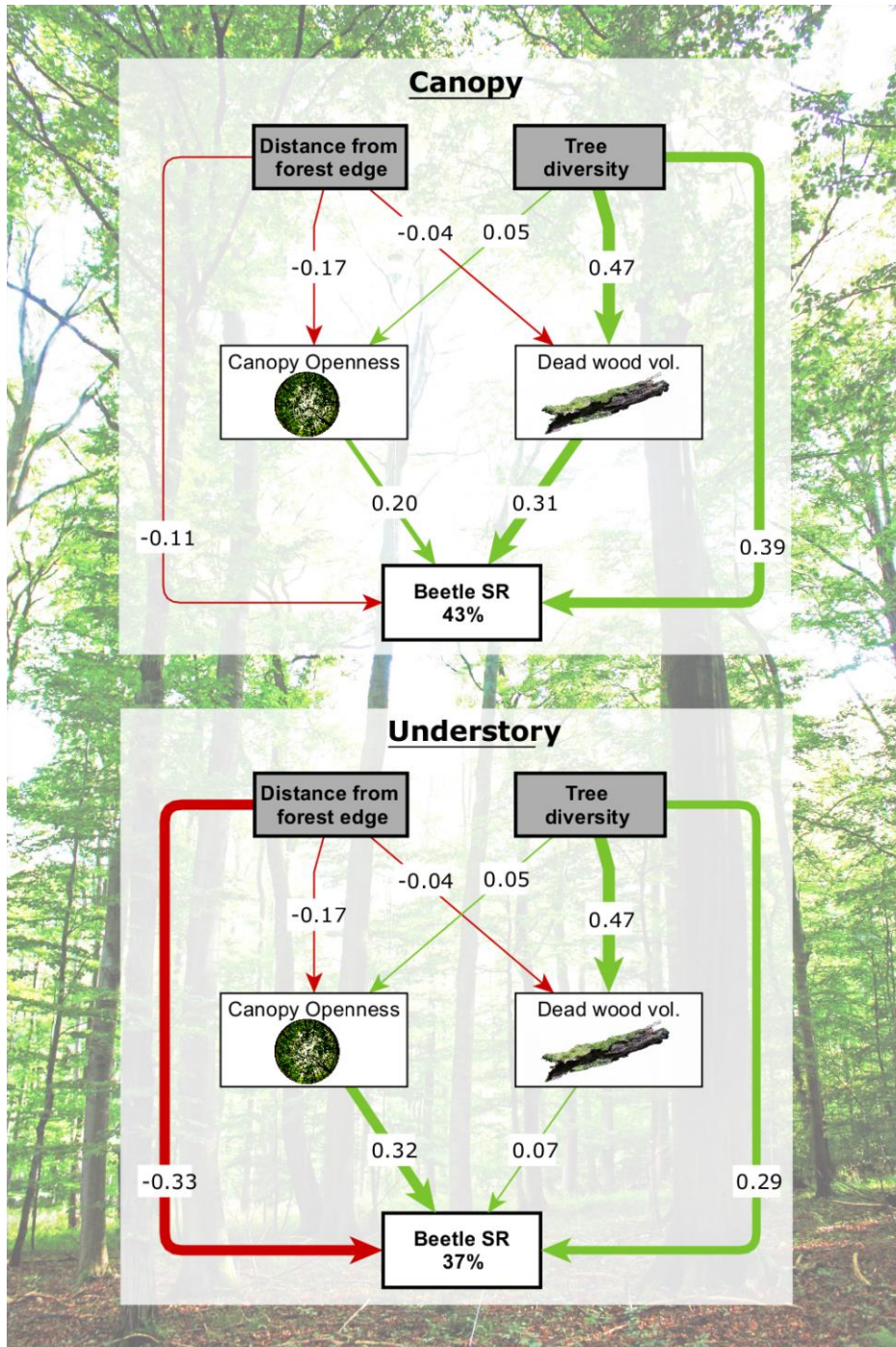


Figure 5 Multi-group structural equation model showing pathways between distance from the forest edge, tree diversity, other forest characteristics and beetle species richness (beetle SR) in (a) the canopy and (b) the understory ($\chi^2 = 1.469$; $P = 0.832$; $DF = 4$; $rmsea = 0.000$; $srmr = 0.023$; $cfi = 1.000$). Numbers next to arrows are standardized coefficients. Green arrows indicate a positive (+) and red arrows a negative (-) relationship. Arrow width shows effect strength. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Discussion

We have shown that three main drivers of forest biodiversity (tree diversity, edge proximity and stratum) influenced each other in determining beetle species richness, community structure (fraction of ecological groups within the community) and community composition in a temperate deciduous forest.

Edge effects

Total species richness increased with edge proximity – a commonly observed pattern at forest edges (Ewers & Didham, 2007; Jokimäki et al., 1998). Stronger edge effects in the understory compared with the canopy are likely to result from differences in microclimatic variability and resource distribution (Tal et al., 2008; Vodka & Cizek, 2013; Wermelinger et al., 2007). Microclimatic conditions in the understory deep inside the forest are often fairly constant (Didham & Ewers, 2014; Tal et al., 2008), but edge proximity can influence parameters such as light availability, litter depth, variability in temperature and humidity, species invasion as well as herb cover and diversity (Murcia, 1995), thus altering environmental heterogeneity and resource distribution for primary and secondary consumers. Forest canopies can be considered vertical edge-like habitats themselves (Didham & Ewers, 2014) and experience a high microclimatic variability during the day and hence may be less prone to being influenced by the forest edge.

Some, but not all species are influenced by edge proximity (Rainio and Niemelä (2003) and references therein). Consequently, ecological groups responded differently, as habitat generalists (only in the understory) and non-saproxyllic species showed a stronger edge response than forest and saproxyllic species. This partly explains the pattern observed for overall beetle species richness. Species from the matrix may rather enter forests close to the ground than in the canopy and therefore cause a higher species richness of non-specialists near the edge in the understory compared with the canopy.

In line with Ewers & Didham (2008) we found that the edge response of beetles occurred on a large spatial scale and extended up to 500 m into the forest interior. For plants and environmental factors, such as soil pH, this has recently been shown (Bergès et al., 2013; Hofmeister et al., 2013; Pellissier et al., 2013). However, evidence of long-ranging edge effects for arthropods are scarce (Ewers & Didham, 2008).

Tree diversity

Tree diversity predicted beetle community composition and increased beetle species richness. Similar results on invertebrates have been shown in comparable systems (Cesarz et al., 2007; Sobek et al., 2009a, 2009b). However, opposing patterns have been found across different study approaches (e. g. observational vs. experimental) and regions (Scherer-Lorenzen, 2014). Overall, tree diversity effects were positive across all ecological groups and strata. *Fagus sylvatica*, the most abundant tree species on our study sites and in most Central European deciduous forests, creates monotonous stand conditions characterised by a dense canopy, nutrient poor acidic leaves, creating thick mats of leaf litter and a low diversity and cover of understory vegetation (Barbier et al., 2008; Mölder et al., 2008; Vockenhuber et al., 2011). Other tree species present on our plots differ from beech in terms of crown architecture, bark structure, leaf budding, nutritional quality, etc. (Barbier et al., 2008; Jacob et al., 2010; Nicolai, 1986). Higher tree diversity also leads to higher understory plant species richness (Mölder et al., 2008). Therefore, higher tree diversity increases environmental heterogeneity as well as niche, structural and resource diversity (Sobek et al., 2009b) both in the canopy and the understory. These factors are regarded as key drivers of arthropod biodiversity (Tews et al., 2004).

Causal pathways

Higher tree diversity increased the overall amount of dead wood of the forest stands fourfold. Gamfeldt et al. (2013) reported similar findings. This may result from tree species specific differences in the amount of dead wood produced, decay rate and the retention time at a tree (Beets et al., 2008; Lofroth, 1998). For example, oak produces more dead wood than beech, and the retention time in the crown is longer (Ammer et al., 2008).

Tree diversity and the overall amount of dead wood in the forest stand were the most important predictors of beetle species richness in the canopy. Forest canopies are structurally very diverse habitats with respect to factors such as crown architecture, dead wood and rot holes (Bouget et al., 2011; Gruppe et al., 2008). A mixture of different tree species with different canopy architectures is likely to further increase this structural diversity (Seidel et al., 2013). A deep-fissured bark structure as found in oak, ash or lime (but not beech), as an example, increases colonisation by epiphytes, but also the accumulation of debris and compost (Nicolai, 1986) and thus leads to higher micro-structural/habitat diversity within the canopy.

In additional SEM analyses (Appendix Fig. D1, Table D1) we separated total dead wood into lying and standing dead wood and additionally included the basal area of oak trees, since these are known to accumulate exceptionally much dead wood in forest canopies (Ammer et al., 2008). All three variables increased with increasing tree diversity. It showed that our results were robust and that indeed beetles sampled in the canopy responded more strongly to downed than to standing dead wood. This can be explained by species moving across strata such as the two most dominant species of the canopy *Corticaria gibbosa* and *Athous vittatus*, which additionally use understory habitats in parts of their life cycle (Honomichl, 1998; Stresemann, 2011). Moreover, beetle species richness showed a strong positive response to oak basal area indicating a link to increased deadwood in the canopy of forest stands rich in tree species.

In the canopy, forest and saproxylic species constituted a higher fraction of the beetle community indicating a more special habitat compared with the understory where habitat generalists stronger dominated the beetle community. Previous studies reported the highest diversity of saproxylic beetles in habitats where both a high dead wood volume and sunlight availability were available (Jonsell et al., 1998; Müller et al., 2008; Vodka & Cizek, 2013; Wermelinger et al., 2007). The forest's overall light regime was of minor importance in the canopy since light availability is in general higher compared with the understory and is thus not a limiting factor. Additionally, some species prefer certain tree species or genera and some tree species house a higher beetle diversity than others (Davies et al., 2008; Irmiler et al., 1996; Jonsell et al., 1998; Lindhe and Lindelöw, 2004; Sprick & Floren, 2008; Weigel & Apfel, 2011). Jonsell et al. (2007) examined saproxylic beetle diversity on logging residues of different tree species and stated that no tree species can be replaced by another without risking biodiversity loss. Matching our results, Walentowski et al. (2014) argued that there are only few beech specialist species and more species associated with other tree species such as *Ulmus*, *Tilia*, *Fraxinus* and *Quercus* because beech only became the dominant tree species of Central Europe in the post-glacial time. Therefore, increased canopy tree diversity is likely to have met the requirements of more specialist species. Since we can assume a higher number of species being associated with certain tree species, one factor contributing to the overall higher beetle diversity (γ -diversity) in forest stands rich in tree species may result from a higher species turnover among trees compared with species poor forest stands. In line with that Sobek et al. (2009a) reported an increase in β -diversity even among conspecific tree individuals in mixed forest stands compared with monospecific forest stands.

Besides the tree species, a forest's understory is characterised by several potentially influential parameters such as herb, shrub and litter layer, but also soil characteristics and light availability – a strong limiting factor where light is scarce (Mölder et al., 2014). Additionally, in the understory fewer saproxylic and forest species were recorded and habitat generalists such as *Meligethes aeneus* strongly dominated the beetle community. Canopy openness and distance from the forest edge increasing in importance indicate that tree diversity effects on beetles in the understory may be less important or rather indirect compared with the canopy.

Beetle community composition changed with increasing distance from the forest edge, but this depended on tree diversity level and forest stratum. Species specific requirements regarding microhabitat, microclimate and resource availability but also interspecific interactions may have shaped the beetle communities along the edge-interior gradient in the high and the low tree diversity level, but also in the canopy and the understory (Bouget et al., 2011; Grimbacher and Stork, 2007). This is reflected in individual species preferring certain forest strata (e. g. *Athous vittatus* or *Ernoporicus fagi*), tree diversity levels (e. g. *Orchestes fagi* or *Phyllobius argentatus*) or forest edge or interior (e. g. *Atomaria linearis*).

Study relevance

The tree diversity effects reported here cannot be clearly separated from beech dominance effects, given that the forests studied here all contained beech (Nadrowski et al., 2010). However, comparable studies by Sobek et al. (2009a,b) and Vockenhuber et al. (2011) showed that including not only beech abundance but also tree diversity considerably improved the explanatory power of statistical models. Taking advantage of natural gradients in tree diversity under comparable site conditions offers the opportunity to obtain results with a high relevance for real-world systems (Leuschner et al., 2009; Pretzsch et al., 2013). Since planted tree diversity experiments (Bruehlheide et al., 2014; Scherer-Lorenzen et al., 2007) are more independent in their study design, thus reducing confounding factors, they indisputably have advantages over observational studies. Yet, they differ from natural old-growth forest stands in many aspects making their results hardly transferable to mature forest stands (Pretzsch et al., 2013). Furthermore, they are unsuitable for studying the full natural beetle diversity, since many species depend on characteristics of mature trees/forest stands (Grove, 2002) – a stage that has in most cases not yet been reached in planted forest biodiversity experiments. Nevertheless, studies on natural tree diversity gradients but with dominant tree species other than beech (Baeten et al., 2013) may help to assess the generality of our results.

