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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.

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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 (Populus alba, 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 × 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.

MaxDBH – highest diameter (in breast height) of tree-trunk found within a circle of 20 m diameter around each trap (in metres).

SumDBH – sum of diameters of all live trees with DBH > 10 cm found within a circle of 20 m diameter around each trap (in metres).

TrapDBH – trunk diameter (in breast height) of the tree where a trap was hung (in metres).

TreeNumber – number of trees with DBH > 10 cm within a circle of 20 m diameter around each trap.

Forestedge20, ForestEdge50 and *ForestEdge100* – length of forest edge (i.e. border between wooded and non-wooded habitats) within circles of 20, 50 and 100 m diameter with traps in their centres. Measured using aerial photographs taken by Geodis Brno in 2006. It serves as measure of forest/non-forest mosaic grain size as well as measure of distance between a trap and nearest forest edge (in metres).

2.4. Analyses

To compare diversity among the four sampled situations, species accumulation curves with confidence intervals were computed using sample-based rarefaction (Mao Tau function) using EstimateS 8.00 software (Colwell, 2006).

The relations among samples were investigated using principal component analysis (PCA). To test for a relationship between sample composition and environmental variables, we used redundancy analysis (RDA), a linear constrained ordination method that relates the species composition of samples to external predictors. We performed five separate RDA analyses: (i) In order to identify variables affecting sample composition, forward selection was applied to all environmental variables and the full dataset (all situations). (ii and iii) RDA with *Height* acting as the explanatory variable was applied to the forest edge dataset (situations edge-canopy and edge-understorey) and to the forest interior dataset (situations interior-canopy and interior-understorey), in order to compare effect of *Height* on assemblages of respective habitat. (iv and v) RDA with the *InteriorDepth* as the explanatory variable was applied to the canopy dataset (situations canopy-edge and canopy-interior) and the understorey dataset (situations understorey-edge and understorey-interior), in order to compare its effect on assemblages of both vertical strata. Ordination analyses were carried out with CANOCO v. 4.51 (ter Braak and Smilauer, 2002), traps represented samples characterised by captures of beetle species, position and surrounding-forest characteristics. Scaling was focused on inter-sample distances; species scores were divided by standard deviations, species counts were log-transformed and centred, samples were neither centred nor standardised. All species with $N > 5$ in the respective dataset were included in analyses.

The following hypotheses were tested: (i) Vertical distribution of individual species does not differ between the forest edge and the interior. (ii) At the forest edge, individual species are evenly distributed between vertical strata. (iii) In the forest interior, individual species are evenly distributed between vertical strata. (iv) Horizontal (edge-interior) distribution of individual species does not differ between the canopy and the understorey layers. (v) In the canopy, individual species are evenly distributed between the edge and the interior. (vi) In the understorey, individual species are evenly distributed between the edge and the interior. The hypotheses (i and iv) were tested using paired *t*-test. (i) Relative abundances of individual species in the canopy of forest edge ($N_{edge-canopy}/N_{edge}$) were compared to their relative abundances in the canopy of interior ($N_{interior-canopy}/N_{interior}$). (iv) Relative abundances of individual species at the edge of the canopy layer ($N_{edge-canopy}/N_{canopy}$) were compared to their relative abundance at the edge of the understorey layer ($N_{edge-understorey}/N_{understorey}$).

The hypotheses (ii, iii, v, vi) were tested using one sample *t*-test comparing relative canopy abundance (ii) at the forest edge, (iii) in the interior, and relative edge abundance in (v) the canopy and the (vi) understorey to hypothetical mean 0.5. The hypothetical mean value 0.5 is expected if species are equally distributed between two positions. All 29 species common ($N > 5$) in both the forest edge and the interior assemblages (i.e. $N_{edge} > 5$ and $N_{interior} > 5$) were used to test hypotheses (i–iii), and all 36 species common ($N > 5$) in both the canopy and the understorey assemblages (i.e. $N_{edge} > 5$ and $N_{interior} > 5$) were used to test the hypotheses (iv–vi). The relative abundance was selected to compare distribution patterns, since it is rather independent of sample size. Values of other measures such as species score (ter Braak and Smilauer, 2002) or species indicator value (Dufrene and Legendre, 1997) do increase with the number of individuals, and would thus reflect also changes in a species abundance among sampled positions.

