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Spatial distribution of saproxylic beetles on trunks of standing Scots pine trees

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Abstract

1. The spatial distribution of saproxylic beetles landing and climbing stems of 12 grown and healthy Scots pine trees (*Pinus sylvestris* L.) was examined in detail during a 3-year trial. The beetles were sampled using sticky traps attached to the tree trunk at three tree parts (i.e., the trunk base, middle part of the trunk, and trunk in crown). Each tree part was sampled using two sticky traps facing opposite cardinal directions (north and south).

2. In total, 4063 individuals representing 169 taxa of saproxylic beetles were yielded in the 1405 obtained samples.

3. Remarkable interstrata diversification of saproxylic beetle assemblages reflecting distribution of breeding substrates in the forest stand was observed. Overall, species richness decreased considerably from the trunk base to the crown, with intermediate values for the middle part of the trunk. However, the abundance of mycetophages and saproxylophages decreased from the trunk base to the crown, with xylophages being the most abundant in the tree crown.

4. The cardinal direction exhibited overall weak effects on abundance, species richness, and composition, but the occurrence of a few particular species was significantly associated with the south (13 species) or north (3 species) facing part of the trunk.

5. Our results suggest that primary attraction and random landing strategies are combined during the substrate selection by many species.

6. High variability in the importance of the studied explanatory variables was observed among taxa, which shows how the species composition recorded in any study might alter its general outcomes.

KEYWORDS
cardinal direction, diversity, guilds, *Pinus sylvestris*, species composition, sticky traps, tree part, vertical

INTRODUCTION

Saproxylic beetles represent one of the most species-rich and functionally diverse groups of organisms that live in forest ecosystems (Grove, 2002; Jonsell et al., 1998; Stokland et al., 2012). Hence, their

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spatial distribution has crucial implications for forest management with respect to the conservation of forest biodiversity, forest ecosystem functions, and forest protection. The vertical and horizontal distributions of saproxylic beetles within forest ecosystems are not homogenous, changing with canopy closure (Horák et al., 2014; Lindhe et al., 2005; Widerberg et al., 2012), distribution of dead wood including the occurrence of specific microhabitats (Horák, 2017; Horák et al., 2016; Martikainen et al., 2000; Ulyshen et al., 2004),

distance from the forest edge (Normann et al., 2016; Vodka & Cizek, 2013; Wermelinger et al., 2007), and height above the ground (Bouget et al., 2011; Prochazka et al., 2018; Vodka & Cizek, 2013). The vertical distribution of saproxylic beetles has been studied repeatedly on diverse boreal and temperate forest ecosystems with partly conflicting results (Hardersen et al., 2014; Hirao et al., 2009; Kappes & Topp, 2004; Normann et al., 2016; Prochazka et al., 2018; Sheehan et al., 2019; Ulyshen & Hanula, 2007; Vance et al., 2003; Vodka et al., 2009; Vodka & Cizek, 2013; Wermelinger et al., 2007). In summary, studies consistently documented differences between strata in species composition and discrepant patterns of beetle abundance and species richness. For instance, according to Ulyshen and Hanula (2007) and Hardersen et al. (2014), species richness is equivalent in the understorey and canopy, and Vodka et al. (2009) and Graf et al. (2022) found the highest species richness in the understorey; in contrast, Kappes and Topp (2004) and Normann et al. (2016) documented peaks in species richness in the canopy. However, some discrepancies in the aforementioned studies might be attributed to the different ranges of taxa investigated or sampling methods. The vertical stratification of saproxylic beetle assemblages in boreal and temperate forests is likely highly variable and can be influenced by spatial structure, tree species composition, and stand age (Gossner, 2009; Ulyshen, 2011; Vodka & Cizek, 2013). Additionally, most studies on vertical distribution compared only two strata (understorey and canopy), with detailed stratification being scarce (Maguire et al., 2014; Prochazka et al., 2018; Sheehan et al., 2019). Hence, further studies addressing the vertical distribution of saproxylic beetles in boreal and temperate forests are needed. In addition, there is a need for complex studies that can cover a broad range of taxa with minimal limitations, conducted across various stand types, and with more detailed sampling of forest stand stratification or specific microhabitats.

The vertical distribution of saproxylic beetles in forest ecosystems is largely driven by individual species' behaviour and specific requirements for breeding substrates, microclimates (humidity, sun exposure, etc.), and other resources (e.g., feeding of adult beetles). A similar mechanism might form distribution of saproxylic beetles with respect to cardinal directions. A few previous studies have documented that the occurrence of emergence holes of several saproxylic beetles (i.e., abundance of successfully developed individuals) is affected by cardinal directions that substrate mantle is facing (Albert et al., 2012; Åström et al., 2013; Foit et al., 2016; Kašák & Foit, 2018), which is likely driven by sun exposure. To our knowledge, there have been no studies addressing the effect of cardinal direction on occurrence of saproxylic beetle adults at the level of assemblages.

