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How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest?

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ABSTRACT

Habitat fragmentation is a major driver of species loss. Here we test the hypotheses that high tree diversity in a large deciduous forest enhances bird diversity and nest survival. We further expect that forest edges support higher bird diversity when different habitat types adjoin, whereas nest predation is not higher, because the large forest area mitigates potential edge effects. We studied how edge-centre differences and tree diversity (beech-dominated vs. tree-species rich) affect the bird community and survival rates of ground breeding birds' nests based on an artificial nest predation experiment in the Hainich National Park, Germany. We surveyed birds three times during the breeding season. We selected six forest stands with low tree diversity (i.e. dominated by beech) and six with high tree diversity (i.e. tree-species rich). Each forest stand contained four bird survey plots (plot 1: 0–30 m, plot 2: 60–90 m, plot 3: 120–150 m and plot 4: 180–210 m distant from edge; altogether 48 bird survey plots). Additionally each plot corner contained one artificial ground nest baited with one Blue-breasted Quail egg and one plasticine egg for eight days of exposure in the middle of the breeding season. Bird abundance and diversity were higher in the first 30 m of the forest. Bird diversity, including ground breeding birds, was also enhanced by higher percentages of bushes, which can provide enhanced food supply, perches as well as sheltering. Nest predation showed no edge effect, supporting the idea that small area of forest fragments causes more important negative effects than the edge in large forest remnants. Predation rates were higher in tree-species rich stands compared to beech-dominated stands, probably due to greater diversity and density of mammalian predators. Edge effects shaped the bird community composition and positively affected abundances of tree and shrub breeding birds, but did not affect ground breeders and the nest predation of ground nests. Shrub breeders accumulating in forest edges might, however, suffer more from nest predation in forest fragments. In conclusion, bird diversity and avian egg predation were affected by both forest edges and tree diversity in surprisingly different ways.

1. Introduction

As a consequence of habitat fragmentation, the global amount of habitat edges increases more and more. Road constructions, housing development, agricultural intensification and forest logging have been shown to lead to an elevated number of artificially created habitat edges (Fahrig, 2003). Edge effects occur at the border of two adjacent ecosystems interacting with each other (Murcia, 1995), and these effects are less pronounced in large fragments due to their smaller perimeter-area ratio (Helzer and Jelinski, 1999). The effects of edges can be due to (1) changing abiotic conditions such as radiation influx, temperature, wind and humidity, (2) direct biotic effects resulting in changed abundance and distribution of a species caused by the physiological tolerance of species, or (3) indirect biological effects such as predator–prey-interactions, parasitism or competition (Murcia, 1995).

Edges can have a positive effect on bird life because of increased abundance and species richness at forest edges (Johnston, 1947). However, higher nest predation risk and nest parasitism rates near forest edges have been shown to influence bird reproductive success (Robinson et al., 1995), with a strong negative effect on bird population densities (Fretwell, 1972). According to this, Gates and Gysel (1978) suggested that edges function as "ecological traps" for nesting birds. After their initial study, nest predation in relation to edge effect was studied all over the world in different habitat types. Results of edge effects on nest predation at forest sites have been variable so far. In a meta-analysis, however, Batáry and Báldi (2004) showed that there is a generally higher nest predation rate in habitat edges compared to habitat interiors. So

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far, there has been no consensus on the question of how far an edge effect can penetrate into a habitat patch (e.g. >200 m Wilcove et al., 1986; <150 m in Laurence, 2000). Most studies found an edge effect penetrating not farther than 150 m into the habitat, presumably about 50 m from the edge (Batáry and Báldi, 2004), but Keyser et al. (1998) found edge effects only in small, not large forests.

The number of tree species in a forest may have additional effects on nest survival of ground breeding birds as well as on bird diversity (Salek et al., 2010). Generally, there should be a positive relationship between habitat heterogeneity, such as by increased tree diversity, and the diversity of associated species such as birds (Balaz and Balazova, 2012). The assumption is that heterogeneous environments provide a greater number of habitat niches and environmental resources leading to increased species diversity (Vivian-Smith, 1997). In forests dominated by one species, such as beech (*Fagus sylvatica*), undergrowth vegetation is less species-rich than in mixed stands (for herb layer from the same study area see Vockenhuber et al., 2011).

Artificial nests are a common tool to study edge effects on nest predation (see e.g. Svobodová et al., 2012), although their reliability has been long debated (Wilson et al., 1998). Parental nest protection as well as conspicuous behaviour, e.g. parent birds leaving the nest, may modify nest predation (Berg, 1996), or even determine nest site selection (Tryjanowski et al., 2000). Since parent birds are not present at artificial nests, artificial nests may not correctly estimate true predation rates (Major and Kendal, 1996). However, for comparative purposes (e.g. comparing different habitats or time periods), artificial nests are a timesaving, non-invasive method that can represent trends in the nest predation rates (Batáry and Báldi, 2005).

