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Saproxylic beetles in tropical and temperate forests – A standardized comparison of vertical stratification patterns

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ABSTRACT

Forests are complex three-dimensional ecosystems, but little is known about the influence of vertical stratification of forest structure on biodiversity and species turnover. Saproxylic beetles make a substantial contribution to forest biodiversity and ecosystem functions such as nutrient cycling. Management measures aimed at supporting saproxylic biodiversity are becoming an integral part of sustainable forest management practices. Yet, monitoring is carried out under the assumption that saproxylic activity at ground level will be a realistic reflection of saproxylic biodiversity in the forest as a whole.

To investigate the validity of this assumption we compare vertical stratification and composition of saproxylic beetle assemblages between three forest types of varying altitude and latitude, including a tropical lowland forest in Panama, a temperate lowland forest and a temperate montane forest, both in the eastern Czech Republic. Beetles were sampled following a standardized sampling protocol using flight intercept traps arranged in vertical transects.

Overall, the tropical forest was estimated to harbour two to three times more saproxylic beetle species than the temperate lowland and the montane forest, respectively. However, point richness estimates within vertical strata were remarkably similar between biomes. Species richness was similar in the understorey of all three forests. It peaked in the canopy of the tropical forest but in the understorey of temperate forests. So, while the beetle assemblages were clearly vertically stratified in all three forest types, stratification patterns varied markedly between tropical and temperate forests. This trend is driven primarily by the high richness of saproxylic beetles in the tropical forest canopy. However these richness differences belie the strong similarities in stratification of feeding guild composition observed all three forest types. This would tend to suggest that similar trophic structuring forces might operate across very different forest biomes of the world.

Similarities in feeding guild composition suggest that management measures aiming at conserving biodiversity of saproxylic beetles are likely to be effective across different forest types. The differences in vertical stratification, however, suggest that understorey monitoring alone will be insufficient to understand management effects on saproxylic biodiversity. In the tropics, in particular, more emphasis will need to be placed on managing the diverse, three-dimensional structure of forest canopies as habitat for saproxylic beetles.

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1. Introduction

Increased exploitation of forests threatens their biodiversity (Hassan et al., 2005). Identifying sustainable forestry practices that minimize the impact of exploitation on forest biodiversity is thus an important priority in forestry research (Brunet et al., 2010; Fedrowitz et al., 2014; Vítková et al., 2018). Beetles associated directly or indirectly with the wood of dead or live trees (i.e. saproxylic beetles) have become model organisms, in many regions, for identifying sustainable forest management practices (Siitonen et al., 2000; Martikainen, 2001; Grove, 2002). They constitute a substantial portion of forest biodiversity and are intensively studied because of the economic importance of some species as pests, and the conservation importance of other species that are threatened with extinction (Stokland et al., 2004; Wermelinger, 2004; Müller et al., 2008; Stokland et al., 2012; Bouget et al., 2013).

Forests are three-dimensional ecosystems in which organisms are not only distributed along various horizontal environmental gradients, but also along the vertical gradient between the forest floor and tree tops (Basset et al., 2003a). Understanding of vertical stratification processes is likely to be fundamental in the development of effective measures for the conservation of arthropod diversity in forest ecosystems (Ulyshen, 2011). Patterns of vertical distribution in a wide range of arthropod taxa, and saproxylic beetles in particular, have thus received growing interest from the scientific community (Intachat and Holloway, 2000; Schulze et al., 2001; Tanabe, 2002; Fermon et al., 2003; Ødegaard, 2004; Leksono et al., 2005; Wermelinger et al., 2007; Bouget et al., 2011; Vodka and Cizek, 2013; Maguire et al., 2014; Basset et al., 2015).

Vertical stratification is considered to be particularly pronounced in tropical forests compared with temperate forests, which has generally been attributed to a greater number of microhabitat niches in tropical forests (Basset et al., 2003a; Ulyshen, 2011). If the complexity of vegetation structure is indeed driving putative tropical vs temperate differences in stratification patterns, then we might also expect a similar phenomenon to occur along altitudinal, as well as latitudinal, gradients, since the vertical vegetation structure of forests is also known to decline in complexity with increasing altitude (e.g. Lieberman et al., 1996; Homeier et al., 2010). There are, however, very few studies that have directly compared the degree of vertical stratification of arthropod communities between tropical and temperate forests, or between forests across altitudinal gradients, using standardized sampling methods (but see Ashton et al., 2016), and none focuses on saproxylic beetles. The majority of generalizations about vertical structuring have been based on comparisons of studies that use different methodologies and sample different taxa (Ulyshen, 2011; Wardhaugh, 2014). Hence, little is known about the way in which the vertical distribution of saproxylic beetles differs between forest types and biomes.

Even less is known about other differences in saproxylic beetle assemblages between temperate and tropical forests. Basic information, such as feeding guild structure, is predominantly anecdotal (e.g. Beaver, 1979), although substantial differences in the ecology of wood decomposition could be expected between the tropical and temperate zones, due to large differences in biotic and abiotic conditions such as climate, tree species diversity, complexity of vertical structure, and the activity of termites, amongst other factors (Grove and Stork, 1999; Ødegaard et al., 2004).

The above mentioned gaps in knowledge of saproxylic beetles distribution may compromise the effectiveness of forest management practices aimed at conserving the diversity of this group and the ecosystem services they provide (Ulyshen, 2016; Fierro et al., 2017). First, most saproxylic beetle monitoring takes place near ground level, and likely misses a considerable portion of the variation in beetle distributional patterns (but see Leidinger et al., 2019), especially in structurally complex forests (Bouget et al., 2011). Second, recommendations for sustainable forest management practices are based on an understanding of saproxylic beetle communities in a few forest types, under the assumption that similar trends will hold true across regions and biomes.