Studies that focus on the spatial distribution of saproxylic beetles in forests used different sampling approaches, which might have a significant effect on the results and their interpretation. While most studies used window-flight traps (Prochazka et al., 2018; Ulyshen & Hanula, 2007; Vodka & Cizek, 2013; Wermelinger et al., 2007), other traps such as malaise traps (Hardersen et al., 2014), yellow pan traps (Wermelinger et al., 2007), fermental traps (Ruchin & Egorov, 2021), or sticky traps (Graf et al., 2022; Saint-Germain et al., 2007) have also been used previously. Further, some studies have been based on rearing insects emerging directly from dead wood substrate (Bouget

FIGURE 1 Photo of the pine-dominated stand where this study was conducted.

et al., 2011; Seibold et al., 2018; Vodka et al., 2009), whereas other studies counted emergence holes on a substrate (Albert et al., 2012; Zhang et al., 1993) or directly examined a substrate for the occurrence of beetles using bark peeling (Cadorette-Breton et al., 2016; Foit, 2010). Whereas, the latter of the approaches, based on the examination of a substrate, shows a direct association of saproxylic beetles with the inhabited substrates, the widely used flight intercept traps reflect the flight activity of beetles, which may be just passing by (Alinvi et al., 2007). Sticky traps attached to the tree stem capture insects landing or climbing on the tree stem—insect activities that are mostly connected to the breeding substrate selection or adult foraging. According to the 'random landing hypothesis', the complete process of discrimination between suitable and unsuitable breeding substrate take place after landing due to short-range olfactory and gustatory cues (Hynum & Berryman, 1980; Moeck et al., 1981), whereas according to 'primary attraction hypothesis' suitable breeding substrate is preselected before landing according to emitted volatile organic compounds (Brattli et al., 1998; Tunset et al., 1993). Some level of primary attraction is probably adopted by most saproxylic beetles (Graf et al., 2022), but both mechanisms are combined and

applied variously at different spatial scales (Saint-Germain et al., 2007). Although saproxylic beetles land more abundantly on suitable deadwood than on unsuitable living trees, the two assemblages do not differ in species composition (Graf et al., 2022).

This study explored spatial distribution of saproxylic beetles in the forest ecosystem using sticky traps attached to the trunks of living trees. Following questions were investigated:

1. What is the vertical distribution of saproxylic beetles landing or climbing on the trunks of living trees in terms of abundance, species composition, richness, and abundance of feeding guilds?

2. Do patterns in saproxylic beetle vertical stratification on living trees (i.e., mostly unsuitable substrate for breeding) correspond to the distribution of their breeding substrates within a forest ecosystem? In other words, is there a certain level of species' affiliation to the individual forest strata as an effect of 'primary attraction hypothesis', but 'random landing hypothesis' applies within each particular stratum?

3. Are there differences in distribution of saproxylic beetles on the tree trunk between cardinal directions, thus, reflecting preferences in breeding substrate selection and/or foraging behaviour of adults?

MATERIALS AND METHODS

Study site and design

The study site is situated in a uniformly aged, 93-year-old (9.58 hectares) mixed stand (Figure 1) in the southern foothills of the Drahanská vrchovina Highland, ~1 km north of Brno (49°15′39″ N, 16°36′20″ E), at 310–340 m a.s.l. on a ~10–15 north-facing slope. Based on daily weather data from 1961 to 1990 from the nearest meteorological station in Brno–Tuřany, the long-term average annual air temperature and precipitation are 8.7°C and 490 mm, respectively, and the growing season lasts 171 days between 23 April and 10 October. The stand was planted in 1928, and its main canopy is composed of Scots pines (*Pinus sylvestris* L.) (>70%) with admixed European larch (*Larix decidua* Mill.) and Norway spruce (*Picea abies* [L.], Karst.). Other interspersed tree species are also present and form mainly understorey: sessile oak (*Quercus petraea* [Matt.] Liebl.), small-leaved linden (*Tilia cordata* Mill.), European hornbeam (*Carpinus betulus* L.) and common ash (*Fraxinus excelsior* L.). The stand basal area reached 42 m^2/ha at the time the study was carried out. Being a typical managed forest, the study stand is characterized by only a moderate amount of deadwood (Stokland et al., 2012) that consists predominantly of older stumps, logging residues, or fallen branches in understorey and suspended dying/dead branches mostly in the canopy layer. The forest in this area has traditionally been managed by clear-cutting followed by prevailing artificial regeneration. Thus, the studied stand is surrounded by a mosaic of even-age mixed stands of various ages.

Twelve apparently healthy Scots pine trees of the main canopy were selected for sampling within the study stand. The trees were not located at the same place, but they were distributed in triads at the vertices of a square of edge length 50 m or slightly more. Thus, four plots were established, each containing three sampled neighbouring Scots pine trees (3–6 m apart of each other). The selected trees ranged between 27 and 48 cm in breast height diameter and 23–28 m in height.

Data collection

Sticky traps were used for sampling saproxylic beetles. The traps consisted of a transparent plastic sheet of 30 cm × 30 cm covered by transparent slightly yellowish insect glue (Chemstop Ecofix, Fytofarm s.r.o. Czechia). Sticky traps were tightly attached to the tree stem. On each tree, three different tree parts were sampled: (a) the base (~2–3 m above the ground), (b) middle trunk where the thin smooth bark begins (6–9 m above the ground), (c) the upper part of the trunk in the crown (17–20 m above the ground). On each part of the tree, two sticky traps were installed, one on the south-facing part of the stem mantle and the second on the opposite north-facing part. In total, beetles landing and crawling on each tree were sampled by six sticky traps. Sampling was carried out throughout the growing season (the beginning of April to the end of September) of 3 years from 2014 to 2016. Sticky traps were gathered and renewed approximately every 30 days while climbing the trees with ladders. Sampling yielded a total of 1405 usable samples for subsequent examination.