Conclusions

This is the first study assessing the relative effects of forest edge, stratum and tree diversity in consideration of interactions among these predictors on beetles in forests.

The outcome of this study emphasizes the relevance of taking large spatial scales into account when addressing edge effect in forests. Many studies examined differences in arthropod communities between forest edge and forest interior and the majority of these studies placed the “interior plots” at max. 100 m away from the forest edge. This appears questionable in the light of our results.

As pointed out by Didham (2010) it still remains unclear why the strength and range of edge effects is so variable. According to Ries & Sisk (2010) and references therein from a conservation perspective, it is not only important to find out where edge effects occur but also where they do not occur. By showing that edge effects in forests are much weaker in the canopy compared to the understory, we hope to contribute a puzzle piece to this debate that has so far been neglected. Our results indicate that the canopy habitat and canopy arthropods may be less impaired by fragmentation induced edge effects, than understory species and habitat. Furthermore, saproxylic beetle species yielded highest numbers in the canopy of forest stands rich in tree species. This is particularly relevant since there are many red-listed species among saproxylic arthropods and they often serve as target species for conservation (Davies et al., 2008; Lachat et al., 2012). Therefore, an increased diversity of deciduous tree species in mature beech forests may help to preserve the diversity of specialist beetle species in Central Europe.

Our results demonstrate that pathways driving beetle diversity in forests may differ across forest strata. Therefore, a multi-layer sampling is recommended (Bouget et al., 2011; Su & Woods, 2001) if the aim is to draw conclusions about the whole system.

Acknowledgements

This study was conducted within the framework of the research training group ‘Graduiertenkolleg 1086: The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests’ and financed by the German Research Foundation (DFG). We thank two anonymous reviewers for constructive comments on an earlier draft of this paper. We highly acknowledge Dominik Seidel for inventing study region specific formulae for the calculation of original tree heights of standing dead wood, our colleague Verena Rösch for improving the English writing and Andreas Weigel and Wolfgang Apfel for their support in beetle identification. Furthermore, we thank the Hainich National Park

administration for providing a map of forest types and for allowing research in the National Park.

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Appendix

Appendix A

Assessment of canopy openness:

Canopy openness was assessed using fish eye photographs taken with a Nikon Coolpix 8400 camera plus Nikon FC-E9 fisheye converter and UR-E16 adapter ring (Nikon Corporation, Chiyoda, Tokyo, Japan). Using Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, California, USA) the photographs were processed in three steps: 1. The image background was converted into an editable layer, 2. the ellipse selection tool was used to select an exactly circular area, excluding the black margin contained in each photograph, 3. in the layers menu, "layer mask" was selected and then "reveal selection" chosen; the formerly black area was thus removed and replaced by a transparent background. Thereafter we used Adobe Photoshop Lightroom 5.2 (Adobe Systems Inc.) and performed adjustments to all photographs in the following way: Contrast was set to -100, highlights were set to -73, whites were set to +7, black was set to -100 and clarity was set to 66. In the tone curve, lights were set to +96. Using SideLook 1.1.01 we (automatically) estimated the optimal threshold for converting photographs into black-and-white pictures (Nobis and Hunziker, 2005). We then calculated canopy openness with Gap Light Analyzer 2.0 (Cary Institute of Ecosystem Studies, Millbrook, New York, USA).

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Appendix B**Table B1**

List of beetle species recorded along the 10 transects. The nomenclature follows de Jong (2013)*. Habitat generalists are defined here as species not explicitly adapted to forests. Forest species = species predominantly occurring in forests; Habitat generalists = species occurring in forests and elsewhere