Therefore, we used the same standardised collecting method to compare the composition and spatial distribution of saproxylic beetles in three very different forest types, including a lowland tropical forest in Panama and a lowland temperate forest and a montane temperate forest in central Europe, testing variation in patterns of fine-scale vertical stratification of species richness and feeding guild composition.

In the light of existing knowledge about differences in arthropod community composition and patterns of vertical distribution in different forests, we formulated the following predictions for the outcome of this study: (i) local species richness and species turnover of saproxylic beetles will be higher in tropical than in temperate forests; (ii) patterns of vertical stratification of species distribution will be more strongly differentiated in tropical than temperate forests; and (iii) these effects will not be uniform across trophic feeding groups, resulting in strong differences in feeding guild composition along vertical gradients in the three forest types.

2. Materials and methods

2.1. Study sites

Field sampling in the tropical lowland forest took place during the IBISCA-Panama project in the San Lorenzo Protected Area (Colón Province, Republic of Panama) which is part of the Mesoamerican Biological Corridor “hotspot” (Weaver and Bauer, 2004). The area is covered by evergreen wet lowland forest, dominated by *Tovomita longifolia* and *Protium panamense*. Extensive further details of the study site are provided in Basset et al. (2007).

Sampling of the temperate forests was performed in a lowland floodplain forest and a montane forest in the Czech Republic. The lowland part of the study was conducted in the oak-dominated alluvial woodlands along the lower Dyje (Thaya) and Morava (March) rivers in southern Moravia. The entire area is considered a hotspot and refuge for the saproxylic fauna (Rozkošný and Vaňhara, 1996; Schlaghamerský, 2000; Miklín and Cizek, 2014).

The montane part of the study was conducted in the Moravian-Silesian Beskids (Beskydy) – a mountain range in the Western Carpathians, situated in north-eastern Moravia. The area is considered one of the refuges for montane saproxylic biodiversity associated with beech-fir forests in the Czech Republic (Vávra and Stanovský, 2013). For a detailed description of the two Czech sampling areas see Weiss et al. (2016).

2.2. Sampling protocol

Sampling in the tropical lowland forest focused on four sites. Three of these were within the reach of the Smithsonian Tropical Research Institute canopy crane, while the fourth was situated on a ridge ~370 m from the crane sites (see Fig. 1). At each of the four sampling sites, three vertical transects were installed. Each vertical transect consisted of six unbaited flight intercept traps suspended at 0, 1.3, 7, 14, 21 and 28 m above the ground (height at the bottom of the interception panels). In total, 72 traps were installed in tropical forest, and beetle samples were collected and sorted every 10–14 days for the period from October 2003 to May 2004 (227 days; 16 344 trap-days sampling effort in total), encompassing the extremes of both the wet and dry seasons of the year (Basset et al., 2007).

In the temperate forests, five sampling sites were selected in each of the lowland and the montane forest locations (see Fig. 1), and three vertical transects were established at each site. Because of the lower tree heights, the vertical transects in the temperate forests were only sampled at five of the six heights, up to 21 m. In total, 75 traps were installed in the temperate lowland forest, and 75 traps in the temperate montane forest. Sampling was carried out in 2007 at the lowland sites and in 2008 at the montane sites. Due to the difference in the length of

