



HAL
open science

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

Matthias Weiss, Raphael K. Didham, Jiri Procházka, Jiri Schlaghamersky, Yves Basset, Frode Ødegaard, Alexey Tichechkin, Juergen Schmidl, Andreas Floren, Gianfranco Curletti, et al.

► To cite this version:

Matthias Weiss, Raphael K. Didham, Jiri Procházka, Jiri Schlaghamersky, Yves Basset, et al.. Saproxylic beetles in tropical and temperate forests – A standardized comparison of vertical stratification patterns. *Forest Ecology and Management*, 2019, 444, pp.50-58. 10.1016/j.foreco.2019.04.021 . hal-02338148

HAL Id: hal-02338148

<https://hal.science/hal-02338148>

Submitted on 17 May 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

1 **Saproxylic beetles in tropical and temperate forests – a standardized comparison**
2 **of vertical stratification patterns**

3 Matthias Weiss^{a,b*}, Raphael K. Didham^{c,d}, Jiri Procházka^e, Jiri Schlaghamerský^e, Yves Basset^{a,b,f,g},
4 Frode Odegaard^h, Alexey Tichechkinⁱ, Juergen Schmidl^j, Andreas Floren^k, Gianfranco Curletti^l,
5 Henri-Pierre Aberlenc^m, Johannes Bailⁿ, Hector Barrios^g, Maurice Leponce^o, Enrique Medianero^g,
6 Laura L. Fagan^p, Bruno Corbara^q, Lukas Cizek^{a,b}

7

8 ^a Biology Centre CAS, Institute of Entomology, České Budějovice, Czech Republic

9 ^b University of South Bohemia, Faculty of Science, Branišovská 31, 370 05 České Budějovice, Czech Republic

10 ^c School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009,

11 Australia

12 ^d Commonwealth Scientific and Industrial Research Organisation, Centre for Environment and Life Sciences, 147

13 Underwood Ave, Floreat WA 6014, Australia

14 ^e Masaryk University, Faculty of Science, Department of Botany and Zoology, Kotlářská 2, 611 37 Brno, Czech

15 Republic

16 ^f Smithsonian Tropical Research Institute, STRI-Research, 080814 Panama City

17 ^g Universidad de Panamá, Maestría de Entomología, 080814 Panama City, SNI members of SENACYT

18 ^h NTNU University Museum, Department of Natural History, NO-7491, Trondheim, Norway

19 ⁱ National Museum of Natural History, Department of Entomology, Washington, DC 20013–7012, United States of

20 America

21 ^j University of Erlangen-Nuremberg, Department of Biology, 91058 Erlangen, Germany

22 ^k Universität Würzburg, Department of Animal Ecology and Tropical Biology, 97070 Würzburg, Germany

23 ^l Museo Civico di Storia Naturale, 10022 Carmagnola, Italy

24 ^m Cirad, Centre de Biologie pour la Gestion des populations, 34988 Montferrier-sur-Lez, France

25 ⁿ Am Ehrenbach 8, 91356 Kirchehrenbach, Germany

26 ^o Institut Royal des Sciences Naturelles de Belgique, Operational Directorate Natural Environment, 1000 Brussels,

27 Belgium

28 ^p Department of Primary Industries and Regional Development, Biosecurity and Regulations – Grain Industry,

29 Entomology and Biosecurity, 3 Baron-Hay Court, South Perth, WA 6151, Australia

30 [¶] CNRS, UMR 6023, 63177 Aubière & Université Blaise Pascal, 63000 Clermont-Ferrand, France

31

32 **Abstract**

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

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

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

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

61

62 **1. Introduction**

63 Increased exploitation of forests threatens their biodiversity (Hassan et al., 2005). Identifying
64 sustainable forestry practices that minimize the impact of exploitation on forest biodiversity is thus
65 an important priority in forestry research (Brunet et al., 2010; Fedrowitz et al., 2014; Vítková et al.,
66 2018). Beetles associated directly or indirectly with the wood of dead or live trees (i.e. saproxylic
67 beetles) have become model organisms, in many regions, for identifying sustainable forest
68 management practices (Siitonen et al., 2000; Martikainen, 2001; Grove, 2002). They constitute a
69 substantial portion of forest biodiversity and are intensively studied because of the economic
70 importance of some species as pests, and the conservation importance of other species that are
71 threatened with extinction (Stokland et al., 2004; Wermelinger, 2004; Müller et al., 2008; Stokland
72 et al., 2012; Bouget et al., 2013).