3. Results

In total, we caught 4739 individuals of 289 species of saproxylic beetles (see Appendix for list of collected species and their abundances). The diversity was at least 50% higher at the forest edge than in the interior, regardless of vertical strata. More species were found in the understorey than in the canopy of the edge, whereas the pattern was the opposite in the forest interior; the differences in diversity between the two strata were not significant, however (Fig. 1, Table 1). There were 29 species (representing 3112 individ-
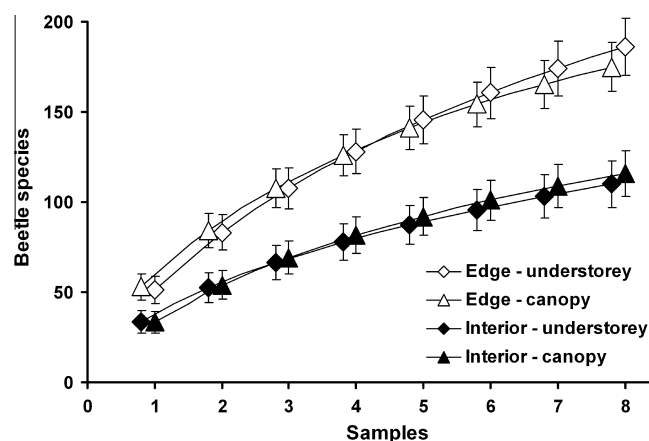
Fig. 1. Diversity (Mao Tau rarefaction, with 95% CI) of saproxylic beetles sampled by flight intercept traps in the canopy and the understorey of the edge and the interior of a deciduous, closed-canopy forest in the SE Czech Republic. Beetle diversity at the forest edge was substantially higher than in the interior, irrespective of vertical forest strata. At the edge, more species were collected in the understorey, whereas the pattern was the opposite in the interior.

Table 1
Number of individuals, species, unique species and singletons of saproxylic beetles sampled by flight intercept traps in a deciduous, closed-canopy forest in the SE Czech Republic.

	Individuals	Species	Uniques	Singletons
CanopyEdge	1667	175	52	31
CanopyInterior	1002	116	12	7
UnderstoreyEdge	1481	186	49	35
UnderstoreyInterior	589	110	15	13
Edge	3148	256	130	66
Interior	1591	159	33	20
Understorey	2070	216	78	48
Canopy	2669	211	73	38
Total	4739	289	–	86

Table 2

Distribution of saproxylic beetles sampled by flight intercept traps in a closed-canopy, deciduous forest in the SE Czech Republic. For the 29 species common at the forest edge and in the interior ($N_{edge} > 5$ and $N_{interior} > 5$), total abundance in sampled positions and relative abundance in the canopy of the forest edge ($N_{canopy-edge}/N_{edge}$) and the interior ($N_{canopy-interior}/N_{edge}$) are given. For the 36 species common in both the canopy and the understorey ($N_{canopy} > 5$ and $N_{underst.} > 5$), total abundance in sampled positions and relative abundance et the forest edge in the canopy ($N_{edge-canopy}/N_{canopy}$) and understorey ($N_{edge-underst.}/N_{underst.}$) layers are given.