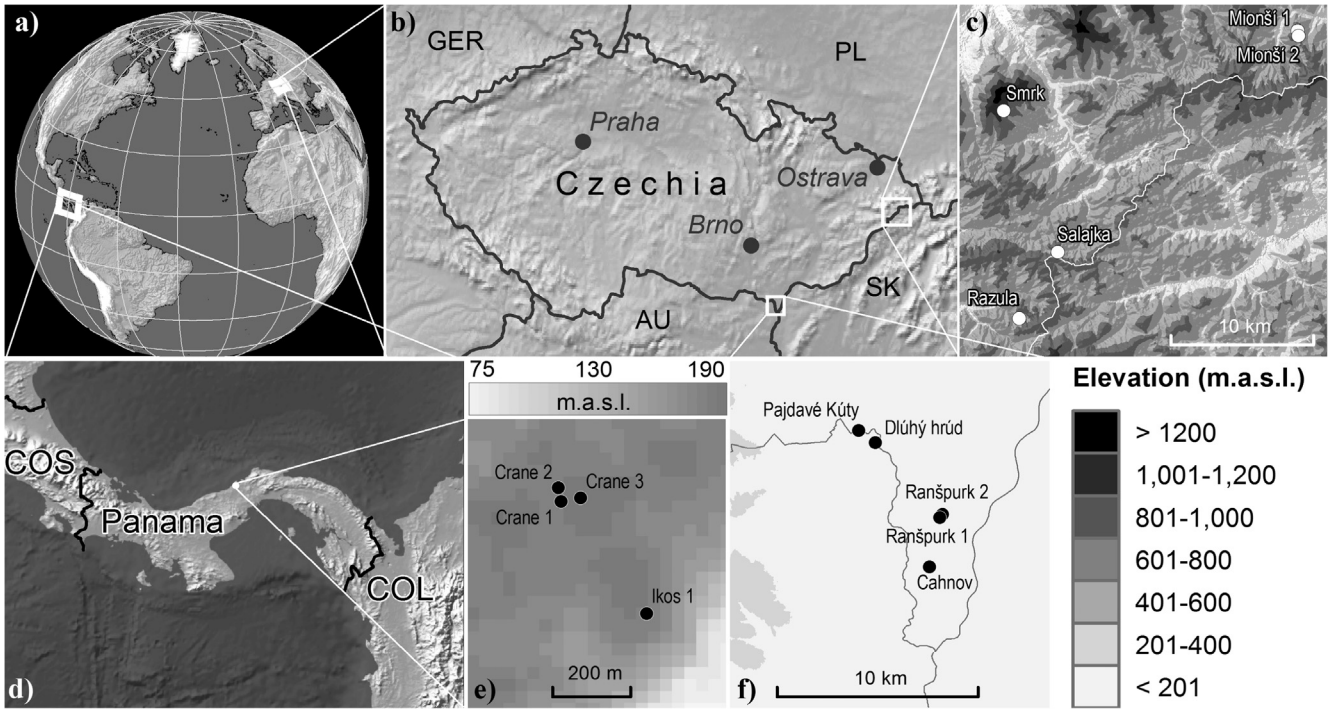

Fig. 1. Global location of the forest sites (a) and location of the two forest sites in the Czech Republic (b). Location of the five sampling sites in the temperate montane forest (c). Location of the study site and the four sampling sites in Panamá (d, e). Location of the five sampling sites in the temperate lowland forest (f).

the vegetation season, traps at the lowland sites were operated from the end of March until the end of September (183 days; 13,725 trap-days sampling effort in total), whereas traps at the montane sites were operated from the end of April (after snow had melted) until the end of September (153 days; 11,475 trap-days sampling effort in total). The sampling thus covered virtually the whole period of beetle activity in both temperate sampling areas.

A list of all sampling sites with all relevant information can be found in the Supplementary Material (Table S1).

The flight intercept traps used were of the cross vane type (the two perpendicular transparent plastic panes were 50 cm high and 25 cm wide) with a roof, and a funnel connected to a collecting bottle with preservative (saturated salt solution with a drop of detergent to eliminate surface tension).

All trapped beetles were sorted and identified to family level, and then families known to contain saproxylic species were sorted further to species or morphospecies. Experienced taxonomic specialists then checked and revised the initial identifications, in order to either confirm species identifications or assign unknown species to higher taxa (mostly genera or tribes). Every saproxylic species was assigned to a feeding guild, as either mycetophagous, xylophagous, zoophagous, or saprophagous based on Leschen et al. (2010), and expert consultations. Larval feeding habits were considered. When unknown, feeding habits were inferred based on known information about closely related taxa. All species associated with fungi, including xylomycetophages and sapromycetophages, were considered as mycetophagous. Staphylinidae were omitted from the dataset due to difficulties with their identification, which is a common approach in previous saproxylic studies and has not been considered to create undue bias in earlier investigations (Sebek et al., 2012; Parmain et al., 2015).

2.3. Data analysis

2.3.1. Species richness and distribution

To compare total observed species richness between the three forest types the expected number of species was interpolated using sample-based rarefaction. The total expected number of species likely to occur at the sites was extrapolated using the classic Chao1 richness estimator with 100 runs for each of the three sampling areas (Chao, 1984). Since sampling covered virtually the entire period of beetle activity in both temperate forest types but only about 60% of the active period in the tropical forest, total richness is likely to be underestimated in the latter case if seasonal species turnover is high (Grimbacher and Stork, 2009). We also tested for a potential undersampling bias between the forest types by calculating incidence based sample coverage estimates (Chao and Jost, 2012; Chao et al., 2014) for all forest types. These analyses were carried out with the iNEXT package (Hsieh et al., 2016) in R 3.5.1 (R Core Team, 2018).

To test the effect of the spatial predictor variables (forest type and vertical strata) on local species richness, we used a generalized linear mixed effects model (GLMM) with Poisson error distribution (and a log-link function) in the lme4 package (Bates et al., 2015) in R 3.5.1 (R Core Team, 2018). To account for the potential confounding influence of sample abundance on richness estimates, we entered the number of beetle specimens as a covariate in the model. We included 'trap height' as a continuous fixed effect and 'forest type' (with three levels: tropical, temperate lowland and temperate montane) as a categorical fixed effect, as well as their interactive effect. 'Sampling transect ID' nested within 'sampling site ID' was used as the random effects structure to account for the non-independence of multiple transects within sites, and multiple traps deployed along each vertical transect. Since there were significant deviations from linear model assumptions for species richness, a 2nd order polynomial function was tested for trap height in the GLMM. Predictors were centred and standardized for model comparisons and model residuals were tested for overdispersion. If overdispersion occurred, 'sample ID' was used as an observation-level random effect (Harrison, 2014). The final, most-parsimonious model was identified following model selection among all possible simplified models using the AICcmodavg package (Mazerolle, 2017) in R 3.5.1 (R Core Team, 2018).

2.3.2. Species dissimilarity

To investigate change in community composition of saproxylic beetles along the vertical transects, a species dissimilarity matrix was

calculated for the samples in each of the three forest types (separately). The Bray-Curtis index was chosen as a measure of dissimilarity since it has proven suitable for ecological comparisons (Legendre and de Cáceres, 2013). From this, we calculated the average pairwise dissimilarity of each beetle sample (N = 72 in the tropical lowland forest, N = 75 in the temperate lowland/montane forests) to the centroid of the respective ground (0 m) samples for that forest type.

We tested the effect of sampling height and forest type on these relative dissimilarity values (referred to hereafter as $Diss_{Rel}$) using a linear mixed effects model (LMM) in the nlme package (Pinheiro et al., 2016) in R 3.5.1 (R Core Team, 2018). We included the log-transform of trap height as a continuous fixed effect and 'forest type' as categorical fixed effect, while 'sampling site ID' and 'sampling transect ID' were included as hierarchical random effects. To meet linear model assumptions, $Diss_{Rel}$ was logit-transformed.

2.3.3. Indicator species

To gain further insight into patterns of vertical distribution, we investigated affinities of individual species to the sampled heights. Characteristic 'indicator species' for trap heights were identified for each of the three forest types as described by Dufrêne and Legendre (1997) using the labdsv package (Roberts, 2016) in R 3.5.1 (R Core Team, 2018). At each vertical height, we counted the number of species that had significant ($p < 0.05$) IndVal values and were an indicator for the particular height.