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Euglenes oculatus</i>	Eugl_ocul	Aderidae	forest species	saproxyllic
<i>Allecula morio</i>	Alle_mori	Alleculidae	forest species	saproxyllic
<i>Mycetochara maura</i>	Myce_maur	Alleculidae	forest species	saproxyllic
<i>Dorcatoma chrysomelina</i>	Dorc_chry	Anobiidae	forest species	saproxyllic
<i>Dorcatoma dresdensis</i>	Dorc_dres	Anobiidae	forest species	saproxyllic
<i>Dryophilus pusillus</i>	Dryo_pusi	Anobiidae	forest species	saproxyllic
<i>Ernobius abietinus</i>	Erno_abie	Anobiidae	forest species	saproxyllic
<i>Ernobius abietis</i>	Erno_abie	Anobiidae	forest species	saproxyllic
<i>Hadrobregmus pertinax</i>	Hadr_pert	Anobiidae	forest species	saproxyllic
<i>Hemicoelus costatus</i>	Hemi_cost	Anobiidae	forest species	saproxyllic
<i>Hemicoelus fulvicornis</i>	Hemi_fulv	Anobiidae	habitat generalist	saproxyllic
<i>Hyperisus plumbeum</i>	Hype_plum	Anobiidae	habitat generalist	saproxyllic
<i>Ptilinus pectinicornis</i>	Ptil_pect	Anobiidae	forest species	saproxyllic
<i>Ptinomorphus imperialis</i>	Ptin_impe	Anobiidae	forest species	saproxyllic
<i>Xestobium rufovillosum</i>	Xest_rufo	Anobiidae	forest species	saproxyllic
<i>Anthribus nebulosus</i>	Anth_nebu	Anthribidae	forest species	saproxyllic
<i>Platystomos albinus</i>	Plat_albi	Anthribidae	habitat generalist	saproxyllic
<i>Tropideres albirostris</i>	Trop_albi	Anthribidae	habitat generalist	saproxyllic
<i>Ceratapion gibbistrostre</i>	Cera_gibb	Apionidae	habitat generalist	non-saproxyllic
<i>Cyanapion spencii</i>	Cyan_spen	Apionidae	habitat generalist	non-saproxyllic
<i>Eutrichapion ervi</i>	Eutr_ervi	Apionidae	habitat generalist	non-saproxyllic
<i>Eutrichapion viciae</i>	Eutr_vici	Apionidae	habitat generalist	non-saproxyllic
<i>Oxystoma cerdo</i>	Oxys_cerd	Apionidae	habitat generalist	non-saproxyllic
<i>Oxystoma craccae</i>	Oxys_crac	Apionidae	habitat generalist	non-saproxyllic
<i>Oxystoma ochropus</i>	Oxys_ochr	Apionidae	habitat generalist	non-saproxyllic
<i>Protapion apicans</i>	Prot_apri	Apionidae	habitat generalist	non-saproxyllic
<i>Protapion fulvipes</i>	Prot_fulv	Apionidae	habitat generalist	non-saproxyllic
<i>Diplocoelus fagi</i>	Dipl_fagi	Biphylidae	forest species	saproxyllic
<i>Odonteus armiger</i>	Odon_armi	Bolboceratidae	habitat generalist	non-saproxyllic
<i>Bruchus rufimanus</i>	Bruc_rufi	Bruchidae	habitat generalist	non-saproxyllic
<i>Byrrhus pilula</i>	Byrr_pilu	Byrrhidae	habitat generalist	non-saproxyllic
<i>Byturus tomentosus</i>	Bytu_tome	Byturidae	habitat generalist	non-saproxyllic
<i>Cantharis decipiens</i>	Cant_deci	Cantharidae	habitat generalist	non-saproxyllic
<i>Cantharis figurata</i>	Cant_figu	Cantharidae	habitat generalist	non-saproxyllic
<i>Cantharis fusca</i>	Cant_fusc	Cantharidae	habitat generalist	non-saproxyllic
<i>Cantharis nigricans</i>	Cant_nigr	Cantharidae	habitat generalist	non-saproxyllic
<i>Cantharis obscura</i>	Cant_obsc	Cantharidae	forest species	non-saproxyllic
<i>Cantharis pellucida</i>	Cant_pell	Cantharidae	habitat generalist	non-saproxyllic
<i>Cantharis rufa</i>	Cant_rufa	Cantharidae	habitat generalist	non-saproxyllic
<i>Cantharis terminata</i>	Cant_term	Cantharidae	forest species	non-saproxyllic
<i>Malthinus flaveolus</i>	Malt_flav	Cantharidae	forest species	non-saproxyllic
<i>Malthodes guttifer</i>	Malt_gutt	Cantharidae	habitat generalist	saproxyllic
<i>Malthodes holdhausi</i>	Malt_hold	Cantharidae	forest species	saproxyllic
<i>Malthodes maurus</i>	Malt_maur	Cantharidae	forest species	saproxyllic
<i>Malthodes minimus</i>	Malt_mini	Cantharidae	forest species	saproxyllic
<i>Malthodes spathifer</i>	Malt_spat	Cantharidae	forest species	saproxyllic
<i>Metacantharis discoidea</i>	Meta_disc	Cantharidae	habitat generalist	non-saproxyllic
<i>Podistra rufotestacea</i>	Podi_rufo	Cantharidae	habitat generalist	non-saproxyllic
<i>Rhagonycha fulva</i>	Rhag_fulv	Cantharidae	habitat generalist	non-saproxyllic
<i>Rhagonycha lignosa</i>	Rhag_lign	Cantharidae	habitat generalist	non-saproxyllic
<i>Rhagonycha lutea</i>	Rhag_lute	Cantharidae	habitat generalist	non-saproxyllic
<i>Rhagonycha nigriiventris</i>	Rhag_nigr	Cantharidae	habitat generalist	non-saproxyllic
<i>Rhagonycha translucida</i>	Rhag_tran	Cantharidae	habitat generalist	non-saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Acupalpus meridianus</i>	Acup_meri	Carabidae	habitat generalist	non-saproxyllic
<i>Amara aenea</i>	Amar_aene	Carabidae	habitat generalist	non-saproxyllic
<i>Amara convexior</i>	Amar_conv	Carabidae	habitat generalist	non-saproxyllic
<i>Amara familiaris</i>	Amar_fami	Carabidae	habitat generalist	non-saproxyllic
<i>Amara montivaga</i>	Amar_mont	Carabidae	habitat generalist	non-saproxyllic
<i>Amara ovata</i>	Amar_ovat	Carabidae	habitat generalist	non-saproxyllic
<i>Amara similata</i>	Amar_simi	Carabidae	habitat generalist	non-saproxyllic
<i>Anchomenus dorsalis</i>	Anch_dors	Carabidae	habitat generalist	non-saproxyllic
<i>Bembidion deletum</i>	Bemb_dele	Carabidae	habitat generalist	non-saproxyllic
<i>Bembidion guttula</i>	Bemb_gutt	Carabidae	habitat generalist	non-saproxyllic
<i>Bembidion lampros</i>	Bemb_lamp	Carabidae	habitat generalist	non-saproxyllic
<i>Bembidion lunulatum</i>	Bemb_lunu	Carabidae	habitat generalist	non-saproxyllic
<i>Bembidion properans</i>	Bemb_prop	Carabidae	habitat generalist	non-saproxyllic
<i>Bembidion quadrimaculatum</i>	Bemb_quad	Carabidae	habitat generalist	non-saproxyllic
<i>Brachinus explodens</i>	Brac_expl	Carabidae	habitat generalist	non-saproxyllic
<i>Dromius agilis</i>	Drom_agil	Carabidae	forest species	saproxyllic
<i>Dromius fenestratus</i>	Drom_fene	Carabidae	forest species	saproxyllic
<i>Dromius quadrimaculatus</i>	Drom_quad	Carabidae	forest species	saproxyllic
<i>Harpalus affinis</i>	Harp_affi	Carabidae	habitat generalist	non-saproxyllic
<i>Leistus spinibarbis</i>	Leis_spin	Carabidae	habitat generalist	non-saproxyllic
<i>Limodromus assimilis</i>	Limo_assi	Carabidae	forest species	non-saproxyllic
<i>Loricera pilicornis</i>	Lori_pili	Carabidae	habitat generalist	non-saproxyllic
<i>Microlestes maurus</i>	Micr_maur	Carabidae	habitat generalist	non-saproxyllic
<i>Notiophilus biguttatus</i>	Noti_bigu	Carabidae	habitat generalist	non-saproxyllic
<i>Poecilus cupreus</i>	Poec_cupr	Carabidae	habitat generalist	non-saproxyllic
<i>Poecilus versicolor</i>	Poec_vers	Carabidae	habitat generalist	non-saproxyllic
<i>Pterostichus diligens</i>	Pter_dili	Carabidae	habitat generalist	non-saproxyllic
<i>Pterostichus oblongopunctatus</i>	Pter_oblo	Carabidae	forest species	non-saproxyllic
<i>Tachys bistratus</i>	Tach_bist	Carabidae	habitat generalist	non-saproxyllic
<i>Trechus obtusus</i>	Trec_obtu	Carabidae	forest species	non-saproxyllic
<i>Trechus quadristriatus</i>	Trec_quad	Carabidae	habitat generalist	non-saproxyllic
<i>Alosterna tabacicolor</i>	Alos_tabac	Cerambycidae	forest species	saproxyllic
<i>Anaglyptus mysticus</i>	Anag_myst	Cerambycidae	habitat generalist	saproxyllic
<i>Anisarthron barbipes</i>	Anis_barb	Cerambycidae	habitat generalist	saproxyllic
<i>Anoplodera sexguttata</i>	Anop_sexg	Cerambycidae	habitat generalist	saproxyllic
<i>Grammoptera abdominalis</i>	Gram_abdo	Cerambycidae	habitat generalist	saproxyllic
<i>Grammoptera ruficornis</i>	Gram_rufi	Cerambycidae	forest species	saproxyllic
<i>Leiopus nebulosus</i>	Leio_nebu	Cerambycidae	forest species	saproxyllic
<i>Mesosa nebulosa</i>	Meso_nebu	Cerambycidae	habitat generalist	saproxyllic
<i>Obrium brunneum</i>	Obri_brun	Cerambycidae	forest species	saproxyllic
<i>Oxymirus cursor</i>	Oxym_curs	Cerambycidae	forest species	saproxyllic
<i>Phymatodes testaceus</i>	Phym_test	Cerambycidae	forest species	saproxyllic
<i>Phytoecia cylindrica</i>	Phyt_cyli	Cerambycidae	habitat generalist	non-saproxyllic
<i>Pogonocherus hispidus</i>	Pogo_hisp	Cerambycidae	forest species	saproxyllic
<i>Rhagium bifasciatum</i>	Rhag_bifa	Cerambycidae	forest species	saproxyllic
<i>Rhagium mordax</i>	Rhag_mord	Cerambycidae	forest species	saproxyllic
<i>Rhagium sycophanta</i>	Rhag_syco	Cerambycidae	forest species	saproxyllic
<i>Rutpela maculata</i>	Rutp_macu	Cerambycidae	forest species	saproxyllic
<i>Saperda scalaris</i>	Sape_scal	Cerambycidae	forest species	saproxyllic
<i>Stenocorus meridianus</i>	Sten_meri	Cerambycidae	habitat generalist	saproxyllic
<i>Stenostola dubia</i>	Sten_dubi	Cerambycidae	habitat generalist	saproxyllic
<i>Stenurella melanura</i>	Sten_mela	Cerambycidae	forest species	saproxyllic
<i>Tetrops praeustus</i>	Tetr_prae	Cerambycidae	habitat generalist	saproxyllic
<i>Tetrops starkii</i>	Tetr_star	Cerambycidae	forest species	saproxyllic
<i>Cerylon deplanatum</i>	Cery_depl	Cerylonidae	forest species	saproxyllic
<i>Cerylon fagi</i>	Cery_fagi	Cerylonidae	forest species	saproxyllic
<i>Cerylon ferrugineum</i>	Cery_ferr	Cerylonidae	forest species	saproxyllic
<i>Cerylon histeroideus</i>	Cery_hist	Cerylonidae	forest species	saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Catops picipes</i>	Cato_pici	Cholevidae	forest species	non-saproxyllic
<i>Catops tristis</i>	Cato_tris	Cholevidae	habitat generalist	non-saproxyllic
<i>Choleva cisteloides</i>	Chol_cist	Cholevidae	habitat generalist	non-saproxyllic
<i>Choleva elongata</i>	Chol_elon	Cholevidae	habitat generalist	non-saproxyllic
<i>Choleva reitteri</i>	Chol_reit	Cholevidae	habitat generalist	non-saproxyllic
<i>Nargus wilkini</i>	Narg_wilk	Cholevidae	forest species	non-saproxyllic
<i>Nemadus colonoides</i>	Nema_colo	Cholevidae	forest species	saproxyllic
<i>Aphthona euphorbiae</i>	Apht_euph	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Chaetocnema aridula</i>	Chae_arid	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Chaetocnema concinna</i>	Chae_conc	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Crepidodera aurata</i>	Crep_aura	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Crepidodera aurea</i>	Crep_aure	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Galeruca tanaceti</i>	Gale_tana	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Longitarsus luridus</i>	Long_luri	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Longitarsus niger</i>	Long_nige	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Orsodacne cerasi</i>	Orso_cera	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Phyllotreta nigripes</i>	Phyl_nigr	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Phyllotreta undulata</i>	Phyl_undu	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Pyrrhalta viburni</i>	Pyrr_vibu	Chrysomelidae	habitat generalist	non-saproxyllic
<i>Cis castaneus</i>	Cis_cast	Ciidae	forest species	saproxyllic
<i>Cis glabratus</i>	Cis_glab	Ciidae	forest species	saproxyllic
<i>Cis micans</i>	Cis_mica	Ciidae	forest species	saproxyllic
<i>Ennearthron cornutum</i>	Enne_corn	Ciidae	forest species	saproxyllic
<i>Orthocis alni</i>	Orth_alni	Ciidae	forest species	saproxyllic
<i>Rhopalodontus perforatus</i>	Rhop_perf	Ciidae	forest species	saproxyllic
<i>Sulcacis fronticornis</i>	Sulc_fron	Ciidae	forest species	saproxyllic
<i>Clambus armadillo</i>	Clam_arma	Clambidae	habitat generalist	non-saproxyllic
<i>Clambus punctulum</i>	Clam_punc	Clambidae	habitat generalist	non-saproxyllic
<i>Opilo mollis</i>	Opil_moll	Cleridae	forest species	saproxyllic
<i>Tillus elongatus</i>	Till_elon	Cleridae	forest species	saproxyllic
<i>Adalia decempunctata</i>	Adal_dece	Coccinellidae	habitat generalist	non-saproxyllic
<i>Anatis ocellata</i>	Anat_ocel	Coccinellidae	forest species	non-saproxyllic
<i>Calvia decemguttata</i>	Calv_dece	Coccinellidae	habitat generalist	non-saproxyllic
<i>Calvia quatuordecimguttata</i>	Calv_quat	Coccinellidae	habitat generalist	non-saproxyllic
<i>Chilocorus renipustulatus</i>	Chil_reni	Coccinellidae	habitat generalist	non-saproxyllic
<i>Coccinella septempunctata</i>	Cocc_sept	Coccinellidae	habitat generalist	non-saproxyllic
<i>Exochomus quadripustulatus</i>	Exoc_quad	Coccinellidae	habitat generalist	non-saproxyllic
<i>Halyzia sedecimguttata</i>	Haly_sede	Coccinellidae	habitat generalist	non-saproxyllic
<i>Harmonia axyridis</i>	Harm_axyr	Coccinellidae	habitat generalist	non-saproxyllic
<i>Nephus bipunctatus</i>	Neph_bipu	Coccinellidae	habitat generalist	non-saproxyllic
<i>Scymnus frontalis</i>	Scym_fron	Coccinellidae	habitat generalist	non-saproxyllic
<i>Scymnus limbatus</i>	Scym_limb	Coccinellidae	habitat generalist	non-saproxyllic
<i>Tytthaspis sedecimpunctata</i>	Tytt_sede	Coccinellidae	habitat generalist	non-saproxyllic
<i>Colon latum</i>	Colo_latu	Colonidae	habitat generalist	non-saproxyllic
<i>Synchita separanda</i>	Sync_sepa	Colydiidae	forest species	saproxyllic
<i>Clypastraea pusilla</i>	Clyp_pusi	Corylophidae	habitat generalist	saproxyllic
<i>Orthoperus nigrescens</i>	Orth_nigr	Corylophidae	habitat generalist	saproxyllic
<i>Antherophagus pallens</i>	Anth_pall	Cryptophagidae	habitat generalist	non-saproxyllic
<i>Atomaria atricapilla</i>	Atom_atri	Cryptophagidae	habitat generalist	non-saproxyllic
<i>Atomaria diluta</i>	Atom_dilu	Cryptophagidae	forest species	saproxyllic
<i>Atomaria fuscata</i>	Atom_fusc	Cryptophagidae	habitat generalist	non-saproxyllic
<i>Atomaria linearis</i>	Atom_line	Cryptophagidae	habitat generalist	non-saproxyllic
<i>Atomaria nigriventris</i>	Atom_nigr	Cryptophagidae	habitat generalist	non-saproxyllic
<i>Atomaria turgida</i>	Atom_turg	Cryptophagidae	forest species	saproxyllic
<i>Cryptophagus pallidus</i>	Cryp_pall	Cryptophagidae	forest species	non-saproxyllic
<i>Cryptophagus pilosus</i>	Cryp_pilo	Cryptophagidae	habitat generalist	non-saproxyllic
<i>Micrambe abietis</i>	Micr_abie	Cryptophagidae	forest species	saproxyllic
<i>Acalles echinatus</i>	Acal_echi	Curculionidae	forest species	saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Anthonomus rectirostris</i>	Anth_rect	Curculionidae	habitat generalist	non-saproxyllic
<i>Anthonomus rubi</i>	Anth_rubi	Curculionidae	habitat generalist	non-saproxyllic
<i>Barypeithes pellucidus</i>	Bary_pell	Curculionidae	unknown	non-saproxyllic
<i>Bradybatus fallax</i>	Brad_fall	Curculionidae	forest species	non-saproxyllic
<i>Bradybatus kellneri</i>	Brad_kell	Curculionidae	forest species	non-saproxyllic
<i>Ceutorhynchus erysimi</i>	Ceut_erys	Curculionidae	habitat generalist	non-saproxyllic
<i>Ceutorhynchus obstructus</i>	Ceut_obst	Curculionidae	habitat generalist	non-saproxyllic
<i>Ceutorhynchus pallidactylus</i>	Ceut_pall	Curculionidae	habitat generalist	non-saproxyllic
<i>Ceutorhynchus sulcicollis</i>	Ceut_sulc	Curculionidae	habitat generalist	non-saproxyllic
<i>Coeliodes rana</i>	Coel_rana	Curculionidae	forest species	non-saproxyllic
<i>Coeliodes transversealbofasciatus</i>	Coel_tran	Curculionidae	forest species	non-saproxyllic
<i>Curculio glandium</i>	Curc_glan	Curculionidae	habitat generalist	non-saproxyllic
<i>Curculio nucum</i>	Curc_nucu	Curculionidae	habitat generalist	non-saproxyllic
<i>Curculio venosus</i>	Curc_veno	Curculionidae	forest species	non-saproxyllic
<i>Hypera nigrirostris</i>	Hype_nigr	Curculionidae	habitat generalist	non-saproxyllic
<i>Hypera postica</i>	Hype_post	Curculionidae	habitat generalist	non-saproxyllic
<i>Mogulones asperifoliarum</i>	Mogu_aspe	Curculionidae	habitat generalist	non-saproxyllic
<i>Orchestes fagi</i>	Orch_fagi	Curculionidae	forest species	non-saproxyllic
<i>Orchestes pilosus</i>	Orch_pilo	Curculionidae	forest species	non-saproxyllic
<i>Phyllobius arborator</i>	Phyl_arbo	Curculionidae	unknown	non-saproxyllic
<i>Phyllobius argentatus</i>	Phyl_arge	Curculionidae	habitat generalist	non-saproxyllic
<i>Phyllobius betulinus</i>	Phyl_betu	Curculionidae	habitat generalist	non-saproxyllic
<i>Phyllobius glaucus</i>	Phyl_glau	Curculionidae	habitat generalist	non-saproxyllic
<i>Phyllobius oblongus</i>	Phyl_oblo	Curculionidae	unknown	non-saproxyllic
<i>Phyllobius roboretanus</i>	Phyl_robo	Curculionidae	unknown	non-saproxyllic
<i>Phyllobius viridicollis</i>	Phyl_viri	Curculionidae	unknown	non-saproxyllic
<i>Polydrusus formosus</i>	Poly_form	Curculionidae	habitat generalist	non-saproxyllic
<i>Polydrusus pilosus</i>	Poly_pilo	Curculionidae	unknown	non-saproxyllic
<i>Polydrusus pterygomalis</i>	Poly_pter	Curculionidae	unknown	non-saproxyllic
<i>Polydrusus tereticollis</i>	Poly_tere	Curculionidae	unknown	non-saproxyllic
<i>Rutera hypocrita</i>	Rute_hypo	Curculionidae	forest species	saproxyllic
<i>Sciaphilus asperatus</i>	Scia_aspe	Curculionidae	unknown	non-saproxyllic
<i>Sitona lineatus</i>	Sito_line	Curculionidae	habitat generalist	non-saproxyllic
<i>Stenocarus ruficornis</i>	Sten_rufi	Curculionidae	habitat generalist	non-saproxyllic
<i>Stereonychus fraxini</i>	Ster_frax	Curculionidae	forest species	non-saproxyllic
<i>Strophosoma melanogrammum</i>	Stro_mela	Curculionidae	unknown	non-saproxyllic
<i>Trachodes hispidus</i>	Trac_hisp	Curculionidae	forest species	saproxyllic
<i>Tychius picirostris</i>	Tych_pici	Curculionidae	habitat generalist	non-saproxyllic
<i>Dascillus cervinus</i>	Dasc_cerv	Dascillidae	habitat generalist	non-saproxyllic
<i>Aplocnemus nigricornis</i>	Aplo_nigr	Dasytidae	forest species	saproxyllic
<i>Dasytes aeratus</i>	Dasy_aera	Dasytidae	habitat generalist	saproxyllic
<i>Dasytes caeruleus</i>	Dasy_caer	Dasytidae	unknown	unkown
<i>Dasytes plumbeus</i>	Dasy_plum	Dasytidae	habitat generalist	saproxyllic
<i>Megatoma undata</i>	Mega_unda	Dermestidae	habitat generalist	saproxyllic
<i>Drilus concolor</i>	Dril_conc	Driliidae	habitat generalist	non-saproxyllic
<i>Hygrotus impressopunctatus</i>	Hygr_impr	Dytiscidae	habitat generalist	non-saproxyllic
<i>Agriotes acuminatus</i>	Agri_acum	Elateridae	habitat generalist	non-saproxyllic
<i>Agriotes lineatus</i>	Agri_line	Elateridae	habitat generalist	non-saproxyllic
<i>Agriotes pallidulus</i>	Agri_pall	Elateridae	habitat generalist	non-saproxyllic
<i>Agriotes pilosellus</i>	Agri_pilo	Elateridae	habitat generalist	non-saproxyllic
<i>Agrypnus murinus</i>	Agry_muri	Elateridae	habitat generalist	non-saproxyllic
<i>Ampedus elongatulus</i>	Ampe_elon	Elateridae	habitat generalist	saproxyllic
<i>Ampedus nigroflavus</i>	Ampe_nigr	Elateridae	forest species	saproxyllic
<i>Ampedus quercicola</i>	Ampe_quer	Elateridae	forest species	saproxyllic
<i>Athous bicolor</i>	Atho_bico	Elateridae	habitat generalist	non-saproxyllic
<i>Athous haemorrhoidalis</i>	Atho_haem	Elateridae	habitat generalist	non-saproxyllic
<i>Athous subfuscus</i>	Atho_subf	Elateridae	habitat generalist	non-saproxyllic
<i>Athous vittatus</i>	Atho_vitt	Elateridae	habitat generalist	non-saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Calambus bipustulatus</i>	Cala_bipu	Elateridae	habitat generalist	saproxylic
<i>Dalopius marginatus</i>	Dalo_marg	Elateridae	habitat generalist	non-saproxylic
<i>Denticollis linearis</i>	Dent_line	Elateridae	forest species	saproxylic
<i>Denticollis rubens</i>	Dent_rube	Elateridae	forest species	saproxylic
<i>Hemicrepidius hirtus</i>	Hemi_hirt	Elateridae	habitat generalist	non-saproxylic
<i>Hemicrepidius niger</i>	Hemi_nige	Elateridae	habitat generalist	non-saproxylic
<i>Hypoganus inunctus</i>	Hypo_inun	Elateridae	forest species	saproxylic
<i>Melanotus villosus</i>	Mela_vill	Elateridae	forest species	saproxylic
<i>Nothodes parvulus</i>	Noth_parv	Elateridae	habitat generalist	non-saproxylic
<i>Endomychus coccineus</i>	Endo_cocc	Endomychidae	forest species	saproxylic
<i>Dacne bipustulata</i>	Dacn_bipu	Erotylidae	forest species	saproxylic
<i>Triplax lepida</i>	Trip_lepi	Erotylidae	forest species	saproxylic
<i>Triplax russica</i>	Trip_russ	Erotylidae	forest species	saproxylic
<i>Tritoma bipustulata</i>	Trit_bipu	Erotylidae	forest species	saproxylic
<i>Eucnemis capucina</i>	Eucn_capu	Eucnemidae	forest species	saproxylic
<i>Hylis cariniceps</i>	Hyli_cari	Eucnemidae	forest species	saproxylic
<i>Hylis olexai</i>	Hyli_olex	Eucnemidae	forest species	saproxylic
<i>Isorhipis melasoides</i>	Isor_mela	Eucnemidae	forest species	saproxylic
<i>Melasis buprestoides</i>	Mela_bupr	Eucnemidae	forest species	saproxylic
<i>Microrhagus lepidus</i>	Micr_lepi	Eucnemidae	forest species	saproxylic
<i>Anoplotrupes stercorosus</i>	Anop_ster	Geotrupidae	forest species	non-saproxylic
<i>Cyphon padi</i>	Cyph_padi	Helodidae	habitat generalist	non-saproxylic
<i>Abraeus granulum</i>	Abra_gran	Histeridae	forest species	saproxylic
<i>Abraeus perpusillus</i>	Abra_perp	Histeridae	forest species	saproxylic
<i>Paromalus flavicornis</i>	Paro_flav	Histeridae	forest species	saproxylic
<i>Plegaderus dissectus</i>	Pleg_diss	Histeridae	forest species	saproxylic
<i>Cryptopleurum minutum</i>	Cryp_minu	Hydrophilidae	habitat generalist	non-saproxylic
<i>Megasternum concinnum</i>	Mega_conc	Hydrophilidae	habitat generalist	non-saproxylic
<i>Cryptolestes ferrugineus</i>	Cryp_ferr	Laemophloeidae	forest species	non-saproxylic
<i>Lagria atripes</i>	Lagr_atri	Lagridae	habitat generalist	non-saproxylic
<i>Lamprohiza splendidula</i>	Lamp_sple	Lampyridae	habitat generalist	non-saproxylic
<i>Lampyris noctiluca</i>	Lamp_noct	Lampyridae	habitat generalist	non-saproxylic
<i>Cartodere nodifer</i>	Cart_nodi	Latridiidae	habitat generalist	non-saproxylic