Species (Family)	% of individuals in canopy of interior	% of individuals in canopy of edge[a]	% of individuals at edge of canopy	% of individuals at edge of understorey[a]	Abundance total (a, b, c, d)[b]
Agrilus convexicollis (Buprestidae)	91.7	88.9			21 (11, 8, 1, 1)
Ampedus pomorum (Elateridae)			70.0	100.0	21 (3, 7, 0, 11)
Anaspis flava (Mordellidae)	71.4	17.6	37.5	87.5	48 (10, 6, 4, 28)
Anaspis frontalis (Mordellidae)	59.0	32.7	70.5	87.6	324 (36, 86, 25, 177)
Arthrolips nana (Corylophidae)	100.0	80.0			23 (8, 12, 0, 3)
Arthrolips obscura (Corylophidae)	100.0	90.0			17 (7, 9, 0, 1)
Atomaria atricapilla (Cryptophagidae)	33.3	18.2	33.3	52.9	23 (4, 2, 8, 9)
Atomaria linearis (Cryptophagidae)	50.0	63.3	88.6	81.8	57 (4, 31, 4, 18)
Corticaria bella (Lathridiidae)	91.3	82.4			40 (21, 14, 2, 3)
Corticarina minuta (Lathridiidae)			100.0	83.3	20 (0, 14, 1, 5)
Corticarina similata (Lathridiidae)	70.6	66.7	25.0	28.6	23 (12, 4, 5, 2)
Cortinicara gibbosa (Lathridiidae)	74.6	66.2	68.6	76.6	803 (173, 378, 59, 193)
Curculio glandium (Curculionidae)			14.3	0.0	24 (12, 2, 10, 0)
Dromius quadrimaculatus (Carabidae)	68.8	66.7	35.3	37.5	25 (11, 6, 5, 3)
Enicmus rugosus (Lathridiidae)	67.7	67.7	67.7	67.7	96 (21, 44, 10, 21)
Enicmus transversus (Lathridiidae)	7.1	50.0	88.9	38.1	30 (1, 8, 13, 8)
Ephistemus reitteri (Cryptophagidae)			100.0	100.0	12 (0, 6, 0, 6)
Ernoporicus caucasicus (Curculionidae)			66.7	75.0	17 (3, 6, 2, 6)
Ernoporus tiliae (Curculionidae)	57.1	19.0	50.0	85.0	56 (8, 8, 6, 34)
Gastrallus laevigatus (Anobiidae)	94.1	91.7			29 (16, 11, 1, 1)
Glischrochilus quadrisignatus (Nitidulidae)	4.8	26.5	90.0	55.6	55 (1, 9, 20, 25)
Hemicoelus rufipennis (Anobiidae)			1.4	21.4	83 (68, 1, 11, 3)
Hemicrepidus hirtus (Elateridae)			77.8	85.7	16 (2, 7, 1, 6)
Hylesinus toranio (Curculionidae)	86.4	88.2	89.6	88.0	208 (19, 164, 3, 22)
Magdalis armigera (Curculionidae)			90.0	100.0	20 (1, 9, 0, 10)
Megatoma undata (Dermestidae)	66.7	64.7	73.3	75.0	23 (4, 11, 2, 6)
Melanophthalma parvicollis (Lathridiidae)	82.6	49.3	49.6	82.8	808 (252, 248, 53, 255)
Melanotus villosus (Elateridae)	44.4	33.3	33.3	44.4	15 (4, 2, 5, 4)
Microrhagus lepidus (Eucnemidae)	50.0	0.0			26 (3, 0, 3, 20)
Mordellistena neuwaldeggiana (Mordellidae)	70.0	23.5	36.4	81.3	27 (7, 4, 3, 13)
Mordellistena variegata (Mordellidae)	18.2	42.0	77.8	51.8	83 (6, 21, 27, 29)
Mordellochroa abdominalis (Mordellidae)	45.5	5.0	28.6	86.4	51 (5, 2, 6, 38)
Mycetochara maura (Tenebrionidae)	86.7	2.4	3.7	90.9	71 (26, 1, 4, 40)
Nemozoma elongatum (Trogositidae)			20.0	20.0	20 (8, 2, 8, 2)
Oligomerus retowskii (Anobiidae)	100.0	75.0			20 (8, 9, 0, 3)
Orthoperus brunnipes (Corylophidae)	50.0	6.7	7.7	53.8	78 (24, 2, 24, 28)
Ptinomorphus imperialis (Anobiidae)			16.7	6.7	33 (15, 3, 14, 1)
Rhyncolus punctatulus (Curculionidae)			33.3	100.0	12 (4, 2, 0, 6)
Sericoderus lateralis (Corylophidae)			88.9	83.3	21 (1, 8, 2, 10)
Symbiotes gibberosus (Endomychidae)	83.3	38.5	50.0	88.9	19 (5, 5, 1, 8)
Tomoxia bucephala (Mordellidae)			92.6	97.1	89 (4, 50, 1, 34)
Xyleborinus saxeseni (Curculionidae)	16.7	71.4	83.3	28.6	13 (1, 5, 5, 2)
Xyleborus monographus (Curculionidae)			93.1	66.7	35 (2, 27, 2, 4)

[a] Missing values indicate abundance bellow threshold.

[b] Abundance in a – interior-canopy, b – edge-canopy, c – interior-understorey, d – edge-understorey.

uals) common (N > 5) at the edge as well as in the interior, while 36 species (representing 3359 individuals) were common in the canopy as well as in the understorey (Table 2).