To test the effect of the spatial predictor variables on the number of 'indicator species', we used a generalized linear mixed effects model (GLMM) with Poisson error distribution in the lme4 package (Bates et al., 2015) in R 3.5.1 (R Core Team, 2018). We used the same model specifications as in the GLMM for species richness (see above).

2.3.4. Feeding guilds

The influence of spatial predictor variables on the relative frequencies of the four feeding guilds (mycetophagous, saprophagous, xylophagous, and zoophagous species) was tested using a log-linear Poisson approach to multinomial analysis. In this approach, the same Poisson GLMM model (with a log-link function) is used as described for the species richness model (see above), except with species counts per functional group as the response variable, and with 'guild' identities entered as an additional fixed categorical predictor variable in the model. The interactions between 'guild' and the other model predictors represent the log-odds that the relative guild frequencies vary with height and between forest types (which are exactly equivalent to the main effects in a multinomial logistic model). We selected the 'zoophagous' guild as the reference category against which relative frequencies of the other three guilds were compared.

3. Results

3.1. Species richness and its vertical distribution

In total, 9247 saproxylic beetle individuals were captured in the tropical lowland forest as opposed to 7429 in the temperate lowland forest and 8939 in the temperate montane forest. The total number of species captured was notably higher in the tropical forest (530 species) than in either the temperate lowland forest (381 species) or temperate montane forest (236 species) (Fig. 2a), and this same trend held true even after standardization of sample abundances (Fig. 2a). Moreover, values of the Chao1 species richness estimator also suggest that undersampling bias was greater at the tropical forest site than at the two temperate sites (Fig. 2a), and this was confirmed with the incidence-based sample coverage estimator, which was markedly higher in the temperate lowland forest (96.5%) and temperate montane forest (96.1%) than in the tropical forest (90.5%).

Species richness peaked in the upper heights of the vertical gradient in the tropical forest, but in the lower vertical heights of both temperate forests (Fig. 2b). Average species richness per trap varied strongly between vertical heights (Fig. 3a), and trends in the vertical distribution of species richness differed significantly between forest types in the GLMM analysis (trap height × forest type interaction effect in Table 1), even after accounting for variation in sample abundances between traps (covariate effect of sample abundance in Table 1). Non-linear trends in vertical distribution were observed at all sites (Table 1), but richness tended to increase from ground to canopy in the tropical forest, and decrease from 1.3 m to canopy in the temperate forests (see Fig. 3a), although the trend was weak in the temperate lowland forest.

3.2. Species dissimilarity

The average dissimilarity between above-ground and ground-level beetle assemblages ($Diss_{Rel}$) increased with trap height in all three forests (Fig. 3b). However, the slope of this increase differed significantly between forest types in the LMM analysis (trap height × forest type interaction effect in Table 2). In both temperate forests the slope was less steep than in the tropical forest with the temperate montane forest showing the least increase along the vertical gradient. The temperate forests also showed a higher dissimilarity among the ground-level beetle assemblages than the tropical forest, particularly in the case of the temperate montane forest (Table 2).

3.3. Indicator species

The number of indicator species per height interval decreased from ground to canopy in all three forests (Fig. 3c) although non-linear trends were evident along the vertical gradient. The slope of this decrease differed significantly between the tropical and the temperate forests (trap height × forest type interaction effect in Table 3) with temperate forests showing a steeper decline in the number of indicator species, whereas the tropical forest had a large peak in indicator species at 21 m but complete absence of indicators species at the uppermost 28 m trap height (Fig. 3c).

3.4. Feeding guilds

There was significant non-uniformity in the distribution of feeding guild proportions along the vertical transect in all forests (Fig. 4). Non-linear trends in vertical distribution were observed for all guilds at all sites. In the tropical forest a significant difference in guild distribution was observed with the proportion of mycetophages decreasing from ground to canopy while that of the other guilds increased (guild × trap height interaction effect in Table 4). This pattern of distribution was highly similar in both temperate forests with a few exceptions. The increase in zoophages from ground to canopy showed a steeper slope in both temperate forests compared to the tropical forest (trap height × forest type interaction effect in Table 4) and the same was true for xylophages (guild X × trap height × forest type interaction effect in Table 4). On the other hand, the proportion of saprophages increased from ground to canopy in the tropical forest but decreased with height in both temperate forests. However, this difference was only significant in the case of the temperate lowland forest (guild S × trap height × forest type interaction effect in Table 4).

4. Discussion

Using a standardized approach, we compared the vertical structuring of saproxylic beetle communities in temperate and tropical forests. Our results provide valuable insights into latitudinal and altitudinal differences in stratification of saproxylic beetles.