All beetles were carefully removed from the sticky traps and cleaned in pure petrol. The captured beetles were subsequently identified and non-saproxylic taxa were omitted. Most of the saproxylic beetles (77.9%) were identified to the species level. However, 22.1% of the saproxylic beetle individuals were identified only to the genus or family level (above all Throscidae—9.1%, Scraptiidae—3.5%, Cryptophagidae—2.6%, Staphylinidae—2.0%, and *Rhyncolus* (Curculionidae)—1.7% of beetle individuals captured).

Classification of beetles

The recorded beetle species (taxa) were assigned to four feeding guilds based on larval feeding habits. The guilds included xylophages (consuming live and fresh deadwood), saproxylophages (consuming partly decomposed wood or other dead organic matter), mycophages (consuming wood-decomposing fungi) and predators (zoophages). The classification was mostly derived from the classification used by Seibold et al. (2015), adjusted and supplemented according to our observations and some additional literature. For the beetle classification used (see Table S1).

Data analysis

To compare species richness among sampled strata and cardinal directions, sample-based rarefaction and extrapolation curves were

constructed using the iNEXT package (function iNEXT) in R 4.0.2. The analyses were conducted on the original samples obtained from a single sticky trap that was used for a period of ~1 month, so that the results would accurately reflect the data collection procedure.

Prior to all the other analyses (that follow) original data were pooled across sampling periods of the whole study (i.e., one sample represented the catch of one sticky trap position through the whole duration of the study). Thus, we obtained 72 (12 trees ×6 trap positions) much larger samples that enabled more robust analyses of spatial distribution of saproxylic beetles.

Generalized linear mixed models (GLMMs) were adopted to test the effects of the tree part and the cardinal direction on the total number of caught individuals and species as well as the abundance of particular feeding guilds. The models were fitted using the Generalized Estimating Equations algorithm in the geepack package (Hojsgaard et al., 2006; function geeglm) in R 4.0.2. GLMMs were computed with the quasi-Poisson distribution, tree identity was treated as a random effect factor, while the tree part and the cardinal direction entered the models as fixed effect factors. The significance of the effect of individual fixed effect factors was evaluated by means of Chi-square-based likelihood ratio tests comparing the full model including the tested fixed effect factor and random effect factors with the reduced model including only random effect factors. Subsequently, the pairs of tree parts that differed significantly were found using post hoc tests in statistical package multcomp (function glht with multiple comparison procedure set up as Tukey all-pair comparisons) in R 4.0.2.

Finally, hierarchical modelling of species communities (HMSC; Ovaskainen et al., 2017) was performed to assess how the occurrence of particular saproxylic beetle taxa as well as overall assemblage species composition depend on random effect factor (i.e., tree identity) and fixed effect factors (i.e., tree part and cardinal direction). The analyses were performed using the package Hmsc (functions: HmscRandomLevel, Hmsc, sampleMcmc, evaluateModelFit) in R 4.0.2. As the response variables in the model were species count data distribution was set as Poisson. The posterior sampling worked with the following settings: thin = 100, samples = 4000, transient = 50,000, and nChains = 4, thus gaining 16,000 posterior samples in total. The overall fit of the model was evaluated according to the computed pseudo-R^2 based on squared Spearman correlation (henceforth c.SR2), which is appropriate for Poisson models. The fitted model was also checked for satisfactory MCMC convergence (effective sample sizes and potential scale reduction factors for beta, gamma, and omega parameters). Subsequently, proportions of variance in each taxon occurrence explained by the model as attributed to particular explanatory variables (functions computeVariancePartitioning and plotVariancePartitioning) were extracted. As the species-level analyses are not informative for species with sparse data, only taxa with at least 10 caught individuals recorded in three or more samples were included in the model. Additionally, for the species included in HMSC analyses, their associations with a particular cardinal direction and tree part(s) were examined through fitting GLMMs using the same methods as described above (except abundances of particular taxa acted as the response variables in these models). Taxa were
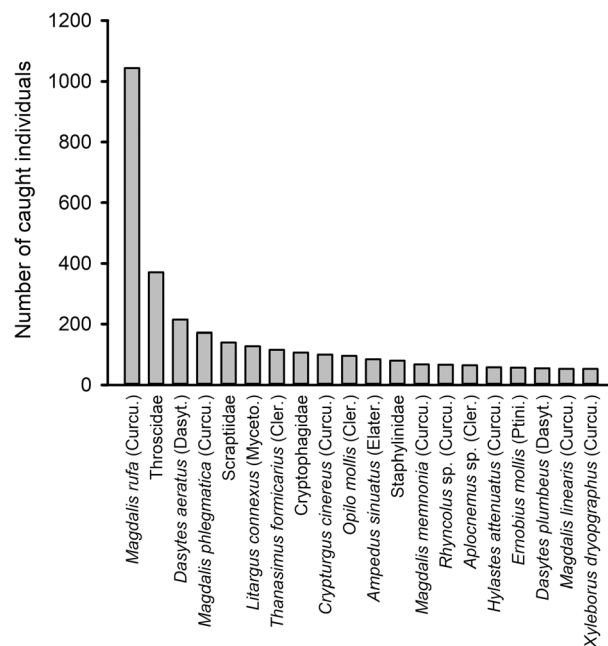

FIGURE 2 Total numbers of individuals of the most abundant taxa caught in this study. The abbreviated name of a beetle family is mentioned next to a species or genus name (i.e., Bupr., Buprestidae; Ceram., Cerambycidae; Cler., Cleridae; Curcu., Curculionidae; Dasyt., Dasytidae; Elater., Elateridae; Hister., Histeridae; Myceto., Mycetophagidae; Ptini., Ptinidae; Tenebr., Tenebrionidae).

considered to be associated with a particular cardinal direction or tree part(s) if the taxa reached the significantly highest abundance there.

