



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



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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 understorey, 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 understorey, 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 saproxyllic species responded less strongly.

The richness of forest and saproxyllic beetles peaked in the canopy, whereas habitat generalists and non-saproxyllic beetles strongly dominated the understorey. 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 understorey.

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1. 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 and Kotze, 2012; Vodka and Cizek, 2013) up to more than 1 km as shown by Ewers and 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 and 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 and 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

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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 and 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 and 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. Saproxylid 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 and 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 saproxylid beetles only (Bouget et al., 2011; Gossner et al., 2013a,b). However, saproxylid 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.

2. Methods

2.1. 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 and 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.

2.2. Tree survey

Around each of the 41 plots we conducted a tree survey (tree relevé sized 20 × 40 m, longer side parallel to forest edge). Each tree (DBH ≥ 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.

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