In the PCA diagram of individual samples based on their species abundance and composition, the samples from the same positions were closer than those from different microhabitats within the same sampling site. Trap position thus affected composition of samples more than sampling site, despite the 1–8 km distance among the sites. This illustrates the high effect of sampled positions and rather similar environmental conditions among sampling sites. The first axis separated the forest-edge samples from the interior samples; and within the interior, it also separated the canopy samples from the understorey samples. The second axis separated the understorey-edge samples from the canopy-edge samples. The first axis explained 19.4% of variance in species data, the second axis explained 10.4% of variance (sum of all canonical eigenvalues was 0.658) (Fig. 2).

In the RDA of the full dataset, the forward selection procedure returned *InteriorDepth*, *Height*, *Evaporation* and *MaxDBH* as variables explaining the highest amount of variance in the species data. After their inclusion to the model, other variables had no effect.

In the RDA of the full dataset with the four above explanatory variables (the first axis: eigenvalue = 0.151, $F = 4.8$, $p < 0.001$; the second axis: eigenvalue = 0.069), the *InteriorDepth* explained 13.4%, *Height* 8.3%, *Evaporation* 9.4% and *MaxDBH* 4.2% of variance not explicable by other variables in the model.

3.1. Vertical stratification at the edge and in the interior

In the RDA of the interior assemblage, the first axis (i.e. *Height*) explained 18.1% of variability in species data (eigenvalue = 0.181, $F = 3.1$, $p < 0.005$) (Fig. 3A). In the identical RDA of the edge assemblage with the *Height* as the explanatory variable, the first axis (identical with the *Height*) explained 15.1% of variability in species data (eigenvalue = 0.151, $F = 2.49$, $p < 0.005$) (Fig. 3B).

29 Species were common (N > 5) at the forest edge and in the interior (see Table 2). Their vertical distribution differed between
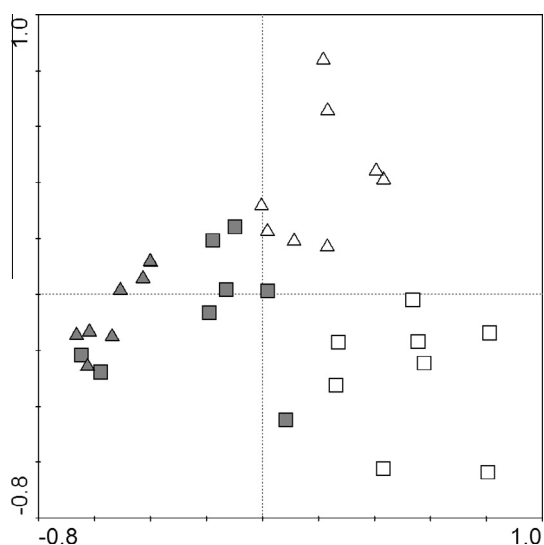
Fig. 2. PCA ordination biplot of saproxylic beetle assemblages sampled by flight intercept traps in the canopy (squares) and the understorey (triangles) of the edge (empty) and the interior (grey) of a deciduous, closed-canopy forest in SE Czech Republic. The first (horizontal) axis explained 19.7% of variance and separated the forest-edge samples from the interior samples; and within the interior, it also separated the canopy samples from the understorey samples. The second (vertical) axis explained 10.9% of variance in species data and separated the understorey-edge samples from the canopy-edge samples.

the two habitats (Edge: Mean = 49.22, SD = 29.61, N = 29. Interior: Mean = 63.52, SD = 27.86, N = 29. Paired t-test: t = 2.56, df = 28, p < 0.05). In the interior, distribution of individual species differed from the hypothetical mean and inclined towards the canopy (One sample t-test: hypothetical/actual mean = 50/63.52, t = 2.61,

df = 28, p < 0.05), whereas the individuals were equally distributed at the forest edge (one sample t-test: hypothetical/actual mean = 50/49.22, t = 0.14, df = 28, p = 0.9) (Fig. 5).

*3.2. Effect of the edge-interior gradient in the canopy and in the understorey*

In the RDA of the canopy assemblage with the *InteriorDepth* as the explanatory variable, the first axis (identical with the *Interior-Depth*) explained 20.5% of variability in the species data (eigen-value = 0.205, F = 3.62, p < 0.0001) (Fig. 4A). In the RDA of the understorey assemblage, the first axis (i.e. *InteriorDepth*) explained 25.9% of variability in the species data (eigenvalue = 0.259, F = 4.89, p < 0.0001) (Fig. 4B).