RESULTS

In total, 4063 individuals of saproxylic beetles representing 169 different taxa were recorded in this study (Table S1). *Magdalis rufa*, with 1043 captured individuals, was by far the most abundant species (Figure 2). The most abundant feeding guilds were xylophagous beetles with 2461 specimens representing 107 taxa, and predators with 859 specimens in 32 different taxa, followed by mycetophages (658 individuals, 12 taxa) and saproxylophages (85 individuals, 18 taxa).

Species richness differed considerably among the sampled tree parts, with decreasing species richness from the trunk base to the crown (Figure 3a). Species richness largely diverged between the trunk base and crown, whereas intermediate species richness associated with the middle trunk exhibited less considerable difference in relation to the crown and even less pronounced difference in relation to the trunk base. No differences in species richness were found between the sampled cardinal directions of the trunk mantle (Figure 3b).

The tree part had a significant effect on the total abundance and species richness of saproxylic beetles and also on the abundances of the feeding guilds (Figure 4). Total abundance was highest in the crown and lowest in the middle part of the trunk, with no significant difference between the crown and the trunk base. Number of species
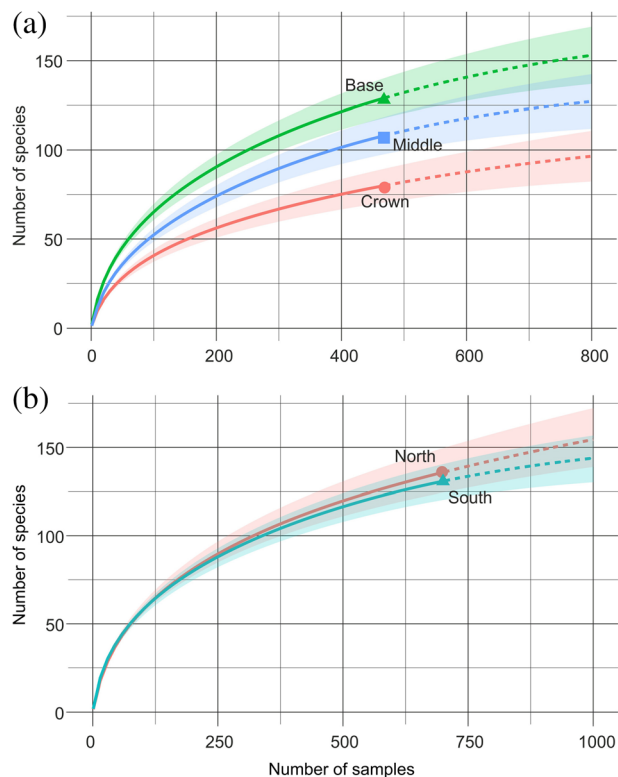
FIGURE 3 Rarefaction curves showing the cumulative number of saproxylic beetle species (taxa) at the studied locality with an increasing number of samples taken from different parts of the trunk (a) and from different cardinal directions of the trunk mantle (b). The rarefaction curves show rarefied (solid lines) and extrapolated numbers of species (dashed lines) with 95% confidence intervals delineated as shaded areas.

decreased from the trunk base to the crown. In the case of feeding guilds, considerable effects were found for the mycetophagous and saproxylophagous beetles, with decreasing abundance from the trunk base to the crown. Another remarkable response was exhibited by xylophagous beetles, with the highest abundance in the crown and the lowest in the middle part of the trunk. Although the abundance of predators was affected by the tree part rather weakly, it decreased significantly from the trunk base to the crown.

In contrast, effects of cardinal direction on the distribution of saproxylic beetles were rather weak (Figure S2). Only total abundance of saproxylic beetles and the abundance of predators were significantly affected by cardinal direction with somewhat higher abundances on the south-facing part of the trunk mantle in both cases.

In total, the HMSC model was able to explain 26.6% (based on c. SR2) of variance in species occurrence (the values ranged from 0.5% to 82.5% in particular taxa) (Figure 5). Although proportions of explanatory power of the studied factors varied considerably among particular species, in general, the highest explanatory power exhibited the fixed effect factor tree part (accounting for 77.9% of the variance explained by the model; Figure 5). The second most important factor was the fixed effect variable cardinal direction (accounting for 11.6% of the variance explained by the model). The explanatory power of the random effect factor tree identity was 10.5%.

Fourteen taxa were found to be associated with the trunk base, 9 taxa associated with both the trunk base and middle part of the trunk, no species associated with the middle part of the trunk, and 9 taxa characteristic of the trunk in the crown (Figure 5). Whereas 13 taxa were assigned as associated with the south-facing part of the trunk mantle, only three species were associated with the north-facing part.