<i>Corticarina minuta</i>	Cort_minu	Latridiidae	habitat generalist	non-saproxylic
<i>Corticarina gibbosa</i>	Cort_gibb	Latridiidae	habitat generalist	non-saproxylic
<i>Dienerella filiformis</i>	Dien_fili	Latridiidae	habitat generalist	non-saproxylic
<i>Enicmus atriceps</i>	Enic_atri	Latridiidae	forest species	saproxylic
<i>Enicmus brevicornis</i>	Enic_brev	Latridiidae	forest species	saproxylic
<i>Enicmus fungicola</i>	Enic_fung	Latridiidae	forest species	saproxylic
<i>Enicmus rugosus</i>	Enic_rugo	Latridiidae	forest species	non-saproxylic
<i>Enicmus transversus</i>	Enic_tran	Latridiidae	habitat generalist	non-saproxylic
<i>Latridius hirtus</i>	Latr_hirt	Latridiidae	forest species	saproxylic
<i>Stephostethus alternans</i>	Step_alte	Latridiidae	forest species	saproxylic
<i>Stephostethus angusticollis</i>	Step_angu	Latridiidae	habitat generalist	saproxylic
<i>Stephostethus lardarius</i>	Step_lard	Latridiidae	habitat generalist	non-saproxylic
<i>Agathidium nigripenne</i>	Agat_nigr	Leiodidae	forest species	saproxylic
<i>Agathidium pseudopallidum</i>	Agat_pseu	Leiodidae	forest species	non-saproxylic
<i>Agathidium seminulum</i>	Agat_semi	Leiodidae	habitat generalist	saproxylic
<i>Agathidium varians</i>	Agat_vari	Leiodidae	habitat generalist	saproxylic
<i>Amphicyllis globiformis</i>	Amph_glob	Leiodidae	forest species	non-saproxylic
<i>Anisotoma humeralis</i>	Anis_hume	Leiodidae	forest species	saproxylic
<i>Platycerus caraboides</i>	Plat_cara	Lucanidae	forest species	saproxylic
<i>Sinodendron cylindricum</i>	Sino_cyli	Lucanidae	forest species	saproxylic
<i>Elateroides dermestoides</i>	Elat_derm	Lymexylidae	forest species	saproxylic
<i>Charopus flavipes</i>	Char_flav	Malachidae	habitat generalist	non-saproxylic
<i>Malachius bipustulatus</i>	Mala_bipu	Malachidae	forest species	saproxylic
<i>Abdera affinis</i>	Abde_affi	Melandryidae	forest species	saproxylic
<i>Abdera flexuosa</i>	Abde_flex	Melandryidae	forest species	saproxylic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Conopalpus testaceus</i>	Cono_test	Melandryidae	forest species	saproxylic
<i>Hallomenus binotatus</i>	Hall_bino	Melandryidae	forest species	saproxylic
<i>Hypulus quercinus</i>	Hypu_quer	Melandryidae	forest species	saproxylic
<i>Melandrya caraboides</i>	Mela_cara	Melandryidae	habitat generalist	saproxylic
<i>Melandrya dubia</i>	Mela_dubi	Melandryidae	forest species	saproxylic
<i>Orchesia minor</i>	Orch_mino	Melandryidae	forest species	saproxylic
<i>Orchesia undulata</i>	Orch_undu	Melandryidae	forest species	saproxylic
<i>Phloiотrya rufipes</i>	Phlo_rufi	Melandryidae	forest species	saproxylic
<i>Monotoma brevicollis</i>	Mono_brev	Monotomidae	habitat generalist	non-saproxylic
<i>Rhizophagus bipustulatus</i>	Rhiz_bipu	Monotomidae	habitat generalist	saproxylic
<i>Rhizophagus depressus</i>	Rhiz_depr	Monotomidae	forest species	saproxylic
<i>Rhizophagus dispar</i>	Rhiz_disp	Monotomidae	forest species	saproxylic
<i>Rhizophagus nitidulus</i>	Rhiz_niti	Monotomidae	forest species	saproxylic
<i>Mordellistena neuwaldeggiana</i>	Mord_neuw	Mordellidae	habitat generalist	saproxylic
<i>Mordellistena variegata</i>	Mord_vari	Mordellidae	habitat generalist	saproxylic
<i>Mordellochroa abdominalis</i>	Mord_abdo	Mordellidae	habitat generalist	saproxylic
<i>Tomoxia bucephala</i>	Tomo_buce	Mordellidae	forest species	saproxylic
<i>Litargus connexus</i>	Lita_conn	Mycetophagidae	forest species	saproxylic
<i>Mycetophagus atomarius</i>	Myce_atom	Mycetophagidae	forest species	saproxylic
<i>Mycetophagus fulvicollis</i>	Myce_fulv	Mycetophagidae	forest species	saproxylic
<i>Mycetophagus piceus</i>	Myce_pice	Mycetophagidae	forest species	saproxylic
<i>Mycetophagus populi</i>	Myce_popu	Mycetophagidae	forest species	saproxylic
<i>Mycetophagus quadripustulatus</i>	Myce_quad	Mycetophagidae	forest species	saproxylic
<i>Amphotis marginata</i>	Amph_marg	Nitidulidae	habitat generalist	saproxylic
<i>Cryptarcha undata</i>	Cryp_unda	Nitidulidae	forest species	saproxylic
<i>Cychramus luteus</i>	Cych_lute	Nitidulidae	forest species	saproxylic
<i>Epuraea aestiva</i>	Epur_aest	Nitidulidae	habitat generalist	non-saproxylic
<i>Epuraea biguttata</i>	Epur_bigu	Nitidulidae	habitat generalist	saproxylic
<i>Epuraea distincta</i>	Epur_dist	Nitidulidae	forest species	saproxylic
<i>Epuraea melanocephala</i>	Epur_mela	Nitidulidae	forest species	non-saproxylic
<i>Epuraea pallescens</i>	Epur_pall	Nitidulidae	forest species	saproxylic
<i>Epuraea terminalis</i>	Epur_term	Nitidulidae	forest species	saproxylic
<i>Glischrochilus hortensis</i>	Glis_hort	Nitidulidae	habitat generalist	non-saproxylic
<i>Glischrochilus quadriguttatus</i>	Glis_quad	Nitidulidae	forest species	saproxylic
<i>Glischrochilus quadrisignatus</i>	Glis_quad	Nitidulidae	habitat generalist	non-saproxylic
<i>Meligethes aeneus</i>	Meli_aene	Nitidulidae	habitat generalist	non-saproxylic
<i>Meligethes denticulatus</i>	Meli_dent	Nitidulidae	habitat generalist	non-saproxylic
<i>Meligethes flavimanus</i>	Meli_flav	Nitidulidae	habitat generalist	non-saproxylic
<i>Meligethes nanus</i>	Meli_nanu	Nitidulidae	habitat generalist	non-saproxylic
<i>Pocadius ferrugineus</i>	Poca_ferr	Nitidulidae	forest species	non-saproxylic
<i>Soronia grisea</i>	Soro_gris	Nitidulidae	habitat generalist	saproxylic
<i>Ischnomera cyanea</i>	Isch_cyan	Oedemeridae	habitat generalist	saproxylic
<i>Omalisus fontisbellaquaei</i>	Omal_font	Omalisidae	habitat generalist	non-saproxylic
<i>Sericoderus lateralis</i>	Seri_late	Orthoperidae	habitat generalist	non-saproxylic
<i>Olibrus flavicornis</i>	Olib_flav	Phalacridae	habitat generalist	non-saproxylic
<i>Stilbus testaceus</i>	Stil_test	Phalacridae	habitat generalist	non-saproxylic
<i>Phloeostichus denticollis</i>	Phlo_dent	Phloeostichidae	forest species	saproxylic
<i>Phloiophilus edwardsii</i>	Phlo_edwa	Phloiophilidae	forest species	saproxylic
<i>Bibloporus bicolor</i>	Bibl_bico	Pselaphidae	forest species	saproxylic
<i>Bibloporus mayeti</i>	Bibl_maye	Pselaphidae	forest species	saproxylic
<i>Bibloporus minutus</i>	Bibl_minu	Pselaphidae	forest species	saproxylic
<i>Bryaxis nodicornis</i>	Brya_nodi	Pselaphidae	habitat generalist	non-saproxylic
<i>Bythinus burrellii</i>	Byth_burr	Pselaphidae	habitat generalist	non-saproxylic
<i>Bythinus macropalpus</i>	Byth_macr	Pselaphidae	habitat generalist	non-saproxylic
<i>Euplectus brunneus</i>	Eupl_brun	Pselaphidae	forest species	saproxylic
<i>Euplectus punctatus</i>	Eupl_punc	Pselaphidae	forest species	saproxylic
<i>Trimium brevicorne</i>	Trim_brev	Pselaphidae	forest species	non-saproxylic
<i>Tychus niger</i>	Tych_nige	Pselaphidae	habitat generalist	non-saproxylic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Acrotrichis atomaria</i>	Acro_atom	Ptiliidae	habitat generalist	non-saproxyllic
<i>Acrotrichis fascicularis</i>	Acro_fasc	Ptiliidae	habitat generalist	non-saproxyllic
<i>Acrotrichis intermedia</i>	Acro_inte	Ptiliidae	habitat generalist	non-saproxyllic
<i>Baeocrara variolosa</i>	Baeo_vari	Ptiliidae	forest species	saproxyllic
<i>Ptenidium pusillum</i>	Pten_pusi	Ptiliidae	habitat generalist	non-saproxyllic
<i>Ptenidium turgidum</i>	Pten_turg	Ptiliidae	forest species	saproxyllic
<i>Pteryx suturalis</i>	Pter_sutu	Ptiliidae	forest species	saproxyllic
<i>Pyrochroa coccinea</i>	Pyro_cocc	Pyrochroidae	forest species	saproxyllic
<i>Pyrochroa serraticornis</i>	Pyro_serr	Pyrochroidae	forest species	saproxyllic
<i>Schizotus pectinicornis</i>	Schi_pect	Pyrochroidae	forest species	saproxyllic
<i>Chonostropheus tristis</i>	Chon_tris	Rhynchitidae	unknown	non-saproxyllic
<i>Deporaus betulae</i>	Depo_betu	Rhynchitidae	habitat generalist	non-saproxyllic
<i>Lasiorrhynchites olivaceus</i>	Lasi_oliv	Rhynchitidae	habitat generalist	non-saproxyllic
<i>Neocoenorrhinus interpunctatus</i>	Neoc_inte	Rhynchitidae	unknown	non-saproxyllic
<i>Lissodema cursor</i>	Liss_curs	Salpingidae	habitat generalist	saproxyllic
<i>Lissodema denticolle</i>	Liss_dent	Salpingidae	habitat generalist	saproxyllic
<i>Rabocerus gabrieli</i>	Rabo_gabr	Salpingidae	habitat generalist	saproxyllic
<i>Salpingus planirostris</i>	Salp_plan	Salpingidae	habitat generalist	saproxyllic
<i>Salpingus ruficollis</i>	Salp_rufi	Salpingidae	habitat generalist	saproxyllic
<i>Vincenzellus ruficollis</i>	Vinc_rufi	Salpingidae	habitat generalist	saproxyllic
<i>Aphodius contaminatus</i>	Apho_cont	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius depressus</i>	Apho_depr	Scarabaeidae	forest species	non-saproxyllic
<i>Aphodius fimetarius</i>	Apho_fime	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius prodromus</i>	Apho_prod	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius pusillus</i>	Apho_pusi	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius rufipes</i>	Apho_rufi	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius rufus</i>	Apho_rufu	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius sphaelatus</i>	Apho_spha	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Aphodius sticticus</i>	Apho_stic	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Gnorimus nobilis</i>	Gnor_nobi	Scarabaeidae	habitat generalist	saproxyllic
<i>Onthophagus coenobita</i>	Onth_coen	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Onthophagus fracticornis</i>	Onth_frac	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Serica brunna</i>	Seri_brun	Scarabaeidae	habitat generalist	non-saproxyllic
<i>Valgus hemipterus</i>	Valg_hemi	Scarabaeidae	habitat generalist	saproxyllic
<i>Prionocyphon serricornis</i>	Prio_serr	Scirtidae	habitat generalist	non-saproxyllic
<i>Cryphalus abietis</i>	Cryp_abie	Scolytidae	forest species	saproxyllic
<i>Dryocoetes autographus</i>	Dryo_auto	Scolytidae	forest species	saproxyllic
<i>Dryocoetes villosus</i>	Dryo_vill	Scolytidae	habitat generalist	saproxyllic
<i>Ernoporicus fagi</i>	Erno_fagi	Scolytidae	forest species	saproxyllic
<i>Hylastes cunicularius</i>	Hyla_cuni	Scolytidae	forest species	saproxyllic
<i>Hylesinus crenatus</i>	Hyle_cren	Scolytidae	forest species	saproxyllic
<i>Hylurgops palliatus</i>	Hylu_pall	Scolytidae	forest species	saproxyllic
<i>Leperisinus fraxini</i>	Lepe_frax	Scolytidae	forest species	saproxyllic
<i>Lymantor coryli</i>	Lyma_cory	Scolytidae	habitat generalist	saproxyllic
<i>Pityogenes chalcographus</i>	Pity_chal	Scolytidae	forest species	saproxyllic
<i>Polygraphus grandiclava</i>	Poly_gran	Scolytidae	habitat generalist	saproxyllic
<i>Scolytus carpini</i>	Scol_carp	Scolytidae	forest species	saproxyllic
<i>Scolytus intricatus</i>	Scol_intr	Scolytidae	forest species	saproxyllic
<i>Taphrorychus bicolor</i>	Taph_bico	Scolytidae	forest species	saproxyllic
<i>Xyleborinus saxeseni</i>	Xyle_saxe	Scolytidae	forest species	saproxyllic
<i>Xyleborus germanus</i>	Xyle_germ	Scolytidae	forest species	saproxyllic
<i>Xyleborus peregrinus</i>	Xyle_pere	Scolytidae	forest species	saproxyllic
<i>Xyloterus domesticus</i>	Xylo_dome	Scolytidae	forest species	saproxyllic
<i>Xyloterus signatus</i>	Xylo_sign	Scolytidae	forest species	saproxyllic
<i>Anaspis flava</i>	Anas_flav	Scrautiidae	habitat generalist	saproxyllic
<i>Anaspis frontalis</i>	Anas_fron	Scrautiidae	forest species	saproxyllic
<i>Anaspis marginicollis</i>	Anas_marg	Scrautiidae	forest species	saproxyllic
<i>Anaspis rufilabris</i>	Anas_rufi	Scrautiidae	forest species	saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Anaspis thoracica</i>	Anas_thor	Scraptiidae	forest species	saproxyllic
<i>Anaspis varians</i>	Anas_vari	Scraptiidae	habitat generalist	saproxyllic
<i>Neuraphes elongatulus</i>	Neur_elon	Scydmaenidae	forest species	non-saproxyllic
<i>Neuraphes rubicundus</i>	Neur_rubi	Scydmaenidae	forest species	non-saproxyllic
<i>Stenichnus collaris</i>	Sten_coll	Scydmaenidae	forest species	non-saproxyllic
<i>Stenichnus scutellaris</i>	Sten_scut	Scydmaenidae	forest species	non-saproxyllic
<i>Dendroxena quadrimaculata</i>	Dend_quad	Silphidae	forest species	non-saproxyllic
<i>Nicrophorus interruptus</i>	Nicr_inte	Silphidae	habitat generalist	non-saproxyllic
<i>Nicrophorus investigator</i>	Nicr_inve	Silphidae	forest species	non-saproxyllic
<i>Nicrophorus vespilloides</i>	Nicr_vesp	Silphidae	forest species	non-saproxyllic
<i>Thanatophilus sinuatus</i>	Than_sinu	Silphidae	habitat generalist	non-saproxyllic
<i>Uleiota planatus</i>	Ulei_plan	Silvanidae	forest species	saproxyllic
<i>Aspidiphorus orbiculatus</i>	Aspi_orbi	Sphindidae	forest species	saproxyllic
<i>Achenium humile</i>	Ache_humi	Staphylinidae	forest species	non-saproxyllic
<i>Acidota crenata</i>	Acid_cren	Staphylinidae	forest species	non-saproxyllic
<i>Aleochara sparsa</i>	Aleo_spar	Staphylinidae	forest species	non-saproxyllic
<i>Alevonota rufotestacea</i>	Alev_rufo	Staphylinidae	habitat generalist	non-saproxyllic
<i>Aloconota coulsoni</i>	Aloc_coul	Staphylinidae	habitat generalist	non-saproxyllic
<i>Aloconota gregaria</i>	Aloc_greg	Staphylinidae	habitat generalist	non-saproxyllic
<i>Amarochara bonmairei</i>	Amar_bonn	Staphylinidae	forest species	saproxyllic
<i>Amischa analis</i>	Amis_anal	Staphylinidae	habitat generalist	non-saproxyllic
<i>Amischa forcipata</i>	Amis_forc	Staphylinidae	forest species	non-saproxyllic
<i>Amischa nigrofusca</i>	Amis_nigr	Staphylinidae	habitat generalist	non-saproxyllic
<i>Anomognathus cuspidatus</i>	Anom_cusp	Staphylinidae	forest species	saproxyllic
<i>Anotylus hamatus</i>	Anot_hama	Staphylinidae	habitat generalist	non-saproxyllic
<i>Anotylus insecatus</i>	Anot_inse	Staphylinidae	habitat generalist	non-saproxyllic
<i>Anotylus mutator</i>	Anot_muta	Staphylinidae	forest species	non-saproxyllic
<i>Anotylus rugosus</i>	Anot_rugo	Staphylinidae	habitat generalist	non-saproxyllic
<i>Anotylus tetracarinatus</i>	Anot_tetr	Staphylinidae	habitat generalist	non-saproxyllic
<i>Anthobium atrocephalum</i>	Anth_atro	Staphylinidae	forest species	non-saproxyllic
<i>Anthophagus angusticollis</i>	Anth_angu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta aegra</i>	Athe_aegr	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta cauta</i>	Athe_caut	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta elongatula</i>	Athe_elon	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta fungi</i>	Athe_fung	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta inquinula</i>	Athe_inqu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta negligens</i>	Athe_negl	Staphylinidae	forest species	non-saproxyllic
<i>Atheta nidicola</i>	Athe_nidi	Staphylinidae	forest species	non-saproxyllic
<i>Atheta oblita</i>	Athe_obli	Staphylinidae	forest species	saproxyllic
<i>Atheta orbata</i>	Athe_orba	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta palustris</i>	Athe_palu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atheta triangulum</i>	Athe_tria	Staphylinidae	habitat generalist	non-saproxyllic
<i>Atreacus affinis</i>	Atre_affi	Staphylinidae	forest species	saproxyllic
<i>Bisnius fimetarius</i>	Bisn_fime	Staphylinidae	habitat generalist	non-saproxyllic
<i>Callicerus obscurus</i>	Call_obsc	Staphylinidae	habitat generalist	non-saproxyllic
<i>Carpelimus corticinus</i>	Carp_cort	Staphylinidae	habitat generalist	non-saproxyllic
<i>Carpelimus pusillus</i>	Carp_pusi	Staphylinidae	habitat generalist	non-saproxyllic
<i>Coprophilus striatulus</i>	Copr_stri	Staphylinidae	habitat generalist	non-saproxyllic
<i>Coryphium angusticollis</i>	Cory_angu	Staphylinidae	forest species	saproxyllic
<i>Cypha longicornis</i>	Cyph_long	Staphylinidae	habitat generalist	non-saproxyllic
<i>Cypha curtula</i>	Cyph_curt	Staphylinidae	forest species	saproxyllic
<i>Dropephylla ioptera</i>	Drop_iopt	Staphylinidae	forest species	saproxyllic
<i>Eusphalerum atrum</i>	Eusp_atru	Staphylinidae	habitat generalist	non-saproxyllic
<i>Eusphalerum limbatum</i>	Eusp_limb	Staphylinidae	habitat generalist	non-saproxyllic
<i>Eusphalerum luteum</i>	Eusp_lute	Staphylinidae	habitat generalist	non-saproxyllic
<i>Eusphalerum minutum</i>	Eusp_minu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Eusphalerum primulae</i>	Eusp_prim	Staphylinidae	habitat generalist	non-saproxyllic
<i>Eusphalerum rectangulum</i>	Eusp_rect	Staphylinidae	habitat generalist	non-saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Eusphalerum semicoleopratum</i>	Eusp_semi	Staphylinidae	habitat generalist	non-saproxyllic
<i>Eusphalerum signatum</i>	Eusp_sign	Staphylinidae	habitat generalist	non-saproxyllic
<i>Haploglossa marginalis</i>	Hapl_marg	Staphylinidae	habitat generalist	saproxyllic
<i>Haploglossa picipennis</i>	Hapl_pici	Staphylinidae	forest species	non-saproxyllic
<i>Haploglossa villosula</i>	Hapl_vill	Staphylinidae	habitat generalist	saproxyllic
<i>Holobus apicatus</i>	Holo_apic	Staphylinidae	forest species	saproxyllic
<i>Hypnogyra angularis</i>	Hypn_angu	Staphylinidae	forest species	saproxyllic
<i>Ischnoglossa obscura</i>	Isch_obsc	Staphylinidae	forest species	saproxyllic
<i>Ischnosoma longicorne</i>	Isch_long	Staphylinidae	habitat generalist	non-saproxyllic
<i>Lathrobium brunnipes</i>	Lath_brun	Staphylinidae	habitat generalist	non-saproxyllic
<i>Leptacinus batychnus</i>	Lept_baty	Staphylinidae	unknown	non-saproxyllic
<i>Leptacinus sulcifrons</i>	Lept_sulc	Staphylinidae	habitat generalist	non-saproxyllic
<i>Leptusa pulchella</i>	Lept_pulc	Staphylinidae	forest species	saproxyllic
<i>Leptusa ruficollis</i>	Lept_rufi	Staphylinidae	forest species	saproxyllic
<i>Lesteva longoelytrata</i>	Lest_long	Staphylinidae	habitat generalist	non-saproxyllic
<i>Liogluta alpestris</i>	Liog_alpe	Staphylinidae	forest species	non-saproxyllic
<i>Liogluta longiuscula</i>	Liog_long	Staphylinidae	forest species	non-saproxyllic
<i>Liogluta microptera</i>	Liog_micr	Staphylinidae	forest species	non-saproxyllic
<i>Lordithon lunulatus</i>	Lord_lunu	Staphylinidae	forest species	non-saproxyllic
<i>Medon brunneus</i>	Medo_brun	Staphylinidae	forest species	non-saproxyllic
<i>Notothecta flavipes</i>	Noto_flav	Staphylinidae	habitat generalist	non-saproxyllic
<i>Ocalea picata</i>	Ocal_pica	Staphylinidae	habitat generalist	non-saproxyllic
<i>Omalium caesum</i>	Omal_caes	Staphylinidae	habitat generalist	non-saproxyllic
<i>Omalium rivulare</i>	Omal_rivu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Oxypoda acuminata</i>	Oxyp_acum	Staphylinidae	habitat generalist	non-saproxyllic
<i>Oxypoda brachyptera</i>	Oxyp_brac	Staphylinidae	habitat generalist	non-saproxyllic
<i>Oxypoda brevicornis</i>	Oxyp_brev	Staphylinidae	habitat generalist	non-saproxyllic
<i>Oxypoda haemorrhoea</i>	Oxyp_haem	Staphylinidae	habitat generalist	non-saproxyllic
<i>Oxypoda opaca</i>	Oxyp_opac	Staphylinidae	habitat generalist	non-saproxyllic
<i>Pella lugens</i>	Pell_luge	Staphylinidae	habitat generalist	non-saproxyllic
<i>Philonthus carbonarius</i>	Phil_carb	Staphylinidae	habitat generalist	non-saproxyllic
<i>Philonthus cognatus</i>	Phil_cogn	Staphylinidae	habitat generalist	non-saproxyllic
<i>Philonthus decorus</i>	Phil_deco	Staphylinidae	forest species	non-saproxyllic
<i>Philonthus laevicollis</i>	Phil_laev	Staphylinidae	habitat generalist	non-saproxyllic
<i>Philonthus sanguinolentus</i>	Phil_sang	Staphylinidae	habitat generalist	non-saproxyllic
<i>Phloeocharis subtilissima</i>	Phlo_subt	Staphylinidae	forest species	saproxyllic
<i>Phloeopora corticalis</i>	Phlo_cort	Staphylinidae	forest species	saproxyllic
<i>Phloeopora scribae</i>	Phlo_scri	Staphylinidae	forest species	saproxyllic
<i>Phloeopora testacea</i>	Phlo_test	Staphylinidae	forest species	saproxyllic
<i>Phyllodrepa floralis</i>	Phyl_flor	Staphylinidae	habitat generalist	saproxyllic
<i>Phyllodrepa melanocephala</i>	Phyl_mela	Staphylinidae	forest species	saproxyllic
<i>Phyllodrepa nigra</i>	Phyl_nigr	Staphylinidae	forest species	saproxyllic
<i>Plataraea brunnea</i>	Plat_brun	Staphylinidae	habitat generalist	non-saproxyllic
<i>Platystethus nitens</i>	Plat_nite	Staphylinidae	habitat generalist	non-saproxyllic
<i>Proteinus atomarius</i>	Prot_atom	Staphylinidae	habitat generalist	non-saproxyllic
<i>Quedius maurus</i>	Qued_maur	Staphylinidae	forest species	saproxyllic
<i>Quedius mesomelinus</i>	Qued_meso	Staphylinidae	habitat generalist	non-saproxyllic
<i>Quedius scitus</i>	Qued_scit	Staphylinidae	forest species	saproxyllic
<i>Rhopalocera clavigera</i>	Rhop_clav	Staphylinidae	unknown	non-saproxyllic
<i>Rhopalotella validiuscula</i>	Rhop_vali	Staphylinidae	habitat generalist	saproxyllic
<i>Rugilus rufipes</i>	Rugi_rufi	Staphylinidae	habitat generalist	non-saproxyllic
<i>Scaphisoma agaricinum</i>	Scap_agar	Staphylinidae	forest species	saproxyllic
<i>Sepedophilus bipunctatus</i>	Sepe_bipu	Staphylinidae	forest species	saproxyllic
<i>Sepedophilus immaculatus</i>	Sepe_imma	Staphylinidae	forest species	non-saproxyllic
<i>Sepedophilus marshami</i>	Sepe_mars	Staphylinidae	habitat generalist	non-saproxyllic
<i>Sepedophilus testaceus</i>	Sepe_test	Staphylinidae	forest species	saproxyllic
<i>Stichoglossa semirufa</i>	Stic_semi	Staphylinidae	forest species	non-saproxyllic
<i>Tachinus laticollis</i>	Tach_lati	Staphylinidae	habitat generalist	non-saproxyllic