36 Species were common (N > 5) in both the canopy and the understorey assemblages (see Table 2). Their horizontal distributions (i.e. relative abundance at the forest edge) in the canopy (Mean = 57.04, SD = 30.79, N = 36) and the understorey (Mean = 66.95, SD = 28.48, N = 36) were only marginally different (Paired t-test: t = −1.91, df = 35, p = 0.06). In the understorey, however, distribution of individual species inclined towards the edge (One sample t-test: hypothetical/actual mean 50/66.95, t = 3.57, df 35, p < 0.01), whereas in the canopy the pattern was insignificant (one sample t-test: hypothetical/actual mean = 50/56.75, t = 1.37, df = 35, p = 0.2).

4. Discussion

The main gradient of saproxylic beetle diversity was found between the forest edge and its interior. The canopy-understorey gradient was much less pronounced. Vertical distribution of individual species, though, differed between edge and interior, and more species inclined towards the canopy in the latter.
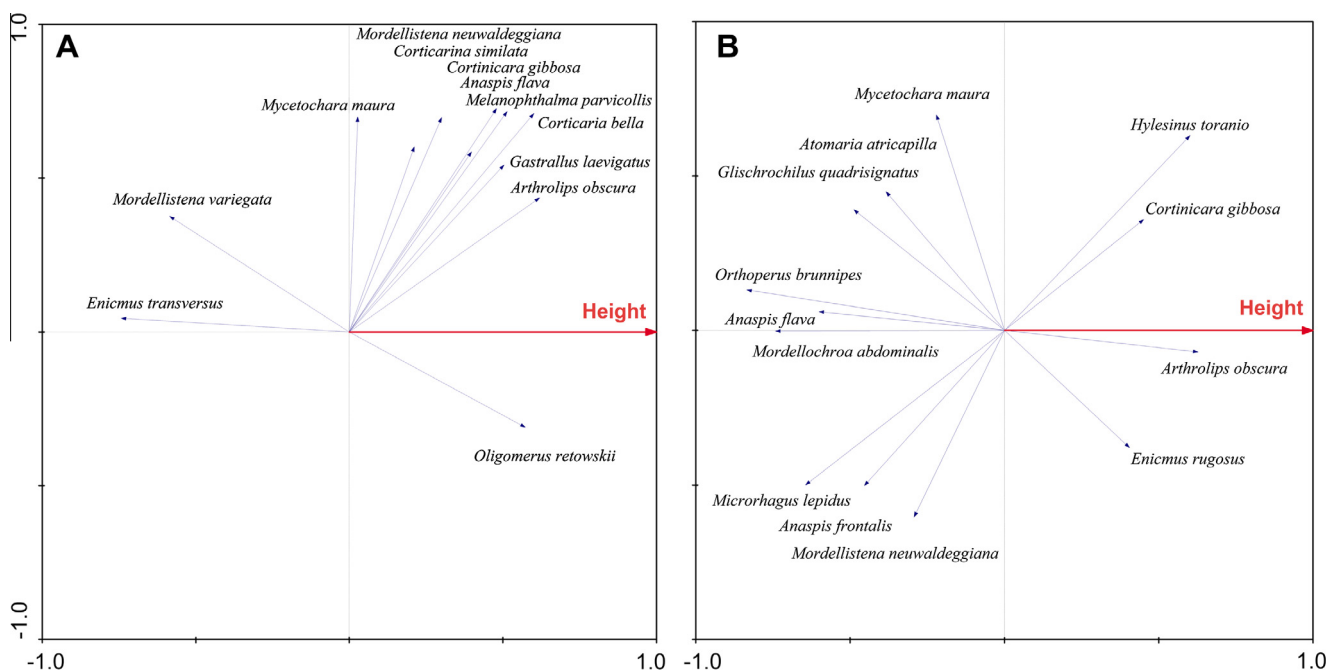
Fig. 3. Saproxylic beetles preferred canopy layer in the interior (A) more than at the edge (B) of a closed-canopy, lowland deciduous forest in SE Czech Republic. RDA ordination biplot relating beetles sampled by flight intercept traps to vertical trap-position: the first (horizontal) axis represents the height of trap above ground, acting as the explanatory variable. It accounted for 15.1% (F = 2.49, p < 0.005) of variance in species data at the edge (A), and for 18.1% (F = 3.1, p < 0.005) of variance in the interior (B). All species common (N > 5) in the respective habitat were analysed, only those with fit-range >30 are depicted.