DISCUSSION

This study documented the spatial distribution of saproxylic beetles on the trunks of living standing Scots pines in a pine-dominated forest stand in southeastern Czechia. Species richness, composition, and abundance significantly changed from the trunk base to the crown. Overall species richness and abundance of mycetophages and saproxylophages considerably decreased from the trunk base to the crown. In contrast, xylophagous taxa were the most abundant in the crown and the least abundant in the middle part of the trunk. Our results suggest that landing and climbing activity of saproxylic beetles tends to be concentrated to the forest stratum where the highest amount of the suitable breeding substrates is available even if sampling is done on unsuitable substrates (living trees). This suggests that both strategies 'primary attraction hypothesis' and 'random landing hypothesis' are employed by many species during the substrate selection. Tree part was the most important factor affecting the occurrence of the species in our study. Although cardinal direction exhibited overall weak effects, a few particular taxa were considerably affected, with south-facing part of the trunk being preferred by most of them. As four of the south-associated taxa were predatory Clerid beetles, not only preferences for breeding substrate selection but most likely also the behaviour of adults (e.g., foraging behaviour or behavioural thermoregulation) underlay these associations. Regardless of all the presented general patterns, the responses of particular taxa largely varied.

Vertical distribution

Surprisingly, the overall abundance of saproxylic beetles was found to be highest in the tree crown (Figure 4a), where it was on average more than twice higher than in the middle part of the trunk and even slightly (but non-significantly) exceeded the abundance at the trunk base. As this study was conducted on apparently healthy trees, only individual dying branches provided breeding substrate for early-arriving xylophagous saproxylic beetles. These beetles are known to reach high abundances if suitable breeding material is available (Lieutier et al., 2004). Thus, the abundance of saproxylic beetles in the crown was inflated by a few locally very abundant species developing in the dying branches, mainly *Magdalis* spp., which corresponds to the lowest species richness (Figures 3–5) as well as species evenness of this tree part (mean Pielou's evenness index ± standard error: trunk base = 0.78 ± 0.04, middle part of the trunk = 0.85 ± 0.05 SE, trunk in the crown = 0.64 ± 0.05). Although this effect could have been
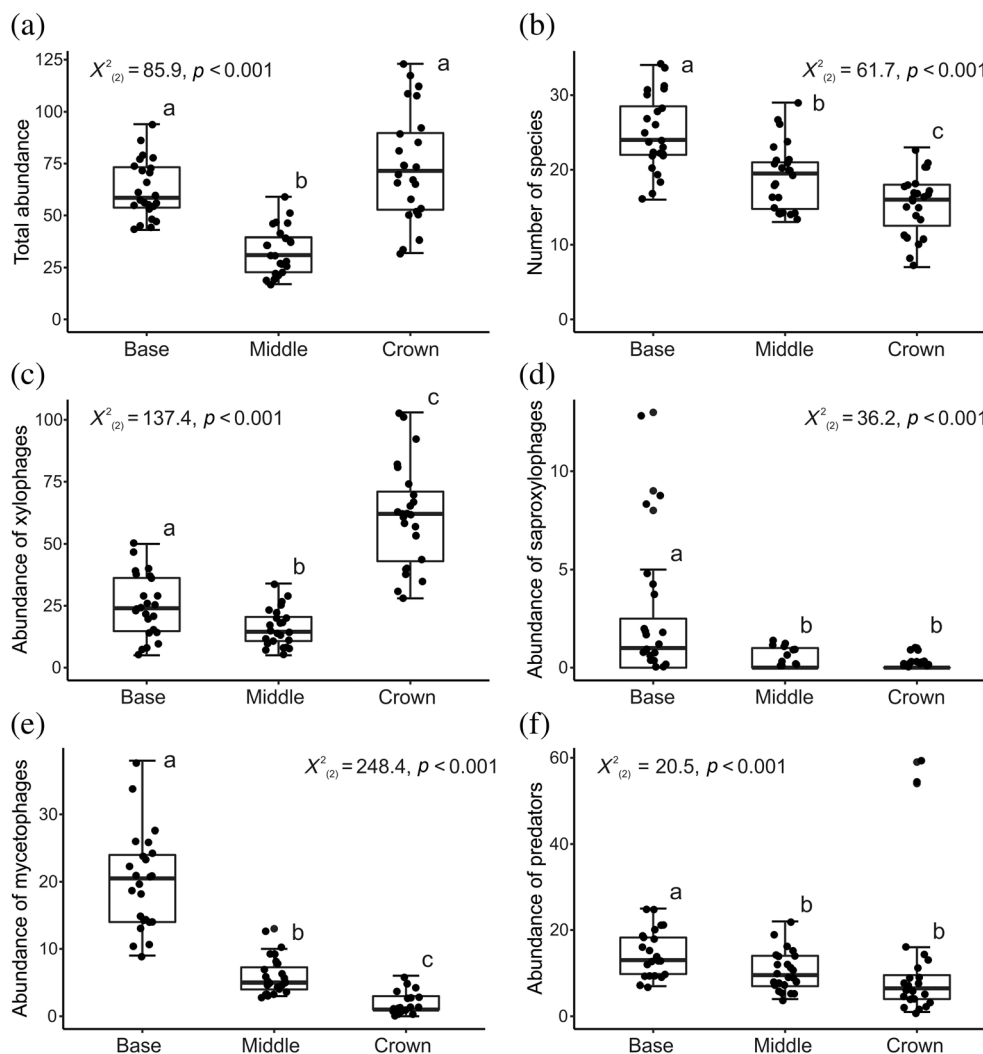
FIGURE 4 Boxplots showing distribution of saproxylic beetles among the sampled tree parts (Base, trunk base; Middle, middle part of the trunk, and Crown, trunk in the crown). Plots illustrate total abundance of saproxylic beetles (a), number of species (b), abundance of xylophagous beetles (c), saproxylophagous beetles (d), mycetophagous beetles (e), and predatory beetles (f). The pooled samples representing the catches from particular sticky traps during the whole study duration are presented. Boxplots consisting of the median, interquartile range, and non-outlier range are accompanied by original data values (depicted as black-filled dots). Significance of differences among tree parts is demonstrated by results of the Chi-square-based likelihood ratio tests of the fitted generalized linear mixed models. In each plot, categories labelled with the same letter did not differ significantly.

intensified by some branches being damaged by climbing the trees during sample collection within this study, the observed pattern is supposed to be generally valid in the case of healthy or slightly declining trees/stands anywhere.

