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The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest

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ABSTRACT

Spatial distribution of arthropods in woodlands has crucial implications for biodiversity conservation and forest management. However, its determinants are insufficiently known. In particular, studies on arthropod vertical distribution in temperate woodlands report contrasting patterns that are difficult to explain in the current theoretical framework. Using flight intercept traps, we investigated vertical and horizontal distribution and diversity of saproxylic beetles in the understorey and the upper canopy at the edge and in the interior of a temperate, closed-canopy, deciduous forest in South-Eastern Czech Republic. At the forest edge, number of species was >60% higher than in the interior. Preference for forest edge were better pronounced in the understorey than in the canopy. Although number of species did not differed between the forest strata, vertical distribution of individual species as well as the whole assemblages differed between edge and interior. In the forest interior, most (~80%) species exhibited higher preference for the canopy than at its edge. Multivariate analysis indicated that beetle distribution was affected by variables related to habitat openness and light availability. The results suggest that: (i) Vertical stratification of arthropod assemblages and individual species is context-dependent and variable even within a single forest patch. (ii) Vertical and horizontal distribution of arthropods is driven mainly by sunlight availability and habitat openness. (iii) In the closed canopy forest, the horizontal edge-interior gradient affects distribution of saproxylic beetles more than the vertical understorey-canopy gradient.

1. Introduction

Insects associated with the wood of live and dead trees (i.e. saproxylic insects) play an important role in forest ecosystems. They affect nutrient cycling, forest structure and dynamics, and constitute a significant portion of forest biodiversity (Edmonds and Eglitis, 1989; Barker, 2008; Müller et al., 2008a; Cobb et al., 2010). Thus, their spatial distribution has crucial implications for the conservation of forest biodiversity and its management. Despite several decades of investigation, determinants of saproxylic insect distribution in forests remain only partly known, especially for temperate forests (Stork et al., 1997, 2001; Basset et al., 2003; Floren and Schmidl, 2008; Bouget et al., 2011). Spatial distribution of saproxylic arthropods has mostly been studied in relation to the amount of available breeding substrate, overall amount of dead wood, vertical forest strata, insolation and habitat openness, forest management intensity, habitat spatial and temporal continuity. Many studies report a direct and close positive relationship between local dead wood volume and saproxylic fauna (Müller et al., 2008b; Martikainen et al., 2000). Other studies, however, have revealed the relationship is more complex, suggesting that type, continuity, placement and overall rather than local supply matter to saproxylic invertebrates (Franc et al., 2007; Wermelinger et al., 2007; Davies et al., 2008; Sverdrup-Thygeson and Birkemoe, 2009; Vodka et al., 2009; Lassauce et al., 2011).

Insect vertical stratification seems to exhibit relatively consistent patterns in humid tropical forests, where the upper layers usually host more diverse assemblages of many taxa and functional groups than those near the forest floor (Hammond et al., 1997; Stork et al., 2008). In temperate woodlands, the observed patterns are often contrasting (Su and Woods, 2001; Wermelinger et al., 2007; Ulyshen and Hanula, 2007; Hirao et al., 2009; Schroeder et al., 2009; Gossner, 2009; Vodka et al., 2009; Bouget et al., 2011). This suggests that vertical stratification of insect assemblages is highly variable and context dependent in temperate woodlands. The type and character of the studied forest, its tree species composition, age and spatial structure, openness, type of management and other factors affect not only the presence or absence of insect species, but also their vertical distribution (Su and Woods, 2001; Ulyshen, 2011; Birtele and Hardersen, 2012).

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Sunlight availability seems to be one of the key factors affecting distribution of saproxylic and other insects in temperate forests (Bílý, 2002; Kappes and Topp, 2004; Wermelinger et al., 2007; Buse et al., 2008; Russo et al., 2011; Horak and Rebl, 2012). Insolation is likely to affect also vertical and horizontal distribution of insects in temperate forests, as sunlight is unevenly distributed between vertical forest strata, between edge and interior, and along canopy-closure gradient (e.g. Gossner, 2009). Many studies on vertical stratification of insects in temperate forests, however, do not consider potentially relevant environmental variables (cf. Bouget et al., 2011). It is thus difficult to interpret and compare findings of different studies and identify factors underlying the observed patterns.

In order to contribute to the understanding of factors affecting distribution of insects in forests, we sampled saproxylic beetles using flight intercept traps in canopy and understorey layers of edge and interior of a lowland, closed-canopy, oak forest in Central Europe. Composition of saproxylic beetle assemblages was then related to forest structure and architecture, volume of available dead wood, and sunlight intensity. The following specific hypotheses were tested to investigate habitat and stratum dependent patterns of saproxylic beetles distribution: (i) Vertical distribution of individual species does not differ between the forest edge and the interior. (ii and iii) Individual species are evenly distributed between vertical strata at the forest edge and in its interior. (iv) Horizontal (edge-interior) distribution of individual species does not differ between the canopy and the understorey layers. (v and vi) Individual species are evenly distributed between the edge and the interior in the canopy and the understorey forest layers.