Species	Abbr.	Family	Habitat preference	Dead wood dependence
<i>Tachinus rufipes</i>	Tach_rufi	Staphylinidae	habitat generalist	non-saproxyllic
<i>Tachyporus hypnorum</i>	Tach_hypn	Staphylinidae	habitat generalist	non-saproxyllic
<i>Tachyporus nitidulus</i>	Tach_niti	Staphylinidae	habitat generalist	non-saproxyllic
<i>Tachyporus obtusus</i>	Tach_obtu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Tachyporus solutus</i>	Tach_solu	Staphylinidae	habitat generalist	non-saproxyllic
<i>Tinotus morion</i>	Tino_mori	Staphylinidae	habitat generalist	non-saproxyllic
<i>Xantholinus linearis</i>	Xant_line	Staphylinidae	habitat generalist	non-saproxyllic
<i>Xantholinus longiventris</i>	Xant_long	Staphylinidae	habitat generalist	non-saproxyllic
<i>Corticeus bicolor</i>	Cort_bico	Tenebrionidae	habitat generalist	saproxyllic
<i>Corticeus unicolor</i>	Cort_unic	Tenebrionidae	forest species	saproxyllic
<i>Diaperis boleti</i>	Diap_bole	Tenebrionidae	forest species	saproxyllic
<i>Tetratoma ancora</i>	Tetr_anco	Tetratomidae	habitat generalist	saproxyllic
<i>Aulonothroscus brevicollis</i>	Aulo_brev	Throscidae	forest species	non-saproxyllic
<i>Trixagus carinifrons</i>	Trix_cari	Throscidae	habitat generalist	non-saproxyllic
<i>Trixagus dermestoides</i>	Trix_derm	Throscidae	habitat generalist	non-saproxyllic
<i>Trixagus lesegneuri</i>	Trix_lese	Throscidae	unknown	non-saproxyllic
<i>Trixagus meybohmi</i>	Trix_meyb	Throscidae	unknown	non-saproxyllic
<i>Trox scaber</i>	Trox_scab	Trogidae	habitat generalist	non-saproxyllic
<i>Nemozoma elongatum</i>	Nemo_elon	Trogositidae	forest species	saproxyllic