Within this study, the vertical gradient represented by the tree part had a large effect on the distribution of saproxylic beetles in the forest stand in many aspects (e.g., abundance, species richness, species composition, and distribution of feeding guilds; Figures 3a–5). This effect seems to be considerably larger than in some other studies (Maguire et al., 2014; Vance et al., 2003; Wermelinger et al., 2007), where only small effects of height above the ground were found. It is possible that sampling beetles landing and climbing on the tree trunk by sticky traps might lead to less blurred interstrata differences compared to those gained by flight intercept traps capturing more just passing by beetles.

In this study, overall species richness was significantly higher at the trunk base than in the crown (Figure 3a), which corresponds well with the results of a former study conducted in a nearby and similar stand (Foit, 2010) that documented decreasing species richness of bark-boring and wood-boring beetles from the trunk base to the branches of standing freshly dead Scots pine trees. As expected, the middle part of the trunk was characterized by an intermediate value of species richness, similar to that reported by Graf et al. (2022) for saproxylic beetles in a beech forest in Germany or by Sheehan et al. (2019) for bark- and wood-boring beetles in a broadleaf temperate forest in Georgia (USA). Different results with the highest species richness in the middle stratum were found by Prochazka et al. (2018) for Scolytid beetles in temperate lowland broadleaf and montane beech-fir forests in Czechia. The found highest species richness at the trunk base (Figure 3a) corresponds well with the high numbers of taxa
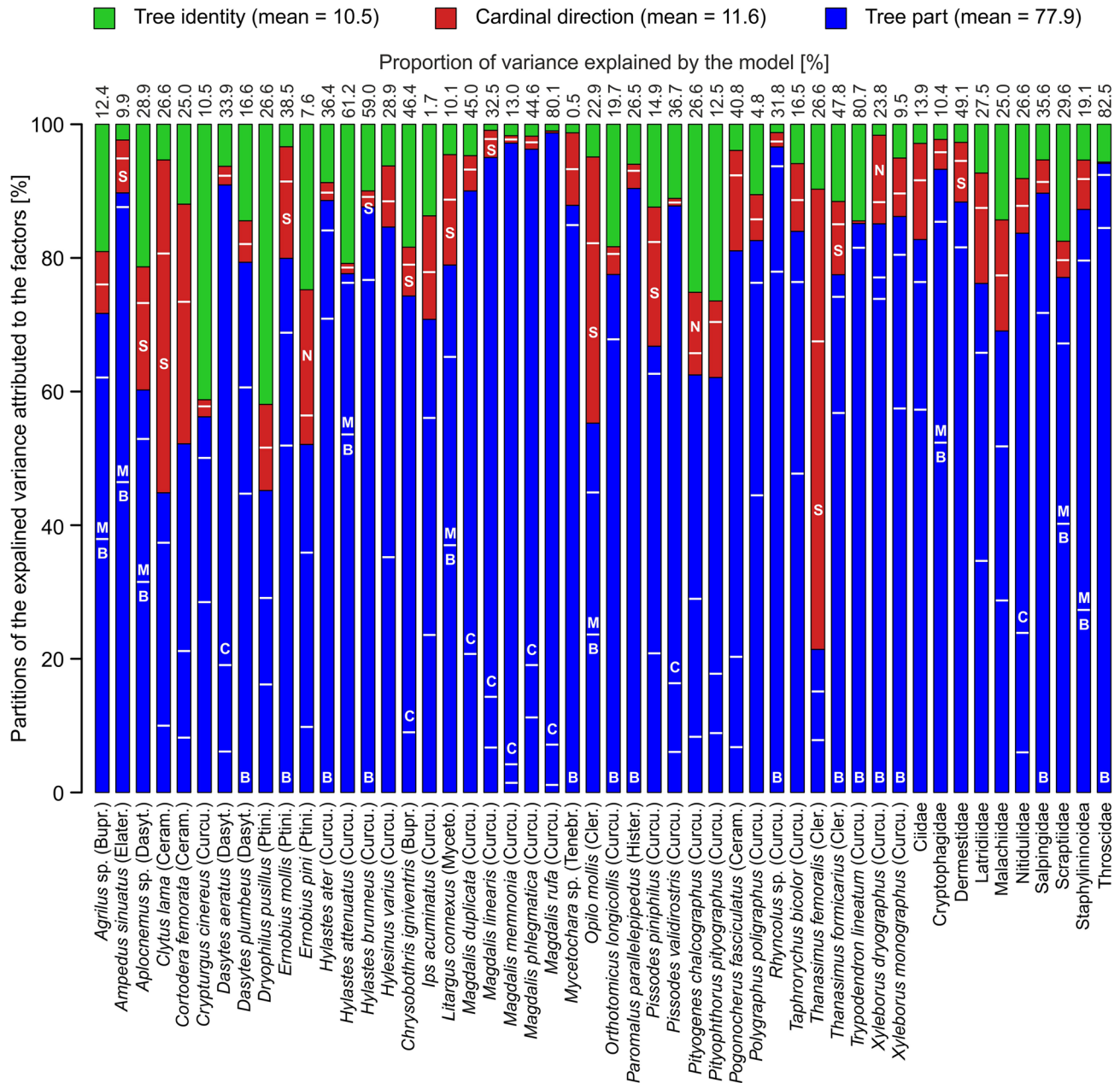
FIGURE 5 Variance partitioning derived from hierarchical modelling of species communities. Plot shows proportions of variance in each taxon occurrence explained by the model and partitioning of the explained variance into components related to the particular explanatory variables. The tree identity was treated as a random effect variable, and the tree part and cardinal direction were treated as fixed effect factors. The mean proportion attributed to each factor (across taxa) is mentioned next to the factor legend in parentheses. Only taxa with at least 10 caught individuals recorded in three or more samples were included in the model. The abbreviated name of a beetle family is mentioned next to a species or genus name (see the legend of Figure 2). Significant associations ($p < 0.05$) of taxa to a particular cardinal direction (S, South; N, North) and tree part(s) (B, trunk base; M, middle part of trunk; C, trunk in crown) as indicated by the fitted generalized linear mixed models are depicted using white characters. Additionally, proportional distribution of the number of captured individuals of each taxon among tree parts and between cardinal directions is illustrated using subdivision of the corresponding bar plot with white crosslines. Thus, blue bars and red bars corresponding to the tree part and the cardinal direction are divided into three parts (from bottom to top: trunk base, middle part of trunk, and trunk in crown) and two parts (south and north), respectively.