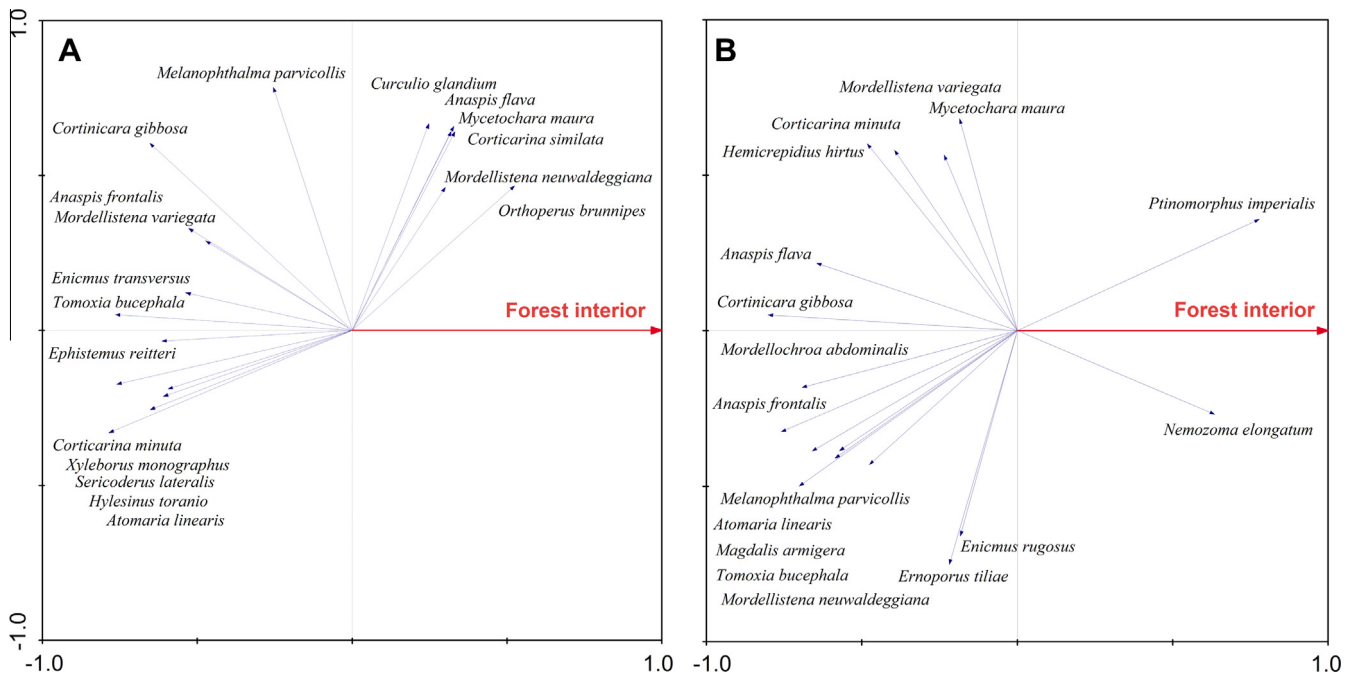
Fig. 4. Saproxylic beetles avoid interior of closed forest regardless to vertical stratum. Beetles were sampled by flight intercept traps in the canopy (A) and the understorey (B) of a deciduous forest in the SE Czech Republic. RDA ordination biplots relating beetles to the distance of a trap from a forest edge. The first (horizontal) axis represents distance to forest edge acting as the explanatory variable. It accounted for 20.5% of variability in the species data ($F = 3.62$, $p < 0.0001$) in the canopy (A) and for 25.9% of variability in the species data ($F = 4.89$, $p < 0.0001$) in the understorey (B). All species common ($N > 5$) in the respective vertical stratum were analysed, only those with fit range >30 are depicted.
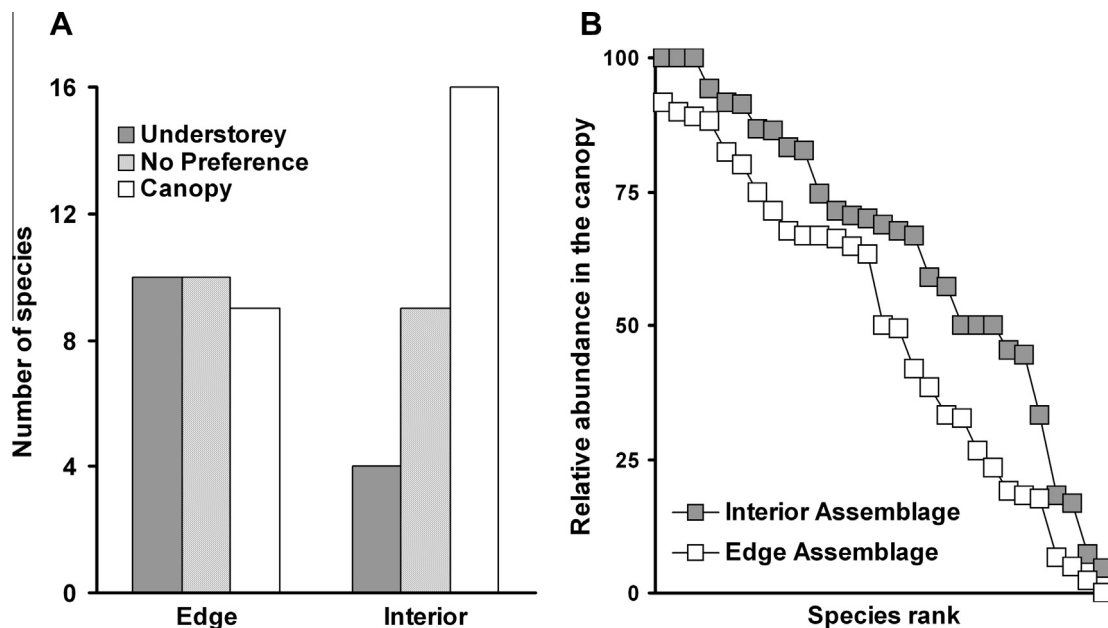
Fig. 5. Habitat affects vertical stratification of saproxylic beetles in a closed-canopy, deciduous forest in the SE Czech Republic. (A) Of the 29 species common in both, the edge and the interior habitats (see Table 2), the majority preferred canopy in the forest interior (chi^2 = 7.5, df = 2, $p < 0.05$), whereas their preferences for vertical forest strata were nearly equal at the forest edge (chi^2 = 0.07, df = 2, $p = 0.97$). (B) Rank ordered diagram of the 29 species according to their relative abundance in canopy of forest interior (*grey squares*) and forest edge (*white squares*). *(A species was classified as preferring understorey (*grey column*) or canopy (*white column*), if more than two-thirds of its individuals from a given assemblage occurred in the respective stratum. Otherwise it was classified as exhibiting no preference (*dashed columns*)).