*De Jong, Y.S.D.M., 2013. Fauna Europaea version 2.6 [WWW Document]. <http://www.faunaeur.org>.

Appendix C

Table C1

Results of the structural equation model (Fig. 5).

	Used	Total
Number of observations per group		
Canopy	45	46
Understory	45	46

Indices of model fit

Estimator	ML	Robust
Minimum Function Test Statistic	1.149	1.469
Degrees of freedom	4	4
P-value (Chi-square)	0.886	0.832
Scaling correction factor for the Yuan-Bentler correction		0.782

Chi-square for each group:

Canopy	0.575	0.735
Understory	0.575	0.735

Parameter estimates:

Information	Observed
Standard Errors	Robust.huber.white

Group 1 [Canopy]:	Estimate	Std.err	Z-value	P(> z)	Std.lv	Std.all
Regressions:						
Deadwood vol~						
logdist	-0.058	0.205	-0.281	0.778	-0.058	-0.039
treediversity	14.459	4.178	3.460	0.001	14.459	0.465
Canopy openness~						
logdist	-0.149	0.146	-1.018	0.309	-0.149	-0.166
treediversity	1.016	2.695	0.377	0.706	1.016	0.054
Beetle SR~						
logdist	-0.122	0.129	-0.947	0.344	-0.122	-0.113
treediversity	8.747	2.904	3.012	0.003	8.747	0.386
Canopy openness	0.236	0.129	1.831	0.067	0.236	0.197
Deadwood vol	0.224	0.136	1.639	0.101	0.224	0.307
Intercepts:						
Deadwood vol	8.117	9.229	0.879	0.379	8.117	0.522
Canopy openness	51.894	8.239	6.299	0.000	51.894	5.493
Beetle SR	30.881	10.271	3.007	0.003	30.881	2.728
logdist	45.330	1.569	28.883	0.000	45.330	4.306
treediversity	0.489	0.075	6.561	0.000	0.489	0.978
Variances:						
treediversity	0.250	0.002	0.250	1.000		
logdist	110.843	16.363	110.843	1.000		
Deadwood vol	189.268	62.376	189.268	0.782		
Canopy openness	86.528	22.591	86.528	0.970		
Beetle SR	73.341	16.935	73.341	0.572		

Group 2 [Understory]:	Estimate	Std.err	Z-value	P(> z)	Std.lv	Std.all
Regressions:						
Deadwood vol~						
logdist	-0.058	0.205	-0.281	0.778	-0.058	-0.039
treediversity	14.459	4.178	3.460	0.001	14.459	0.465
Canopy openness~						
logdist	-0.149	0.146	-1.018	0.309	-0.149	-0.166
treediversity	1.016	2.695	0.377	0.706	1.016	0.054
Beetle SR~						
logdist	-0.455	0.166	-2.742	0.006	-0.455	-0.329
treediversity	8.638	3.461	2.496	0.013	8.638	0.290
Canopy openness	0.487	0.31	1.573	0.116	0.487	0.316
Deadwood vol	0.069	0.081	0.855	0.393	0.069	0.074
Intercepts:						
Deadwood vol	8.117	9.229	0.879	0.379	8.117	0.522
Canopy openness	51.894	8.239	6.299	0.000	51.894	5.493
Beetle SR	41.883	11.834	3.539	0.000	41.883	2.880
logdist	45.330	1.569	28.883	0.000	45.330	4.306
treediversity	0.489	0.075	6.561	0.000	0.489	0.978
Variances:						
treediversity	0.250	0.002	0.250	1.000		
logdist	110.843	16.363	110.843	1.000		
Deadwood vol	189.268	62.376	189.268	0.782		
Canopy openness	86.528	22.591	86.528	0.970		
Beetle SR	133.176	36.452	133.176	0.630		

R-Square Group 1 [Canopy]:

Deadwood vol	0.218
Canopy openness	0.030
Beetle SR	0.428

R-Square Group 2 [Understory]:

Deadwood vol	0.218
Canopy openness	0.030
Beetle SR	0.370

Appendix D

Additional structural equation model including tree diversity level and distance from forest edge as design variables, canopy openness, lying dead wood and standing dead wood separately, basal area oak (including *Quercus robur* and *Q. petraea*) and beetle species richness. Detailed modeling procedure was as described for the structural equation model Fig. 5