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

80 Ødegaard, 2004; Leksono et al., 2005; Wermelinger et al., 2007; Bouget et al., 2011; Vodka and
81 Cizek, 2013; Maguire et al., 2014; Basset et al., 2015).

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

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

102 The above mentioned gaps in knowledge of saproxylic beetles distribution may compromise the
103 effectiveness of forest management practices aimed at conserving the diversity of this group and the
104 ecosystem services they provide (Ulyshen, 2016; Fierro et al., 2017). First, most saproxylic beetle

105 monitoring takes place near ground level, and likely misses a considerable portion of the variation
106 in beetle distributional patterns (but see Leidinger et al., 2019), especially in structurally complex
107 forests (Bouget et al., 2011). Second, recommendations for sustainable forest management practices
108 are based on an understanding of saproxylic beetle communities in a few forest types, under the
109 assumption that similar trends will hold true across regions and biomes.

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

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

122

123 **2. Materials and Methods**

124 **2.1 Study sites**

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

130 Sampling of the temperate forests was performed in a lowland floodplain forest and a montane
131 forest in the Czech Republic. The lowland part of the study was conducted in the oak-dominated
132 alluvial woodlands along the lower Dyje (Thaya) and Morava (March) rivers in southern Moravia.
133 The entire area is considered a hotspot and refuge for the saproxylic fauna (Rozkošný and Vaňhara,
134 1996; Schlaghamerský, 2000, Miklín and Cizek 2014).

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

140

141 *2.2 Sampling protocol*

142 Sampling in the tropical lowland forest focused on four sites. Three of these were within the reach
143 of the Smithsonian Tropical Research Institute canopy crane, while the fourth was situated on a
144 ridge ~ 370 meters from the crane sites (see Fig. 1). At each of the four sampling sites, three vertical
145 transects were installed. Each vertical transect consisted of six unbaited flight intercept traps
146 suspended at 0, 1.3, 7, 14, 21 and 28 meters above the ground (height at the bottom of the
147 interception panels). In total, 72 traps were installed in tropical forest, and beetle samples were
148 collected and sorted every 10-14 days for the period from October 2003 to May 2004 (227 days; 16
149 344 trap-days sampling effort in total), encompassing the extremes of both the wet and dry seasons
150 of the year (Basset et. al 2007).

151 In the temperate forests, five sampling sites were selected in each of the lowland and the montane
152 forest locations (see Fig. 1), and three vertical transects were established at each site. Because of the
153 lower tree heights, the vertical transects in the temperate forests were only sampled at five of the six
154 heights, up to 21 meters. In total, 75 traps were installed in the temperate lowland forest, and 75

155 traps in the temperate montane forest. Sampling was carried out in 2007 at the lowland sites and in
156 2008 at the montane sites. Due to the difference in the length of the vegetation season, traps at the
157 lowland sites were operated from the end of March until the end of September (183 days; 13 725
158 trap-days sampling effort in total), whereas traps at the montane sites were operated from the end of
159 April (after snow had melted) until the end of September (153 days; 11 475 trap-days sampling
160 effort in total). The sampling thus covered virtually the whole period of beetle activity in both
161 temperate sampling areas.

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

164

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

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

180

181 **2.3 Data Analysis**182 *2.3.1 Species richness and distribution*

183 To compare total observed species richness between the three forest types the expected number of
184 species was interpolated using sample-based rarefaction. The total expected number of species
185 likely to occur at the sites was extrapolated using the classic Chao1 richness estimator with 100 runs
186 for each of the three sampling areas (Chao, 1984). Since sampling covered virtually the entire
187 period of beetle activity in both temperate forest types but only about 60 % of the active period in
188 the tropical forest, total richness is likely to be underestimated in the latter case if seasonal species
189 turnover is high (Grimbacher and Stork, 2009). We also tested for a potential undersampling bias
190 between the forest types by calculating incidence based sample coverage estimates (Chao & Jost,
191 2012; Chao et al., 2014) for all forest types. These analyses were carried out with the iNEXT
192 package (Hsieh et al., 2016) in R 3.5.1 (R Core Team, 2018).

193 To test the effect of the spatial predictor variables (forest type and vertical strata) on local species
194 richness, we used a generalized linear mixed effects model (GLMM) with Poisson error distribution
195 (and a log-link function) in the lme4 package (Bates et al., 2015) in R 3.5.1 (R Core Team, 2018).