associated with this tree part alone (14) and with the trunk base together with the middle part of the trunk (9) (Figure 5). Whereas a considerable number (9) of taxa was also found to be associated with the tree crown, no species was determined as characteristic of the middle part of the trunk itself, which suggests that the middle stratum

of the forest stand almost did not offer unique microhabitats for saproxylic beetles that can be found in other strata (e.g., roots, stumps, basal parts of trunks with thick bark, downed humid dead wood, or dying thin twigs). Moreover, the total amount of saproxylic beetle microhabitats in this stratum was probably the most limited, as

evidenced by the observed lowest abundance of saproxylic beetles in the middle part of the trunk. Other studies, such as Vance et al. (2003), Ulyshen & Hanula, 2007, Bouget et al. (2011), and Vodka and Cizek (2013), have also confirmed the presence of unique species in both the understorey and canopy strata. In contrast, the middle stand stratum was found to host no or only a limited number of unique species. Therefore, the assemblages of saproxylic beetles in this stratum may largely represent combined nested subsets of ground and canopy assemblages, which highlights the importance of microhabitats along forest strata.

Also, distribution of feeding guilds was largely affected by the vertical stratification. The most considerable effects of the tree part were found in the case of mycetophagous, saproxylophagous, and xylophagous species (Figure 4). Xylophagous species were the most abundant in the crowns (considerable amount of available dying branches), less abundant at the trunk base (only limited amount of fresh deadwood available), and were the least abundant in the middle part of the trunk (virtually no available suitable breeding substrate in this stratum). In contrast, species associated with later decay stages (mycetophagous and saproxylophagous) were by far the most abundant next to the ground (the trunk base), where higher amount of suitable breeding substrate in the form of decaying deadwood with sufficient moisture favouring growth of fungi occurred (older logging residues, stumps, etc.; Stokland et al., 2012). This is in line with the results of some other studies (Bouget et al., 2011; Floren et al., 2014; Gossner, Floren, et al., 2013) reporting the highest abundance of mycetophages in the understorey and xylophages in the canopy.

Since beetles landing on and climbing living trees (an unsuitable breeding substrate) were sampled, most of them probably exhibited random landing strategy during the substrate selection, likely moving from one tree to another until a suitable habitat was found for reproduction. On the other hand, the found patterns of saproxylic beetle vertical distribution largely reflected the availability of breeding substrates in particular strata of the studied stand. This suggests that mechanisms of primary attraction hypothesis guide saproxylic beetles at least to the appropriate forest strata to search for a suitable substrate. For example, crowns with individual dying branches were likely releasing host volatiles that attracted a specific community (e.g., *Chrysobothris igniventris* or *Magdalis* sp.) to this forest stratum, while downed wood throughout the stand provided habitat for another specialists (e.g., *Hylastes* sp. or *Trypodendron lineatum*) that dispersed at lower heights. Correspondingly, scale-dependent combined strategy of substrate selection was suggested by Saint-Germain et al. (2007) and the study by Graf et al. (2022) documented that besides primary attraction random landing took place as well.

Cardinal direction

In contrast to the tree part, cardinal direction was documented to have weak and limited effects on the distribution of saproxylic beetles in this study (Figures 3b, 5, and S2), namely, certain effects on the total abundance, distribution of predatory species, and the occurrence