4.1. Species richness and vertical stratification patterns

The estimated number of beetle species in the tropical forest was

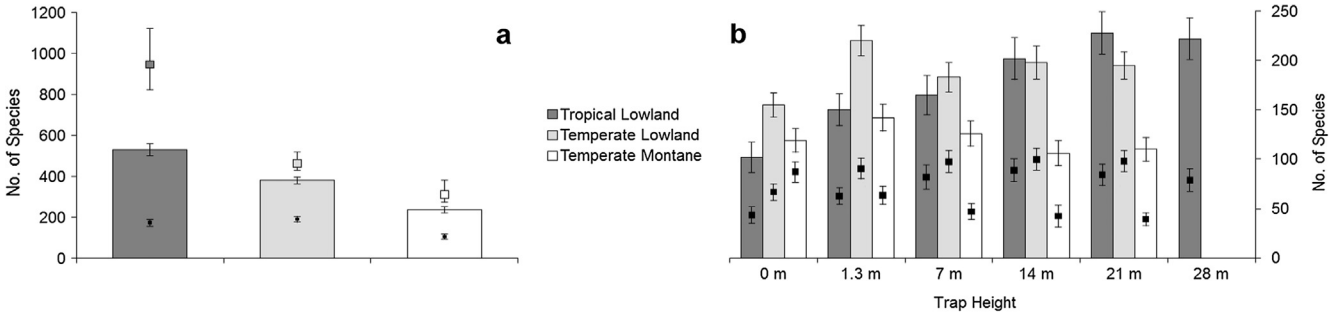

Fig. 2. Species richness estimates for saproxylic beetles in two temperate and one tropical forest. Observed total species richness (bars), estimated total species richness using the Chao1 species richness estimator (squares) and rarefied species richness standardized to a sample of 1000 specimens (black dots) (a). Observed total species richness (bars) and species richness standardized to a sample of 300 individuals (black squares) along the vertical gradients in two temperate and one tropical forest (b) All error bars represent 95% confidence limits.

between two to three times higher than in the temperate lowland and montane forests, respectively. An overall difference of this magnitude is to be expected, considering the latitudinal gradient in insect diversity (Stork, 1988). However the vertical distribution of saproxylic richness differed between the temperate and tropical forests. While the number of species increased almost uniformly with height in the tropical forest and peaked in the canopy (21 m), the vertical trend in species richness was strikingly different in the two temperate forests, with a peak in richness in the understorey at 1.3 m (even after standardising for variation in sample abundance between vertical heights). One implication of this finding is that point alpha diversity in a temperate forest understorey could, at times, be substantially higher than in a tropical rainforest understorey, especially given the pronounced seasonality in temperate forests.

The comparatively low richness near the ground in tropical forests is also likely to be an explanation for the rather low dissimilarity among near-ground samples, and rapid increase in dissimilarity with height in the tropical forest. In temperate forests, by comparison, the among-sample dissimilarity is rather high near the ground, but its rate of change with height is lower. The very high dissimilarity near the ground in the temperate montane forest might partly be attributed to the higher variability due to a wider area being sampled and rugged mountain terrain. The most important finding from the dissimilarity model is that the slopes (reflecting the rate of change in dissimilarity with vertical trap height) clearly differ among the three forests. In this respect, the two lowland forests are more similar to each other than to the montane forest, where dissimilarity shows the lowest increase along the vertical gradient.

The above mentioned diversity patterns are in line with known stratification patterns in tropical (Wardhaugh, 2014) and temperate forests (Ulyshen, 2011). Nevertheless, this study performs the first direct comparison of species richness of entire saproxylic beetle assemblages between tropical and temperate forest ecosystems. The high differences in tree species richness (see Table S1) among sampling sites are not mirrored by beetle diversity, suggesting rather low host specificity of saproxylic beetles in the tropics (or a very long tail of rare, unsampled specialists that we did not encounter). Similarly, low host specificity has also been suggested in previous studies (e.g. Beaver, 1979; Tavakilian et al., 1997; Ødegaard et al., 2000). However, a limitation of our study was the higher undersampling bias in the tropical forest compared to the temperate ones (as estimated by sample coverage measures; Chao and Jost, 2012), and admittedly our sampling only included a portion of the seasonal variation in beetle activity periods in the tropical forest (e.g. Grimbacher and Stork, 2009).

The vertical stratification of beetle species richness and community composition in the three forest types can perhaps be best explained through variation in resource availability and partly also resource competition. Firstly, the stratification of arthropod communities has been linked to the complexity of vertical forest structure (Basset et al., 2003a). Tropical rainforests typically have a higher vertical complexity than temperate forests (Smith, 1973; Terborgh, 1985). The temperate montane forest has, in turn, a simpler vertical structure than the lowland forest (for a detailed description of the structure of both forests see Janik et al., 2013). Sun-lit dead wood is an important resource to many saproxylic beetle species (e.g. Franc et al., 2007), but is virtually absent in the tropical forest understorey where almost no sunlight reaches the ground (Parker, 1995). Close intertwining with lianas, on the other hand, ensures a higher occurrence of standing and especially suspended dead wood in the canopy of tropical forests compared to temperate ones (Martius and Bandeira, 1998). Furthermore, the concentration of supplementary resources such as flowers and fruits, which sustain adults of many beetle species, is much higher in tropical canopies. Another reason for the lower species richness on the forest floor could also be competition from termites (Ødegaard et al., 2000). They are an important part of the saproxylic community in tropical forests and are more active on and near the forest floor than in the canopy (Roisin et al., 2006).

4.2. Indicator species along the vertical gradient

Analysis of the frequency and distribution of potential indicator species (i.e., with high fidelity to specific vertical heights), points to further differences in patterns of beetle vertical stratification between tropical and temperate forests. While the number of indicator species decreased towards the upper vertical heights in all forests, the slope of the relationship was less steep in the tropical forest due to a secondary peak of indicator species at 21 m. This suggests that there is a very distinct community of saproxylic beetles near the ground, adapted to the dark and humid conditions near the forest floor, and in tropical forest this is complemented by a distinct community of species that prefers the drier, sun exposed canopy at 21 m above ground. No species appeared to prefer outer-canopy heights of 28 m in the tropical forest, despite the high observed species richness. Beetles from the lower canopy possibly frequent this height in search of resources, such as flowers, or use it as a dispersal flight route in order to avoid navigating in the denser foliage underneath, but do not appear to live exclusively in this zone.