196 To account for the potential confounding influence of sample abundance on richness estimates, we
197 entered the number of beetle specimens as a covariate in the model. We included ‘trap height’ as a
198 continuous fixed effect and ‘forest type’ (with three levels: tropical, temperate lowland and
199 temperate montane) as a categorical fixed effect, as well as their interactive effect. ‘Sampling
200 transect ID’ nested within ‘sampling site ID’ was used as the random effects structure to account for
201 the non-independence of multiple transects within sites, and multiple traps deployed along each
202 vertical transect. Since there were significant deviations from linear model assumptions for species
203 richness, a 2nd order polynomial function was tested for trap height in the GLMM. Predictors were
204 centred and standardized for model comparisons and model residuals were tested for

205 overdispersion. If overdispersion occurred, ‘sample ID’ was used as an observation-level random
206 effect (Harrison 2014). The final, most-parsimonious model was identified following model
207 selection among all possible simplified models using the AICcmodavg package (Mazerolle, 2017)
208 in R 3.5.1 (R Core Team, 2018).

209

210 2.3.2 *Species dissimilarity*

211 To investigate change in community composition of saproxylic beetles along the vertical transects, a
212 species dissimilarity matrix was calculated for the samples in each of the three forest types
213 (separately). The Bray-Curtis index was chosen as a measure of dissimilarity since it has proven
214 suitable for ecological comparisons (Legendre and de Cáceres, 2013). From this, we calculated the
215 average pairwise dissimilarity of each beetle sample (N=72 in the tropical lowland forest, N=75 in
216 the temperate lowland/montane forests) to the centroid of the respective ground (0m) samples for
217 that forest type.

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

224

225 2.3.3 *Indicator species*

226 To gain further insight into patterns of vertical distribution, we investigated affinities of individual
227 species to the sampled heights. Characteristic ‘indicator species’ for trap heights were identified for
228 each of the three forest types as described by Dufrêne and Legendre (1997) using the labdsv
229 package (Roberts, 2016) in R 3.5.1 (R Core Team, 2018). At each vertical height, we counted the

230 number of species that had significant ($p < 0.05$) IndVal values and were an indicator for the
231 particular height.

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

236

237 *2.3.4. Feeding guilds*

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

248

249 **3. Results**

250 *3.1 Species richness and its vertical distribution*

251 In total, 9 247 saproxylic beetle individuals were captured in the tropical lowland forest as opposed
252 to 7 429 in the temperate lowland forest and 8 939 in the temperate montane forest. The total
253 number of species captured was notably higher in the tropical forest (530 species) than in either the
254 temperate lowland forest (381 species) or temperate montane forest (236 species) (Fig. 2a), and this

255 same trend held true even after standardization of sample abundances (Fig. 2a). Moreover, values of
256 the Chao1 species richness estimator also suggest that undersampling bias was greater at the
257 tropical forest site than at the two temperate sites (Fig. 2a), and this was confirmed with the
258 incidence-based sample coverage estimator, which was markedly higher in the temperate lowland
259 forest (96.5%) and temperate montane forest (96.1%) than in the tropical forest (90.5%).
260 Species richness peaked in the upper heights of the vertical gradient in the tropical forest, but in the
261 lower vertical heights of both temperate forests (Fig. 2b). Average species richness per trap varied
262 strongly between vertical heights (Fig. 3a), and trends in the vertical distribution of species richness
263 differed significantly between forest types in the GLMM analysis (trap height \times forest type
264 interaction effect in Table 1), even after accounting for variation in sample abundances between
265 traps (covariate effect of sample abundance in Table 1). Non-linear trends in vertical distribution
266 were observed at all sites (Table 1), but richness tended to increase from ground to canopy in the
267 tropical forest, and decrease from 1.3 m to canopy in the temperate forests (see Fig. 3a), although
268 the trend was weak in the temperate lowland forest.

269

270 *3.2 Species dissimilarity*

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

278

279 *3.3 Indicator species*

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

286

287 *3.4 Feeding Guilds*

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

300

301 **4. Discussion**

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

305

306 *4.1 Species richness and vertical stratification patterns*

307 The estimated number of beetle species in the tropical forest was between two to three times higher
308 than in the temperate lowland and montane forests, respectively. An overall difference of this
309 magnitude is to be expected, considering the latitudinal gradient in insect diversity (Stork, 1988).

310 However the vertical distribution of saproxylic richness differed between the temperate and tropical
311 forests. While the number of species increased almost uniformly with height in the tropical forest
312 and peaked in the canopy (21 m), the vertical trend in species richness was strikingly different in the
313 two temperate forests, with a peak in richness in the understorey at 1.3 m (even after standardising
314 for variation in sample abundance between vertical heights). One implication of this finding is that
315 point alpha diversity in a temperate forest understorey could, at times, be substantially higher than
316 in a tropical rainforest understorey, especially given the pronounced seasonality in temperate
317 forests.