In the present study we analysed how forest edges and tree diversity affect (i) the bird communities and (ii) survival rates of ground breeding birds' nests based on an artificial nest predation experiment. Data collection took place in the largest, connected deciduous non-managed forest in Germany (Vockenhuber et al., 2011), so that the forest centre should be minimally affected by the edge. We tested the following main hypotheses: (1) Edge effects: predation rates in artificial ground nests are higher at forest edges than in forest interiors. Further, both species richness and abundance will be higher at forest edges than in forest interiors, because of higher microhabitat heterogeneity and availability of nesting sites and food resources. (2) Effects of tree diversity: bird species richness and abundance are higher in tree-species rich forest stands due to the availability of more niches and food resources than in the beech-dominated stands. In addition, we expected higher predation rates on artificial ground nests in species-rich forest stands due to higher predator diversity. (3) Interactions between edge effects and tree diversity: edge effects on nest predation and bird abundance will be more pronounced in forest stands with low tree diversity (hereafter termed "beech-dominated" stands), where the contrast between the more heterogeneous forest edge and the more uniform forest interior is greater than at forest stands with high tree diversity (hereafter called "species rich" stands). (4) Finally, examining three major breeding types (tree breeders, shrub breeders and ground breeders), we expected the strongest edge and tree diversity effects on the abundance of shrub breeders due to their special nesting site requirements.

2. Methods

2.1. Study area and sampling design

The study was conducted in the Hainich National Park in the federal state of Thuringia, Germany. With a size of about 16.000 hectares, the Hainich is the largest continuous deciduous forest area in Germany (Sobek et al., 2009; Vockenhuber et al., 2011). The National Park (covering 7.500 ha) is located on a mountain range of shell limestone reaching a maximum elevation of 494 m a.s.l. (mean annual temperature: 7.5 °C, mean annual rainfall: 640 mm; Mölder et al., 2006). Although the forests of the Hainich had been used to extract timber over centuries, the stands remained semi-natural compared with other German forests, and forest management has been stopped at least 50y ago.

Before mid-19th century the forest stands had been irregularly used as coppice-with-standards for many years. Later on, management was changed to a multiple aged forest system called "Plenter forest" (Schmidt et al., 2009). Plenter forests are high forests that are permanently regenerated by selective cutting of mature trees. In 1964, the study site became a military training area, which enabled the development of a large area of near-natural forests. Finally, in 1997, the area was turned into a National Park, and recently became part of the UNESCO world natural heritage (Mölder et al., 2006). Today almost 90% of the total area of the National Park is not managed at all, only a few marginal areas are still used as a pasture.

The most abundant tree species in the area is the common beech (*F. sylvatica*); however, in given stands tree diversity is high with numerous deciduous tree species such as ash (*Fraxinus spp.*), lime (*Tilia spp.*) and maple (*Acer spp.*; Knohl et al., 2008). Around 70% of the area is covered by woodruff beech forest (*Galio odorati-Fagetum*).

Within the Hainich National Park, we selected twelve study forest stands for data collection. Six stands were dominated by beech (mean beech dominance: 81.4%, mean tree species richness: 3.1) and the other six stands contained more tree species (mean beech dominance: 25.1%, mean tree species richness: 6.4). All stands were distributed homogenously along the northern, eastern and southern borders of the National Park, which is surrounded by arable land or grassland. The distance between forest stands was at least one kilometre to ensure independence of replicates (see Appendix A.1in Supporting information).

At each stand, a transect was laid out starting at the forest edge with a total length of 210 m. The length of transects was limited to this distance in order to meet the criteria that each transect should be situated in a forest part that has similar tree diversity. Forest edges consisted of dense shrubs and saplings such as blackthorn (*Prunus spinosa*) and common ash (*Fraxinus excelsior*) reaching a width of around 5 m. Each forest stand contained four bird survey plots (plot 1: 0–30 m; plot 2: 60–90 m; plot 3: 120–150 m; plot 4: 180–210 m) with a plot size of 30 × 60 m (width × length) (Fig. A.1 in Supporting information). This plot design was chosen to ensure a sufficient number of non-overlapping counting points within stands.

2.2. Bird survey

Birds were surveyed using a point-counting method with three bird survey rounds covering the whole breeding season: end of April, end of May and middle of June. Surveys started at sunrise within 4 h, restricted to good weather conditions (no rain or storm). For each plot, sampling took 5 min in which all birds were registered via listening and sighting while standing still in the middle of each plot. Sampling was limited to 5 min, which was enough time to register even inconspicuous bird species, but not too long to risk double counting. We took special attention not to count the same bird individual more than once. Birds flying through were not counted. For later analyses, bird species were classified according to their nesting site as tree-, shrub- and ground breeders (Table A.1 in Supporting information; Bezzel, 1993). Within one day we surveyed four forest stands. The order in which the forest