In both temperate forests the distribution of indicator species followed the pattern of species richness more closely. In temperate forests, with their lower structural complexity, dead wood is more abundant near the ground (e.g. Green and Peterken, 1997; Fridman and Walheim, 1999; Ulyshen, 2011), sunlight availability gradients are less pronounced and there is less competition for the dead wood from e.g. fungi and/or termites. More indicator species thus occur at the heights where most dead wood is accumulated. The lower overall number of indicator species in tropical forests may be attributed at least partly to a much higher proportion of rare species than in temperate forests (Price et al., 1995; Novotný and Basset, 2000).

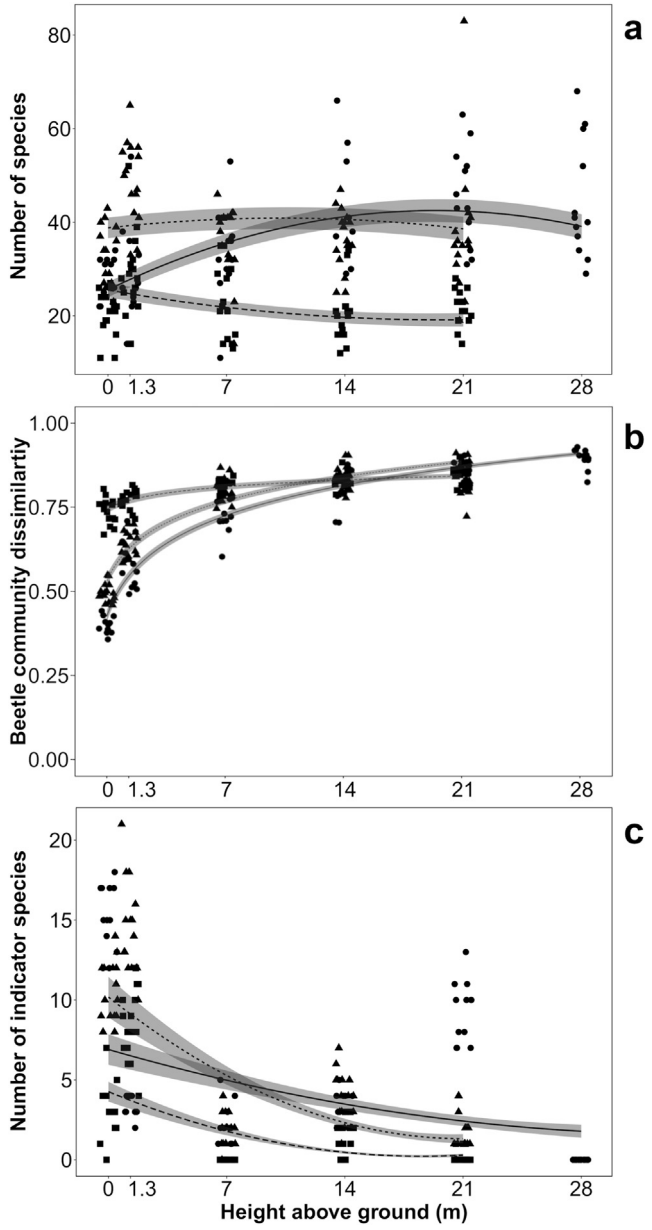

Fig. 3. Observed species richness of saproxylic beetles per sampling point along the vertical transects at each of the respective tropical and temperate sites (a). Beetle community dissimilarity ($Diss_{Rel}$) between each vertical height and the average ground-level community composition at the respective tropical and temperate sites (b). Species richness of indicator beetle species per sample along the vertical transect at the respective tropical and temperate sites (c). In all cases, the fitted lines represent model-predicted estimates (± 1 SE) from mixed-effects models (see methods for further details). Overlapping data points are offset for clarity. (Samples: Tropical lowland = circles; Temperate lowland = triangles; Temperate montane = squares; Fitted Lines: Tropical lowland = solid line; Temperate lowland = dotted line; Temperate montane = broken line).

4.3. Guild composition along the vertical gradient

Saproxylic beetle communities in this study were also stratified in terms of guild composition, as evidenced by all four feeding guilds being influenced by trap height in the three forests studied.

There were subtle, but statistically significant, differences in the vertical distribution of feeding guilds between the forest types. The saprophages showed the most distinctive differences, with a higher proportion near the ground in temperate forests, most likely due to the fact that dead organic matter generally accumulates on the forest floor. In the tropical forest the proportion of saprophages increased with trap height. The reason for this might be that the more complex forest structure ensures that dead organic matter is more evenly vertically distributed in tropical forests (Nadkarni and Longino, 1990). Moreover, the beetles might face more competition on the forest floor from fungi or termites, for example, which have been found to be more prevalent in woody debris on the ground and in the understorey, than in the canopy of tropical forests (Meier et al., 2010, Roisin et al. 2006).

Despite the differentiation of guild composition across vertical heights, patterns of stratification in guild composition were predominantly quite similar between the three forests. For instance, the proportion of mycetophages decreased with height in all three forests. This phenomenon most likely stems from the relatively moist

Table 1
Vertical stratification of beetle species richness in three forest types. Results of a generalised linear mixed effects model (GLMM) showing the influence of sample abundance, trap height (by its 2nd degree polynomials; L = linear component, Q = quadratic component), forest type (TeL = temperate lowland forest, TeM = temperate montane forest) and the interaction between these factors on the number of saproxylic beetle species per sample. SE = Standard error of the model estimate.