of several particular species were confirmed. Three particular species were found to be associated with the north-facing part of the trunk mantle (*Ernobius pini*, *Pityogenes chalcographus*, and *Xyleborus dryographus*; Figure 5), but the south-facing part of the trunk mantle was preferred by much more (13) species with a significant association. Correspondingly, some scolytid beetles were documented to prefer shady, more humid microhabitats (Foit, 2015; Gossner, Lachat, et al., 2013; Holusa et al., 2021; Peltonen & Heliövaara, 1999), but most saproxylic beetles are referred to as favouring increased sun exposure in more open habitats (Horák et al., 2014; Horák & Rébl, 2013; Lindhe et al., 2005; Vodka & Cizek, 2013). Additionally, detailed studies on the occurrence of several endangered species mostly revealed higher abundances of emergence holes on the south-facing part of the trunk (Albert et al., 2012; Åström et al., 2013; Foit et al., 2016; Kašák & Foit, 2018). The determined effect of cardinal direction on the occurrence of predatory beetles (Figure S2) largely reflects the association of Clerid beetles (*Aplocnemus* sp., *Opilo mollis*, *Thanasimus femoratus*, and *Thanasimus formicarius*) to the south-facing part of the trunk, which emphasizes a possible role of foraging or thermoregulation behaviour of adult beetles in the case of cardinal direction selection. These findings agree with Gossner, Floren, et al. (2013) and Seibold et al. (2015), who classified these beetles as being associated with sunny habitats.

Importance of variability in responses of individual taxa

Regardless of the general patterns, a high variability in the importance of particular studied explanatory variables (tree identity, tree part and cardinal direction) was observed among taxa (Figure 5). For instances, remarkable responses to generally less important explanatory variables were exhibited by some taxa (especially *Clytus lama*, *Cortodera femorata*, *O. mollis*, and *Thanasimus femoralis* to the cardinal direction and *Crypturgus cinereus* and *Dryophilus pusillus* to the tree identity). This observation highlights how particular taxa exhibit largely different patterns in occurrence and behaviour. Our study emphasizes that the recorded species composition of the assemblages can significantly affect the general results of the study. This indicates one of the possible reasons for the inconsistencies observed among various studies that investigate the distribution of saproxylic beetles in forest stands, as discussed in the Section 1.

Limitations of the study

However, this study is based on a sufficiently large dataset (3 years of sampling gaining 1405 usable samples with 4063 captured saproxylic beetle individuals), there are several issues limiting the general validity of the results: (i) the observed patterns of saproxylic beetle distribution are partly given by actual characteristics of the study stand (vertical structure, tree species composition, the amount of dead wood, etc.). Similarly, results might be slightly influenced by the variability in

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the individual study trees and by differences in species composition and health condition of surrounding trees. On the other hand, the performed analyses revealed an overall weak effect of tree identity (Figure 5), which indicates the general validity of the found patterns throughout the study stand. As the study stand represented a typical managed forest stand in the region, the results are supposed to be widely valid in similar forest stand types. (ii) A certain level of bias might arise from the fact that 22.1% of the saproxylic beetle individuals were identified only to the genus or family level. More than half of such beetles (12.6%) were represented by just two families, Throscidae and Scraptiidae (Figure 2), each rather consistent in its ecology. Moreover, based on the more precisely determined testing subsamples, the vast majority of individuals belonging to the mentioned families represented a single species (i.e., *Aulonothroscus brevicollis* (Bonvouloir, 1859) and *Anaspis frontalis* (Linnaeus, 1758) for Throscidae and Scraptiidae, respectively). A similar situation was observed in some of the other families (Biphyllidae, Cryptophagidae, Lycidae, and Salpingidae). Thus, the possible inaccuracy of the results was most likely negligible. (iii) The use of sticky traps could lead to the underestimation of larger species occurrence because larger robust species are able to escape from the trap. *Monochamus galloprovincialis* (Olivier, 1800) or *Spondylis buprestoides* (Linnaeus, 1758) are examples of large species occurring at the locality but never caught by a sticky trap. Such species would probably not reach sufficient abundance in samples to affect the result considerably.

CONCLUSIONS

Previous studies (sampling beetles actively flying or developing in/emerging from breeding substrates) documented the occurrence of saproxylic beetles within forest stands can vary along a vertical gradient (Bouget et al., 2011; Graf et al., 2022; Hardersen et al., 2014; Normann et al., 2016). This study confirmed remarkable interstrata changes in saproxylic beetle assemblages within a forest stand even for beetles landing and climbing on the tree trunk. A gradual decrease in species richness from the understorey to the canopy with intermediate richness in the middle forest stratum was documented. Regardless of this general pattern, there are contrasting responses of particular species and feeding guilds to forest stratification (predators, mycetophages, and saproxylophages being the most abundant at the trunk base, xylophages being the most abundant in the crown). The distribution of feeding guilds among forest strata is obviously driven by the distribution of their breeding substrates. Hence, the actual observed patterns of guild distribution might be altered according to forest stand characteristics (stand structure, occurrence of declining trees, dead wood distribution, etc.), which might be investigated by future studies. The effect of cardinal direction on the occurrence of saproxylic beetles is limited; however, this effect can be remarkable as in the case of particular species, which saw the southern part of the trunk being preferred more often. This study promotes the idea that strategies corresponding to both 'primary attraction hypothesis' and 'random landing hypothesis' are combined during the substrate selection by many species. Detailed analyses of species' responses to the explanatory variables studied in this study revealed unexpectedly large variability among particular species, which suggests that the usually used approach of extracting just general patterns likely represents an oversimplification of reality and that the actual species composition of assemblages recorded within a given study can easily shift the results of the study.

AUTHOR CONTRIBUTIONS

Jiří Foit: Data curation; methodology; project administration; supervision; visualization; writing—original draft; writing—review and editing. **Václav Čermák:** Data curation; methodology; project administration; writing—review and editing. **Tomáš Kudláček:** Data curation; methodology; writing—review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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SUPPORTING INFORMATION

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Table S1:

Figure S2:

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