2. Methods

2.1. Study area and focal group

The study was conducted in alluvial woodlands of Southern Moravia, Czech Republic (alt. 160–170 m, 16°45′–16°55′E, 48°45′–48°50′N), in a floodplain of the lower Dyje (Thaya) river within a landscape of managed hardwood forests and meadows with old solitary trees. The terrain is flat, the prevailing trees are pedunculate oak (*Quercus robur*), narrowleaf ash (*Fraxinus angustifolia*), hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), limes (*Tilia cordata, T. platyphyllos*), European white elm (*Ulmus laevis*), poplars (*Populusalba , P. nigra*), and black alder (*Alnus glutinosa*). Historically, the forests were managed as coppice with standards or pasture woodland. These practices were abandoned 60–150 years ago in favour of growing high forest (i.e. forest raised wholly or mainly from seed) with 90–150 year rotation (Vrška et al., 2006). The forests are mainly even-aged oak, ash and poplar plantations, with occasional remnants of coppice with standards and pasture woodlands. The entire area is rich in saproxylic organisms, forming their hot spot within the Czech Republic and Central Europe (Rozkosny and Vanhara 1995–1996). The traps were exposed in a mature, closed-canopy forest that could be characterised as high forest, formerly managed as coppice with standards. The coppicing was abandoned >60 years ago, and through thinning the stands were gradually transformed into a high forest. The standards were already gone from the sampled patches, but the forest was prior its first clear-cut harvest. It thus retained continuity, high tree species richness and also structural diversity.

Beetles (Coleoptera) associated with dead wood (=saproxylic and xylophagous beetles) were used as model group in order to avoid contamination of the dataset by species not associated with woodland habitats and/or lacking resources in either of the sampled situations (*see below*). All beetle individuals in samples were sorted, and identified to families; saproxylic groups were identified to species level. Species identity was revised by experienced specialists except for Dasytes sp. (Dasytidae), and some Mordella and Mordellistena (Mordellidae) assigned only to morphospecies. Staphylinidae were omitted from the dataset due to difficulties with their identification. This is a common approach, unlikely to affect our results (Sebek et al., 2012).

2.2. Sampling design

Beetles were collected with flight intercept traps with crossed transparent polycarbonate sheets sized 25×50 cm (width $\times$ height) and saturated salt solution and detergent as conservation liquid. The traps were exposed in the canopy and understorey of the forest edge and interior. Four positions were thus sampled: (i) interior-canopy, (ii) interior-understorey, (iii) edge-canopy, and (iv) edge-understorey. The canopy traps were suspended in the upper tree layer, 14–26 m (mean 20.3) aboveground. The understorey traps were suspended 1–2.5 m aboveground. The understorey traps were hung as close as possible below their corresponding canopy traps. The interior traps were located 36–88 m (mean 56.6 m) from the respective forest edge. The four traps exposed at a sampling site were located within as homogenous a forest patch as possible. There were a total of eight trapping sites, located 1–8 km apart. Each of the four positions was sampled by one trap at each site. We thus had eight replicates for each position, with 32 traps in total. The traps were active from 30th April to 2th September 2006. Samples were collected every 2 weeks. The sampling period has been selected to maximise effectivity of the sampling, and covers main period of saproxylic beetle activity in the area. By not sampling during April and September, we have probably missed ca 13% of individuals and ca 7% of species (*unpublished data*).

2.3. Explanatory variables

The effect of the following variables on sample composition was considered:

Canopy openness – tree crowns' relative cover (%) above trap as recorded by a fish-eye objective (16 mm focal length) and analysed in software GapLightAnalyzer (Frazer et al., 1999).
Evaporation – measured as water evaporated from a 20 cm long water-filled tube (0.5 cm diameter) vertically attached to each trap (in centimetres). Height of the water level was measured twice in July and August, during two-week intervals, and data per trap were summed together.
Height – height of individual trap above ground (in metres).
InteriorDepth – distance of individual trap to the nearest forest edge (in metres).
Dead wood volume (DWV) – it was estimated as the amount of all dead wood (in m^3 per 1 ha) surrounding a trap and situated in conditions corresponding to the exposure conditions of a trap. For the interior, DWV within a circle of 50 m diameter with a trap in its centre was considered. Forest edge is a linear habitat, DWV within a rectangle of 10×50 m, situated along the forest edge with a trap in its centre. For canopy samples, we considered dead wood situated in the section of canopy from 5 m below the trap to the tree tops; and for understorey, we considered dead wood up to 5 m above the ground within the above-defined sections of the forest. The data were standardised per area unit and square root-transformed.
Total dead wood volume – estimated as the *Dead wood volume*, but all dead wood from ground to upper canopy was considered. The data were standardised per area unit and square root-transformed.