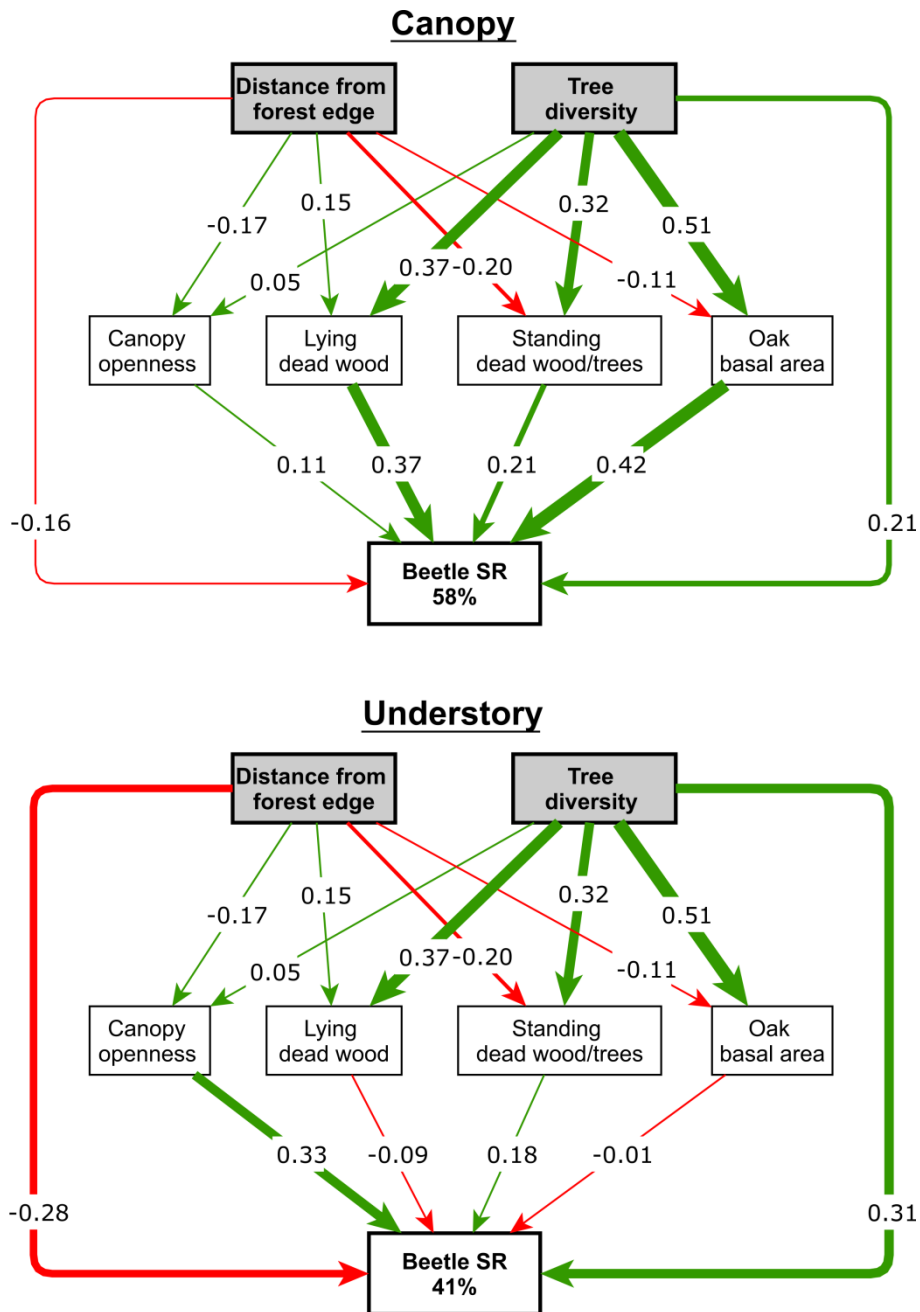


Figure D1

Structural equation model results showing pathways between distance from the forest edge, tree diversity, lying and standing dead wood, oak basal area and beetle species richness (Beetle SR) in a) the canopy and b) the understory ($\chi^2 = 11.811$; $P = 0.621$; $DF = 14$; $rmsea = 0.000$; $smr = 0.054$; $cfi = 1.000$). Numbers next to arrows are standardized coefficients. Green arrows indicate a positive (+) and red arrows a negative (-) relationship. Arrow width shows effect strength.

Table D1
Results of the additional structural equation model.

	Used	Total
Number of observations per group		
Canopy	45	46
Ground	45	46

Estimator	ML	Robust
Minimum Function Test		
Statistic	11.519	11.811
Degrees of freedom	14	14
P-value (Chi-square)	0.645	0.621
Scaling correction factor for the Yuan-Bentler correction		0.975

Chi-square for each group:

Canopy	5.760	5.906
Understory	5.760	5.906

Parameter estimates:

Information	Observed
Standard Errors	Robust.huber.white

Group 1 [Canopy]:	Estimate	Std.err	Z-value	P(> z)	Std.lv	Std.all
Regressions:						
lying deadwood	~					
logdist	0.148	0.188	0.789	0.43	0.148	0.149
treediversity	0.374	0.135	2.77	0.006	0.374	0.374
standing deadwood	~					
logdist	-0.198	0.103	-1.912	0.056	-0.198	-0.197
treediversity	0.317	0.143	2.219	0.026	0.317	0.316
basal area oak	~					
logdist	-0.11	0.139	-0.792	0.429	-0.11	-0.11
treediversity	0.506	0.131	3.851	0	0.506	0.505
canopy openness	~					
logdist	-0.166	0.163	-1.018	0.309	-0.166	-0.166
treediversity	0.054	0.143	0.377	0.706	0.054	0.054
beetle SR	~					
logdist	-0.16	0.079	-2.026	0.043	-0.16	-0.163
treediversity	0.206	0.107	1.936	0.053	0.206	0.21
canopy openness	0.11	0.07	1.574	0.116	0.11	0.113
lying deadwood	0.368	0.166	2.213	0.027	0.368	0.374
standing deadwood	-0.054	0.139	-0.389	0.697	-0.054	-0.055
basal area oak	0.406	0.129	3.149	0.002	0.406	0.415
Intercepts:						
lying deadwood	0	0.135	0	1	0	0
standing deadwood	0	0.137	0	1	0	0
basal area oak	0	0.126	0	1	0	0
canopy openness	0	0.145	0	1	0	0
beetle SR	0	0.093	0	1	0	0
logdist	0	0.147	0	1	0	0
treediversity	0	0.147	0	1	0	0
Variances:						
treediversity	0.978	0.006	0.978	1		
logdist	0.978	0.144	0.978	1		

lying deadwood	0.816	0.463	0.816	0.838
standing deadwood	0.845	0.417	0.845	0.861
basal area oak	0.719	0.284	0.719	0.733
canopy openness	0.949	0.248	0.949	0.97
beetle SR	0.391	0.07	0.391	0.416

Group 2 [Understory]:

	Estimate	Std.err	Z-value	P(> z)	Std.lv	Std.all
Regressions:						
lying deadwood	~					
logdist	0.148	0.188	0.789	0.43	0.148	0.149
treediversity	0.374	0.135	2.77	0.006	0.374	0.374
standing deadwood	~					
logdist	-0.198	0.103	-1.912	0.056	-0.198	-0.197
treediversity	0.317	0.143	2.219	0.026	0.317	0.316
basal area oak	~					
logdist	-0.11	0.139	-0.792	0.429	-0.11	-0.11
treediversity	0.506	0.131	3.851	0	0.506	0.505
canopy openness	~					
logdist	-0.166	0.163	-1.018	0.309	-0.166	-0.166
treediversity	0.054	0.143	0.377	0.706	0.054	0.054
beetle SR	~					
logdist	-0.281	0.119	-2.364	0.018	-0.281	-0.279
treediversity	0.314	0.149	2.102	0.036	0.314	0.312
canopy openness	0.331	0.199	1.667	0.095	0.331	0.329
lying deadwood	-0.094	0.093	-1.015	0.31	-0.094	-0.093
standing deadwood	0.184	0.12	1.535	0.125	0.184	0.183
basal area oak	-0.012	0.141	-0.087	0.931	-0.012	-0.012
Intercepts:						
lying deadwood	0	0.135	0	1	0	0
standing deadwood	0	0.137	0	1	0	0
basal area oak	0	0.126	0	1	0	0
canopy openness	0	0.145	0	1	0	0
beetle SR	0	0.114	0	1	0	0
logdist	0	0.147	0	1	0	0
treediversity	0	0.147	0	1	0	0
Variances:						
treediversity	0.978	0.006	0.978	1		
logdist	0.978	0.144	0.978	1		
lying deadwood	0.816	0.463	0.816	0.838		
standing deadwood	0.845	0.417	0.845	0.861		
basal area oak	0.719	0.284	0.719	0.733		
canopy openness	0.949	0.248	0.949	0.97		
beetle SR	0.588	0.155	0.588	0.593		

R-Square Group 1 [Canopy]:

lying deadwood	0.162
standing deadwood	0.139
basal area oak	0.267
canopy openness	0.03
beetle SR	0.584

R-Square Group 2 [Understory]:

lying deadwood	0.162
standing deadwood	0.139
basal area oak	0.267
canopy openness	0.03
beetle SR	0.407

SUMMARY

SUMMARY

Major threats to global biodiversity include the continuous increase of forest fragmentation and the associated augmentation of forest edge zones. How much edge effects penetrate into the forest interior can be influenced by habitat structure with tree species composition weakening or strengthening edge effects. Here, we address for the first time forest edge and tree diversity effects and their potential interactions on the understory vegetation and arthropods, focusing on the Hainich National Park, Germany's largest connected deciduous forest.

A total of 12 transects extending from the forest edge up to 500 m into the forest interior were established – six of them in forest stands dominated by beech with a low tree species diversity and six in forest stands rich in tree species, containing up to nine deciduous tree species e. g. oak, ash, lime and maple. Understory vegetation and arthropods were studied along each transect.

In the **first manuscript (chapter 2)** of this thesis we studied the understory vegetation along the edge-interior gradient.

The herb layer plant species richness was influenced by an interaction of tree diversity and edge effects. In the high tree diversity forest stands herb species richness was not affected by edge proximity, whereas in beech dominated forest stands it strongly declined with increasing distance from the forest edge. This resulted in higher plant species richness in the forest interior of the high tree diversity level. The fraction of forest specialist species increased, while the fraction of forest generalists decreased from the forest edge towards the forest interior. The dominance of forest specialists was much stronger in the low tree diversity level. Plant community composition differed with tree diversity level and edge proximity and it was more variable in the high tree diversity forest stands and closer to the edge. Tree diversity mediated leaf litter thickness, which was identified as the most important predictor of plant species richness.

The **second manuscript (chapter 3)** focuses on ground-dwelling arthropods (ground beetles, rove beetles and spiders) and the effect of body size and habitat specialisation on their response to tree diversity and forest edge proximity.

While no consistent pattern was found for total species richness, the tree diversity and edge response across all three taxa depended on habitat specialisation and body size. Neither tree diversity nor edge effects clearly affected the richness of forest species and body size was also not important. However, individual species suffered, whereas others were promoted by increased tree diversity. The species richness of habitat generalists strongly declined from the

forest edge towards the forest center in the low tree diversity level. This effect was mitigated in the high tree diversity level (except for spiders) and the species richness of habitat generalists, and among these the small species in particular, benefited from increased tree diversity. Individual habitat generalist species were generally positively affected. Changes in environmental conditions and habitat heterogeneity induced by tree diversity and edge proximity are most likely the reason for the observed patterns.

In the **third manuscript (chapter 4)** forest stratum as a third component was added to the study approach. We studied the forest in its full three-dimensionality by addressing edge and tree diversity effects on beetles across forest strata. Therefore, flight interception traps were installed both in the canopy and the understory along ten of the transects for a seven month period from April until November.

Edge effects influenced beetle species richness and community composition on a large spatial scale extending up to 500 m into the forest interior. However, edge effects were weaker in the canopy than in the understory - likely a result of higher, edge-like microclimatic variability and harshness in the canopy. Tree diversity did not influence edge effects. The edge response of total beetle species richness was driven by habitat generalists, which strongly declined with increasing distance from the forest edge, whereas saproxylic and forest species only responded weakly. Habitat generalists and non-saproxylic species dominated the forest understory. The richness of saproxylic and forest species peaked in the canopy. Tree diversity enhanced beetle diversity across all strata and forest specialisation groups. Structural equation modelling revealed that pathways driving beetle richness differed across strata. Tree diversity, dead wood amount and (partly) canopy openness were the most important drivers in the canopy, whereas canopy openness, edge proximity and to a lesser extent tree diversity were important in the understory. In conclusion, in the canopy tree diversity effects were stronger and more direct than in the understory.

Overall, we conclude that for a deeper understanding of forest fragmentation the relative importance of edge, stratum and tree diversity, but also species' life-history traits (e. g. body size) and habitat specialisation should be considered.

Increasing the abundance and diversity of deciduous tree species in Central European forests may help to preserve the regional species diversity of plants and arthropods. However, some forest species may rely on old-growth pure beech forests. These have received special attention in the UNESCO World Heritage sites "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany".