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

328 The above mentioned diversity patterns are in line with known stratification patterns in tropical
329 (Wardhaugh, 2014) and temperate forests (Ulyshen, 2011). Nevertheless, this study performs the
330 first direct comparison of species richness of entire saproxylic beetle assemblages between tropical

331 and temperate forest ecosystems. The high differences in tree species richness (see Table S1) among
332 sampling sites are not mirrored by beetle diversity, suggesting rather low host specificity of
333 saproxylic beetles in the tropics (or a very long tail of rare, unsampled specialists that we did not
334 encounter). Similarly, low host specificity has also been suggested in previous studies (e.g. Beaver,
335 1979; Tavakilian et al., 1997; Ødegaard et al., 2000). However, a limitation of our study was the
336 higher undersampling bias in the tropical forest compared to the temperate ones (as estimated by
337 sample coverage measures; Chao and Jost, 2012), and admittedly our sampling only included a
338 portion of the seasonal variation in beetle activity periods in the tropical forest (e.g. Grimbacher and
339 Stork, 2009).

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

356

357 ***4.2 Indicator species along the vertical gradient***

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

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

378

379 ***4.3 Guild composition along the vertical gradient***

380 Saproxylic beetle communities in this study were also stratified in terms of guild composition, as

381 evidenced by all four feeding guilds being influenced by trap height in the three forests studied.
382 There were subtle, but statistically significant, differences in the vertical distribution of feeding
383 guilds between the forest types. The saprophages showed the most distinctive differences, with a
384 higher proportion near the ground in temperate forests, most likely due to the fact that dead organic
385 matter generally accumulates on the forest floor. In the tropical forest the proportion of saprophages
386 increased with trap height. The reason for this might be that the more complex forest structure
387 ensures that dead organic matter is more evenly vertically distributed in tropical forests (Nadkarni
388 and Longino, 1990). Moreover, the beetles might face more competition on the forest floor from
389 fungi or termites, for example, which have been found to be more prevalent in woody debris on the
390 ground and in the understorey, than in the canopy of tropical forests (Meier et al., 2010, Roisin et al.
391 2006).

392 Despite the differentiation of guild composition across vertical heights, patterns of stratification in
393 guild composition were predominantly quite similar between the three forests. For instance, the
394 proportion of mycetophages decreased with height in all three forests. This phenomenon most likely
395 stems from the relatively moist conditions near the forest floor that provide better conditions for the
396 fungi that these species rely on (Floren et al., 2014; Ulyshen, 2011). The relative proportion of
397 xylophages generally increased along the vertical gradient in all three forests. Many xylophagous
398 beetles, especially in the families Cerambycidae, Curculionidae and Buprestidae, are known to
399 prefer sun-exposed wood often found in the canopy (e.g. Ødegaard, 2003; Kappes and Topp, 2004).
400 The increasing proportion of zoophages with trap height was also a common phenomenon in all
401 examined forest types. An important reason for this is, most likely, that many species of this guild
402 are predatory as larvae as well as adults (Leschen et al., 2010). Therefore the imagines are usually
403 highly mobile and will prefer the upper parts of the forest where vegetation is less dense and
404 insolation is higher (at least in temperate forests). In the tropical forest, the preference of predators
405 for the upper heights of the canopy can best be explained by the higher amount of resources, such as

406 leaves, flowers and fruits, which attract a higher abundance of prey (Basset et al., 2003b).

407

408 *4.4 Implications for forest management*

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

430

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

437

438 **Acknowledgements**

439 We would like to thank Peter Cate, Jon Cooter, Luboš Dembický, Milada Holecová, Jan Horák,
440 Josef Jelínek, Paul J. Johnson, Miloš Knížek, Vítězslav Kubáň, Pavel Průdek, Tomáš Sitek,
441 Vladimír Švihla (†), Jiří Vávra, and Petr Zahradník, for assistance with material identification,
442 sorting and guild identification, and David Hauck, Stanislav Němejč, Petr Bejdák, Lukáš Bureš, Jan
443 Čížek, Petr Čechovský jr., and Lenka Petráková for help with trap installation and operation.
444 Furthermore we want to thank Jan Miklín for creating the map of the study sites and Marc-Oliver
445 Adams for statistical advice. The Ministry of the Environment of the Czech Republic, and the
446 Forests of the Czech Republic, a state enterprise, permitted us to work in the forests under their
447 direction. The study and its authors were funded from the Grant Agency of the Czech Academy of
448 Sciences (grant No. KJB600960705), Grant Agency of the University of South Bohemia (grant No.
449 04-168/2013/P), the Czech Science Foundation (grant No. P504/12/1952), the Ministry of
450 Education, Youth and Sports of the Czech Republic (Research Plan MSM 0021622416) and the
451 project Biodiversity of Forest Ecosystems (CZ.1.07/2.3.00/20.0064) co-financed by the European
452 Social Fund and the state budget of the Czech Republic. The Panama based authors also received
453 founding from the Secretaria Nacional de Ciencia y Tecnologia (SENACYT). IBISCA-Panama was
454 an initiative of Pro-Natura International, Blaise Pascal University, Universidad de Panama and
455 Smithsonian Tropical Research Institute (STRI) with core funding from SolVin-Solvay SA, the