4.1. Determinants of saproxylic beetle distribution

Sample composition was affected mainly by variables directly related to openness and amount of solar radiation received by the sampled positions, including *InteriorDepth*, *Height*, and *Evapo-* *ration*. The fact that *Canopy openness* itself was not selected into final model should not confuse the reader. Its effect was significant; it was, however, correlated with *InteriorDepth* as well as with *Evaporation*. Also, the fish-eye based estimations may suffer from bias as close objects (e.g., low branches) have much higher effect on

the estimate than distant ones. In the closed forest, there is more sun at the edge and in the canopy than in the interior and the understorey. The evaporation is affected by the solar radiation and air circulation that again relates to habitat openness. This is in line with the fact that saproxylic beetles often require sunny forest habitats (e.g. Jonsell et al., 1998; Wermelinger et al., 2007; Sugiura et al., 2009; Sverdrup-Thygeson and Birkemoe, 2009; Albert et al., 2012), and many are poor fliers (e.g. Hedin et al., 2008). They may thus avoid closed forest due to lack of sunshine and/or low ability to navigate through dense growth (Dubois and Vignon, 2008). It is important to note that herein reported patterns of the adult beetles distribution are in agreement with results obtained by rearing of xylophages at the same area and positions (Vodka et al., 2009). Adult distribution and flight activity thus likely reflect patterns in oviposition preferences, and/or larval microhabitat requirements. The observed high affinity of saproxylic beetles to sunny habitats has crucial consequences for their conservation in lowland woodlands.