ZUSAMMENFASSUNG

Die fortschreitende Fragmentierung von Wäldern ist eine der Hauptursachen für den Verlust von Biodiversität weltweit. Mit zunehmender Fragmentierung steigt der Anteil an Waldrandzonen, in denen die Eigenschaften eines Waldes stark verändert sein können. Wie stark diese Randeffekte ein Fragment beeinflussen, kann von der Habitatstruktur abhängen. Die Habitatstruktur ist wiederum maßgeblich durch die Baumartenzusammensetzung beeinflusst.

Die vorliegende Arbeit untersucht zum ersten Mal gleichzeitig die Einflüsse von Randeffekten und Baumartenvielfalt und deren mögliche Interaktionen auf Krautschichtvegetation und Arthropoden.

Die Untersuchungen hierzu wurden im Nationalpark Hainich, Deutschlands größtem zusammenhängenden Laubwaldgebiet, durchgeführt. Dafür wurden 12 Transekte angelegt, die vom Waldrand bis zu 500 m in das Waldesinnere hineinreichten. Sechs Transekte in baumartenarmen Waldstandorten mit einem hohen Buchenanteil (*Fagus sylvatica* L.) und weitere sechs in baumartenreichen Waldstandorten mit einem niedrigen Buchenanteil. Baumartenreiche Standorte wiesen bis zu neun Baumarten auf, wie z.B. Eiche, Esche, Linde und Ahorn. Entlang der Transekte wurden die Krautschichtvegetation und die Arthropodengemeinschaften untersucht.

Im **ersten Manuskript (Kapitel 2)** dieser Arbeit) wurde die Krautschichtvegetation entlang des Rand-Innen-Gradienten aufgenommen.

Eine Interaktion zwischen Randeffekten und Baumartenvielfalt beeinflusste den Pflanzenartenreichtum. In Waldbereichen mit hoher Baumartenvielfalt blieb die Artenzahl der Krautschicht vom Rand bis ins Waldesinnere konstant, wohingegen sie in baumartenarmen Bereichen stark abfiel. Die Krautschicht war somit in baumartenreichen Waldstandorten im Waldesinneren höher. Der Anteil an Waldspezialistenarten nahm mit zunehmender Entfernung vom Waldrand zur Mitte zu. Parallel dazu nahm der Anteil an Waldgeneralistenarten ab. Die Dominanz der Waldspezialisten war in buchendominierten Standorten stärker ausgeprägt, als in baumartenreichen. Auch die Artenzusammensetzung der Krautschicht wurde von der Distanz zum Waldrand und der Baumartenvielfalt beeinflusst. Sie wies in baumartenreichen Standorten und mit zunehmender Nähe zum Rand eine hohe Variabilität auf. Die Baumartenvielfalt steuerte die Dicke der Streuschicht, die unter allen untersuchten Umweltfaktoren den größten Einfluss auf die Diversität der Krautschicht hatte.

Im **zweiten Manuskript (Kapitel 3)** dieser Arbeit) wurden bodenlebende Arthropoden (Laufkäfer, Kurzflügelkäfer und Spinnen) untersucht.

Die Reaktion der Gesamtartenzahl auf Baumartenvielfalt und Entfernung zum Waldrand war je nach Taxon unterschiedlich. Allerdings zeigten sich übereinstimmende Muster, nachdem die Arten hinsichtlich ihrer Habitataffinität und Körpergröße in Gruppen eingeteilt worden waren. Über alle Taxa hinweg wurde die Anzahl der Waldarten weder von der Baumartenvielfalt noch von der Randnähe nennenswert beeinflusst und die Körpergröße der Waldarten spielte keine Rolle. Allerdings reagierten einzelne Waldarten positiv auf eine erhöhte Baumartenvielfalt, während andere davon negativ beeinflusst waren. Die Artenzahl der Habitatgeneralisten nahm vom Waldrand zur Waldmitte hin stark ab. Dieser Effekt wurde jedoch, außer bei den Spinnen, durch eine höhere Baumartenvielfalt abgeschwächt. Die Artenzahl der Habitatgeneralisten, insbesondere der kleinen Arten, reagierte positiv auf eine erhöhte Baumartenvielfalt im Waldesinneren. Die beobachteten Effekte sind höchstwahrscheinlich das Resultat von durch Baumartenvielfalt und Randnähe veränderten Umweltfaktoren und einer erhöhten Habitatheterogenität am Waldboden.

Im **dritten Manuskript (Kapitel 4)** dieser Arbeit wurde untersucht, ob sich Rand- und Baumartendiversitätseffekte zwischen verschiedenen Straten unterscheiden. Hierzu wurden entlang von zehn Transekten sowohl im Kronenraum als auch unmittelbar über dem Boden Kreuzfensterfallen installiert. In einem Zeitraum von sieben Monaten (April bis November 2012) wurde dadurch die fliegende Käferfauna erfasst.

Randeffekte auf Käfer wurden bis zu einer Distanz von 500 m vom Waldrand hin nachgewiesen. Im Kronenraum waren die Randeffekte schwächer ausgeprägt als im Unterholz, vermutlich durch eine höhere „randähnliche“ mikroklimatische Variabilität im Kronenraum. Die Gesamtartenzahl der Käfer nahm mit zunehmender Distanz zum Waldrand ab. Dieses Muster wurde vor allem durch die Habitatgeneralisten getrieben, wohingegen die Artenzahl der Waldarten und der xylobionten Arten kaum auf die Randnähe reagierten. Eine Beeinflussung des Randeffekts durch Baumartenvielfalt konnte nicht gezeigt werden. Habitatgeneralisten und nicht-xylobionte Arten dominierten die Käfergemeinschaft im Unterholz. Im Kronenraum wurden die höchsten Artenzahlen von Waldarten und xylobionten Arten nachgewiesen. Baumartendiversität wirkte sich über alle Straten und ökologischen Gruppen positiv auf die Artenvielfalt der Käfer aus. Besonders ausgeprägt war dieser Effekt im Kronenraum. Die Haupteinflussfaktoren, die den Käferartenreichtum steuerten, unterschieden sich also zwischen den Straten. So waren im Kronenraum Baumartenvielfalt, die Totholzmenge und zu einem geringen Teil der Kronenschluss die entscheidenden Faktoren. Im Unterholz hingegen war der Einfluss der Baumartenvielfalt geringer und die

Distanz zum Waldrand und der Kronenschluss besonders wichtig. Insgesamt waren die Effekte von Baumartenvielfalt im Unterholz indirekter und im Kronenraum direkter.

Um Konsequenzen von Waldfragmentierung umfangreich zu verstehen, ist es nicht nur notwendig den Einfluss von Randeffekten, Baumartenvielfalt und Straten zu berücksichtigen, sondern auch die Eigenschaften (z. B. Körpergröße) und die Habitataffinität der beobachteten Arten.

Diese Arbeit zeigt, dass eine erhöhte Baumartenvielfalt in zentraleuropäischen Wäldern zum Erhalt der Biodiversität von Pflanzen und Arthropoden beitragen kann. Das allein ist jedoch nicht ausreichend, da auch gezeigt wurde, dass einzelne Arten buchendominierte Wälder bevorzugen und es Unterschiede in der Artenzusammensetzung zwischen den verschiedenen Baumartendiversitätsstufen gibt. Dies hebt die Bedeutung des Erhalts alter Buchenwälder, verankert in den UNESCO-Welterbeflächen „Buchenurwälder in den Karpaten und alte Buchenwälder in Deutschland“, als besondere Schutzaufgabe hervor.

ACKNOWLEDGEMENTS/DANKSAGUNG

Ich möchte mich bei folgenden Menschen bedanken, die mich unterstützt und zum Gelingen dieser Arbeit beigetragen haben. Ich danke...

...Teja Tschardt für die Bereitstellung des Themas, immer konstruktiven Gesprächen, klares Feedback und die gute Atmosphäre bei den Agrarökologen

...Christoph Scherber für die intensive Betreuung, erhellende statistische Momente, eine andere Sichtweise auf die Dinge und unterhaltsame Gespräche

...Prof. Stefan Vidal für die Übernahme des zweiten Gutachtens

...der Deutschen Forschungsgemeinschaft für das Stipendium innerhalb des Graduiertenkollegs 1086: „The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests“

...Manuela Armenat, Ann-Cathrin Fender und Lars Köhler für die Organisation des Graduiertenkollegs

...Verena Rösch für support auf allen Ebenen, sei es inhaltlich, sprachlich, kulinarisch oder gärtnerisch. Auch für ein stets offenes Ohr und musikalische Momente

...Hella Schlinkert, Urs Kormann, Iris Motzke und Ines Vollhardt, weil sie toll waren und weil ich immer mit meinen Fragen kommen durfte

...Pierre Gras für nervenaufreibende aber auch erhellende Gespräche

...Christine Venjakob, Maria Rosa Rossetti, Kristy Udy, Hannah Reininghaus, Erin Treanore für schöne und erholsame Mittagspausen

...Margaritha Hottmann für die gemeinsame Zeit im Hainich und den Unterschlupf

...allen anderen Agrarökos für die freundliche und kollegiale Atmosphäre, besonders Maraja Riechers, Stefanie Fronczek, Kristin Krewenka, Lydia Betz, Julia Tiede, Björn Klatt, Jochen

ACKNOWLEDGEMENTS

Fründ, Hagen Andert, Kevin Darras, Catrin Westphal, Péter Batary, Anika Hass und Alette Baillo

...Thomas Österreich und Siegfried Opolka für die administrative Hilfe

...den großartigen TA's Susanne Schiele, Ulrike Kierbaum, Susanne Jahn und Brigitte Jünemann für die praktische Hilfe und schöne Gespräche im Aufarbeitungsraum, besonders aber bei Susanne Jahn und Brigitte Jünemann deren Imker-Azubi ich sein durfte

...Jutta Gilles für ihre Herzlichkeit und verwaltungstechnische Unterstützung

...der Nationalparkverwaltung Hainich für die Zusammenarbeit, insbesondere bei Manfred Großmann, Andreas Henkel, Jens Wilhelm und Michael Hornschuh

...Andreas Weigel, Ronald Bellstedt, Frank Fritzlar für entomologische Unterstützung

...Anna, Ann-Kathrin, Elli, Bene, Marc, Christoph, Katrin, Anouk, Jakob und Luise – meinen Göttinger Wegbegleitern außerhalb der Uni

...meiner Familie, die immer hinter mir steht, an mich glaubt und mich immer unterstützt hat

...Matthias Bruckner für den Gegenpol in meinem Leben, liebevollen Bestand und viel, viel Geduld.

PUBLICATIONS

Journal articles

Normann C., Tschardtke T., Scherber C. (2016) How forest edge-center transitions in the herb layer interact with beech dominance versus tree diversity. *Journal of Plant Ecology*, First published online: January 19

Normann C., Tschardtke T., Scherber C. (*submitted*) Tree diversity and species' traits moderate forest edge responses of ground-dwelling beetles and spiders

Normann C., Tschardtke T., Scherber C. (2016) Interacting effects of forest stratum, edge and tree diversity on beetles. *Forest Ecology and Management*, **361**, 421-431.

Normann C., Scherber C., Tschardtke T. (2014) Wie beeinflussen Baumartenvielfalt und Randeffekte die Artenvielfalt von Krautschichtpflanzen und Laufkäfern in Wäldern? *Treffpunkt Biologische Vielfalt XIII - BfN-Skripten*, **370**, Bundesamt für Naturschutz, Bonn – Bad Godesberg.

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Conference contributions

Normann C., Tschardtke T., Scherber C. (2013) Does tree diversity change forest edge effects on plant and carabid beetle communities? Talk at the 43rd Annual Meeting of the Ecological Society of Germany, Austria & Switzerland (GfÖ), "Building bridges in ecology - linking systems, scales and disciplines", Universität Potsdam, 09.09-13.09.2013

Normann C., Tschardtke T., Scherber C. (2013) Baumartenvielfalt in Wäldern und Artenvielfalt von Krautschichtpflanzen und Insekten. Talk at the Interdisziplinäre

PUBLICATIONS

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PhD thesis: “Interacting effects of forest edge, tree diversity and forest stratum on the diversity of plants and arthropods in Germany’s largest deciduous forest”
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THESIS DECLARATION

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

I confirm that the chapters 2, 3 and 4 are a series of manuscript that have been published or will be submitted to peer-reviewed journals. I am the overall author of all manuscripts presented in this thesis. I have personally set up the study design, collected and analysed the data for all manuscripts, developed the main ideas presented in the manuscripts, written all manuscripts and created tables, figures and appendices. The co-authors gave advices and contributed to various parts of the studies such as analysis, discussions and writing. All co-authors contributed to finalising the manuscripts.

Declaration plagiarism

I declare that that I have written this doctoral thesis independently, that I have not used other sources or facilities other than the ones mentioned, that I have not used unauthorized assistance and that I have not submitted this thesis previously in any form for another degree at any university or institution.

Osnabrück, March 2016

(Claudia Normann)