Predictor	Estimate	SE	P-Value
Intercept (Tropical forest)	3.63	0.06	< 0.001
Sample abundance	0.31	0.03	< 0.001
Trap Height: L	0.46	0.06	< 0.001
Trap Height: Q	−0.42	0.09	< 0.001
Forest Type: TeL	0.08	0.08	0.361
Forest Type: TeM	−0.60	0.09	< 0.001
Trap Height: L × Forest Type: TeL	−0.45	0.08	< 0.001
Trap Height: Q × Forest Type: TeL	0.27	0.18	0.144
Trap Height: L × Forest Type: TeM	−0.73	0.09	< 0.001
Trap Height: Q × Forest Type: TeM	0.63	0.22	< 0.01

Table 2
Dissimilarity in beetle species composition along vertical gradients in three forest types. Results of a linear mixed effects model (LMM) showing the influence of trap height, forest type (TeL = temperate lowland forest, TeM = temperate montane forest) and the interaction between these factors on the species dissimilarity of saproxylic beetle communities to the average ground-level community at the same site ($Diss_{Rel}$). SE = Standard error of the model estimate.

Predictor	Estimate	SE	P-Value
Intercept (Tropical forest)	−0.38	0.07	< 0.001
log(Trap Height)	0.72	0.02	< 0.001
Forest Type: TeL	0.45	0.10	< 0.01
Forest Type: TeM	1.43	0.10	< 0.001
log(Trap Height) × Forest Type: TeL	−0.13	0.03	< 0.01
log(Trap Height) × Forest Type: TeM	−0.52	0.03	< 0.001

Table 3
Distribution of beetle species associated with certain heights (indicator species) along the vertical gradient in three forest types. Results of a generalised linear mixed effects model (GLMM) showing the influence of trap height, forest type (TeL = temperate lowland forest, TeM = temperate montane forest) and the interaction between these factors on the number of indicator species of saproxylic beetles. SE = Standard error of the model estimate.

Predictor	Estimate	SE	P-Value
Intercept (Tropical forest)	1.46	0.10	< 0.001
log(Trap Height)	−0.87	0.18	< 0.001
Forest Type: TeL	−0.10	0.14	0.464
Forest Type: TeM	−1.33	0.18	< 0.001
Trap Height × Forest Type: TeL	−0.92	0.29	< 0.01
Trap Height × Forest Type: TeM	−1.59	0.39	< 0.001

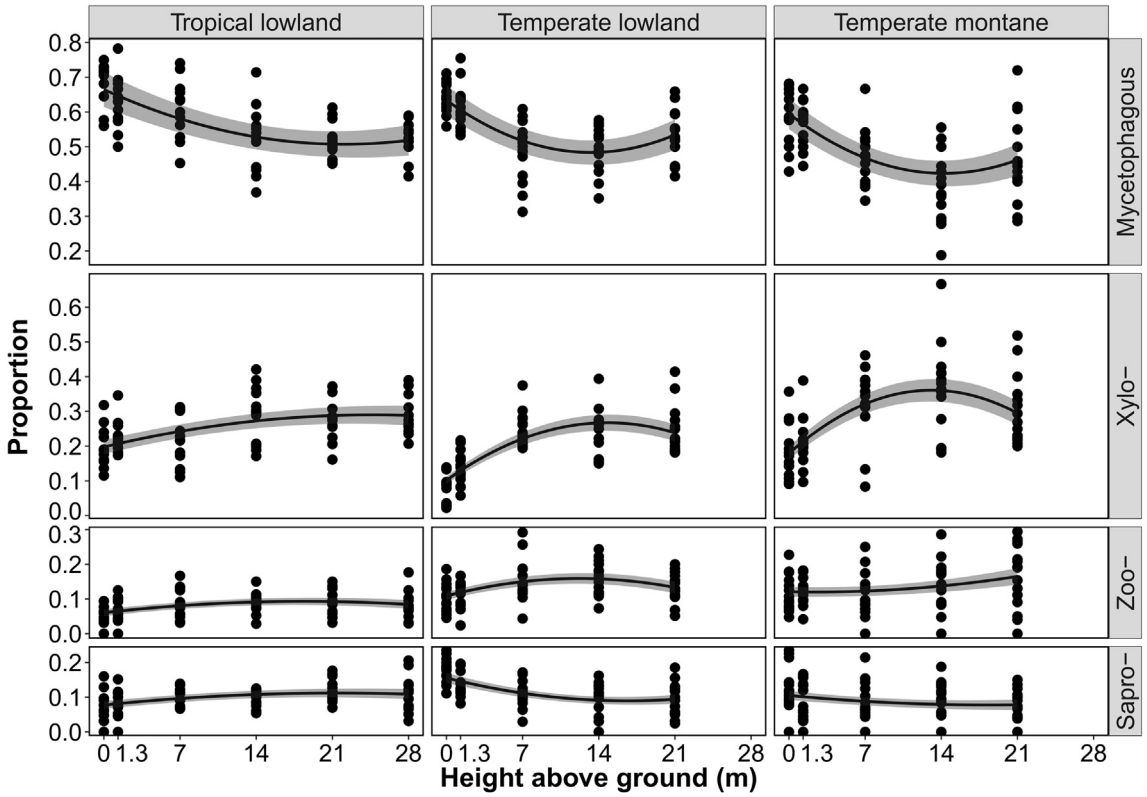

Fig. 4. Variation in the proportions of saproxylic beetle individuals belonging to each of the four feeding guilds along vertical gradients in each forest type. Fitted lines (and confidence intervals) represent model-predicted estimates (± 1 SE) from a log-linear Poisson generalized linear mixed effects model (GLMM). See methods for further details.

conditions near the forest floor that provide better conditions for the fungi that these species rely on (Floren et al., 2014; Ulyshen, 2011). The relative proportion of xylophages generally increased along the vertical gradient in all three forests. Many xylophagous beetles, especially in the families Cerambycidae, Curculionidae and Buprestidae, are known to prefer sun-exposed wood often found in the canopy (e.g. Ødegaard, 2003; Kappes and Topp, 2004). The increasing proportion of zoophages with trap height was also a common phenomenon in all examined forest types. An important reason for this is, most likely, that many species of this guild are predatory as larvae as well as adults (Leschen et al., 2010). Therefore the imagines are usually highly mobile and will prefer the upper parts of the forest where vegetation is less dense and insolation is higher (at least in temperate forests). In the tropical forest, the preference of predators for the upper heights of the canopy can best be explained by the higher amount of resources, such as leaves, flowers and fruits, which attract a higher abundance of prey (Basset et al., 2003b).