It underlines the need for active management measures in protected lowland woodlands. In Europe, forest reserves mostly lack key disturbance factors such as large wild herbivores (Vera, 2000), or fire dynamics (Niklasson et al., 2010) for hundreds of years. In absence of "natural" disturbance factors, traditional woodland managements (e.g. coppicing, pollarding, litter raking, grass mowing, and wood pasture) facilitated for survival of sunloving forest organisms for hundreds of years (e.g. Konvicka et al., 2008; Hédl et al., 2010; Kopecký et al., 2013; Sebek et al., 2013). In reserves, cesation of the traditional managements has lead to full canopy closure, diminution or absence of sunny forest habitats, and exclusion of disturbance dependent, often keystone trees such as oak and fir (Vera, 2000; Vrska et al., 2009). Increased canopy closure in formerly open forests also leads to decline of old trees (Altman et al., 2013). The above has inevitably resulted in decline or local extinctions of numerous woodland organisms. Restoration of natural disturbance regime or active management increasing habitat diversity is thus needed to prevent further decline in biodiversity of European forests (Bengtsson et al., 2000).

No effect of dead wood volume (DWV) on sample composition has been detected in this study. It should not be inferred from our results, however, that dead wood volume is not important to saproxylic beetles (see e.g. Lachat et al., 2012). Our sampling design allows for investigation of the differences among assemblages of studied positions rather than for detection of the more complex effect of DWV. On the other hand, there is consistently more dead wood in the understorey than in the canopy, and there is certainly not less dead wood in the interior than at the edge. Beetle distribution, though, shows different patterns. Our results thus demonstrate that in the closed canopy forest and on the small spatial scale studied, DWV in the vicinity of a trap is certainly not the most important factor affecting sample composition. Other studies have also found a weak relationship between local DWV and saproxylic beetle diversity (Siitonen, 1994; Økland et al., 1996; Vodka et al., 2009), concluding that the overall supply of DWV in wider landscapes is probably more important than its local amounts (Franc et al., 2007).

4.2. Vertical stratification as a function of forest structure?

Vertical stratification of assemblages as well as individual species is clearly affected by edge-interior gradient. Except for sunlight availability, most potentially relevant environmental factors (i.e. dead wood volume, forest age, tree species composition) were identical, or nearly identical between the edge and the interior. This suggests that vertical stratification of insects in forests is a function of sun availability/habitat openness, and thus is affected mainly by forest spatial structure. This is supported by fact that diversity of insect assemblages may be lower or higher in the can-

opy than in the understorey of the identical forest, depending on canopy cover (Gossner, 2009), and/or undergrowth density (Ulyshen et al., 2010). Oak, on the other hand, has high light requirements, and oak woodlands were open woodlands for most of their recent history (Rackham, 1998). It is thus possible that oak-associated arthropods require more solar radiation than those associated with shade tolerant trees (Jonsson et al., 2005; Gossner, 2009). The described pattern would than be less pronounced in woodlands dominated by tolerant trees such as e.g. beech or spruce. Saproxylic beetles in our data, however, mostly are generalists also exploiting wood of shade tolerant trees.

Although species with high preference for canopy clearly do exist in temperate woodlands (e.g. *Agrilus convexicollis*, *Arthrolips* spp. in the presented data), sampling focused on forest interior is likely to overestimate their incidence. Sun-requiring species, clearly prevailing in the studied community, appear as preferring canopy in the interior, but may exhibit no preference or even prefer understorey at the edge (e.g. *Anaspis flava* and *Mordellistena neuwaldeggiana*). It remains unclear how general this pattern is geographically and taxonomically. Observation of vertical stratification of beetle and neuropteran assemblages on the forest edge and the interior (Duelli et al., 2002; Wermelinger et al., 2007), and vertical stratification of heteropteran assemblages along canopy cover gradient (Gossner, 2009) suggest it might be widespread among various insect orders in temperate forests. It might be valid also in the tropics as suggested by the fact that localization of flight height in Lepidoptera is less developed in open than in closed tropical forests (Holloway in Basset et al., 2003), and that shift of vertical preferences of individual species as a reaction to canopy closure was observed for arboreal dung beetles (Davis and Sutton, 1998; Tregidgo et al., 2010).

Both the differences in the structure of sampled woodlands and the effect of dominant tree species may explain for inconsistent and often contrasting outcomes of studies dealing with vertical stratification of insects in forests (cf. Vance et al., 2003; Hirao et al., 2009; Schroeder et al., 2009; Bouget et al., 2011). Despite the growing number of studies investigating insect vertical stratification in forests, studies considering the key environmental parameters such as canopy closure and undergrowth density remain rare. Although substantial progress has been made in recent years (Bouget et al., 2011; Ulyshen, 2011) to allow for synthesis of patterns of arthropod vertical distribution in temperate woodlands and their underlying factors, emphasis needs to be put on studying arthropod vertical distribution in the context of their environment.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.04.007.

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