4.4. Implications for forest management

Forest management practices that minimize the negative effects of forest use on biodiversity have become an integral part of the forest industry, and underpin core values in the certification of sustainable forest products (Johansson et al., 2013; Jonsson et al., 2016). However, effective management practices must be supported by empirical evidence about the distribution of biodiversity in managed forests. While most saproxylic monitoring surveys assume that sampling at ground level provides a good representation of biodiversity in the forest as a whole (but see Bouget et al., 2011), our study has shown that this is not the case. There were substantial differences in the diversity, species composition and feeding guild proportionality of saproxylic beetles across vertical strata in all forest types sampled. Consequently, management practices aimed at conserving saproxylic beetle diversity, and maintaining important ecosystem services, will need to be tailored to the type of forest in question. In the tropical forest, the understorey stratum was rather species-poor, and contained a distinct suite of indicator species that were not representative of the diversity and composition of saproxylic beetles in higher forest canopy layers. In order to understand potential forest management influences on saproxylic biodiversity, monitoring would have to take vertical stratification patterns into account, especially in forests with complex vertical structure. In temperate forests, on the other hand, ground-level monitoring could provide a much better representation of stand-wide saproxylic communities (comparatively speaking), particularly in forests of lower vertical complexity. Management emphasis might then be best placed on maintaining structurally diverse understories. This is fully in line with previous findings that high canopy closure simplifies understorey vegetation and may threaten saproxylic biodiversity of certain forests (Götmark, 2013; Vodka and Cizek, 2013; e.g. Sebek et al., 2015).

In conclusion, we showed clear vertical stratification of saproxylic beetle communities in tropical and temperate forests at different altitudes. The overall community structure and stratification of feeding guilds were relatively similar between forest types, but the vertical distribution of species richness differed. These patterns may at least partly be due to variation in microclimate and amount and quality of resources. However, research with specific focus on these factors would be required for a more holistic understanding of the spatial distribution of saproxylic species.

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Table 4
Vertical stratification of beetle feeding guilds from three forest types. Results of a generalised linear mixed effects model (GLMM) showing the influence of trap height (by its 2nd degree polynomials; L = linear component, Q = quadratic component), forest type (TeL = temperate lowland forest, TeM = temperate montane forest, reference state = tropical forest), feeding guild (M = mycetophagous, X = xylophagous, S = saprophagous, Z = zoophagous) and the interaction between these factors on the frequency of saproxylic beetle individuals. SE = Standard error of the model estimate.

Predictor	Estimate	SE	P-Value
Intercept (Tropical forest; Guild Z)	1.14	0.12	< 0.001
Guild M	1.87	0.11	< 0.001
Guild S	0.17	0.13	0.2031
Guild X	1.10	0.11	< 0.001
Trap Height: L	0.82	0.19	< 0.001
Trap Height: Q	−0.63	0.28	< 0.05
Forest Type: TeL	0.69	0.15	< 0.001
Forest Type: TeM	−0.07	0.17	0.6840
Guild M × Trap Height: L	−0.64	0.20	< 0.01
Guild S × Trap Height: L	−0.05	0.25	0.8264
Guild X × Trap Height: L	−0.05	0.21	0.7985
Guild M × Trap Height: Q	0.57	0.29	0.0502
Guild S × Trap Height: Q	0.13	0.36	0.7110
Guild X × Trap Height: Q	0.18	0.31	0.5556
Guild M × Forest Type: TeL	−0.73	0.14	< 0.001
Guild S × Forest Type: TeL	−0.62	0.19	< 0.01
Guild X × Forest Type: TeL	−0.64	0.16	< 0.001
Guild M × Forest Type: TeM	−0.63	0.17	< 0.001
Guild S × Forest Type: TeM	−0.59	0.23	< 0.05
Guild X × Forest Type: TeM	−0.08	0.18	0.6497
Trap Height: L × Forest Type: TeL	−0.67	0.23	< 0.01
Trap Height: Q × Forest Type: TeL	0.07	0.46	0.8853
Trap Height: L × Forest Type: TeM	−0.76	0.24	< 0.01
Trap Height: Q × Forest Type: TeM	1.11	0.55	< 0.05
Guild M × Trap Height: L × Forest Type: TeL	0.21	0.23	0.3769
Guild S × Trap Height: L × Forest Type: TeL	−0.67	0.30	< 0.05
Guild X × Trap Height: L × Forest Type: TeL	0.61	0.26	< 0.05
Guild M × Trap Height: Q × Forest Type: TeL	0.71	0.48	0.1413
Guild S × Trap Height: Q × Forest Type: TeL	1.24	0.64	0.0516
Guild X × Trap Height: Q × Forest Type: TeL	−0.77	0.54	0.1586
Guild M × Trap Height: L × Forest Type: TeM	0.12	0.26	0.6246
Guild S × Trap Height: L × Forest Type: TeM	−0.47	0.34	0.1690
Guild X × Trap Height: L × Forest Type: TeM	0.31	0.28	0.2649
Guild M × Trap Height: Q × Forest Type: TeM	−0.29	0.59	0.6172
Guild S × Trap Height: Q × Forest Type: TeM	−0.13	0.82	0.8759
Guild X × Trap Height: Q × Forest Type: TeM	−1.67	0.63	< 0.01

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Appendix A. Supplementary material

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