456 United Nations environment Programme, the Smithsonian Institution (Walcott fund), the European
 457 Science Foundation and the Global Canopy Programme.

458

459 **References:**

- 460 Ashton, L.A., Nakamura, A., Basset, Y., Burwell, C.J., Cao, M., Eastwood, R., Odell, E., de Oliveira, E.G., Hurley, K.,
 461 Katabuchi, M., Maunsell, S., McBroom, J., Schmidl, J., Sun, Z., Tang, Y., Whitaker, T., Laidlaw, M.J.,
 462 McDonald, W.J.F., Kitching, R.L., 2016. Vertical stratification of moths across elevation and latitude. *J.*
 463 *Biogeogr.* 43, 59-69.
- 464 Basset, Y., Hammond, P.M., Barrios, H., Holloway, J.D., Miller, S.E., 2003a. Vertical stratification of arthropod
 465 assemblages, in: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), *Arthropods of Tropical Forests*.
 466 Cambridge University Press. pp. 4-7.
- 467 Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., 2003b. Conclusion: arthropods canopies and interpretable patterns,
 468 in: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), *Arthropods of Tropical Forests*. Cambridge
 469 University Press. pp. 394-405.
- 470 Basset, Y., Corbara, B., Barrios, H., Cuénoud, P., Leponce, M., Aberlenc, H., Bail, J., Bito, D., Bridle, J.R., Castaño-
 471 Meneses, G., Cizek, L., Cornejo, A., Curletti G., Delabie, J.H.C., Dejean, A., Didham, R.K., Dufrêne, M.,
 472 Fagan, L.L., Floren, A., Frame, D.M., Hallé, F., Hardy, O.J., Hernandez, A., Kitching, R.L., Lewinsohn, T.M.,
 473 Lewis, O.T., Manumbor, M., Medianeiro, E., Missa, O., Mitchell, A.W., Mogia, M., Novotny, V., Ødegaard, F.,
 474 de Oliveira, E., Orivel, J., Ozanne, C.M.P., Pascal, O., Pinzón, S., Rapp, M., Ribeiro, S.P., Roisin, Y., Roslin,
 475 T., Roubik, D.W., Samaniego, M., Schmidl, J., Sørensen, L.L., Tishechkin, A., van Osselaer, C., Winchester,
 476 N.N., 2007. IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a
 477 lowland rainforest: rationale, study sites and field protocols. *Bull. Inst. Roy. Sc. Nat. Belg. Ent.* 77, 39-69.
- 478 Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A.K., Schmidl, J.,
 479 Winchester, N.N., Roubik, D.W., Aberlenc, H.P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G.,
 480 Corbara, B., Curletti, G., da Rocha, W.D., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A.,
 481 Kitching, R.L., Medianero, E., de Oliveira, E.G., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y.,
 482 Schmidt, J.P., Sørensen, L., Lewinsohn, T.M., Leponce, M. 2015. Arthropod distribution in a tropical
 483 rainforest: Tackling a four dimensional puzzle. *PLOS One* doi:10.1371/journal.pone.0144110.
- 484 Bates, D., Maechler M., Bolker B., Walker S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*
 485 67, 1-48. doi:10.18637/jss.v067.i01.

- 486 Beaver, R.A., 1979. Host specificity of temperate and tropical animals. *Nature* 281, 139–141.
- 487 Bouget, C., Brin, A., Brustel, H., 2011. Exploring the “last biotic frontier”: Are temperate forest canopies special for
488 saproxylic beetles? *Forest Ecol. Manag.* 261, 211-220.
- 489 Bouget, C., Larrieu, L., Parmain, G., Nusillard, B., 2013. In search of the best local habitat drivers for saproxylic beetle
490 diversity in temperate deciduous forests. *Biodivers. Conserv.* 22, 2111-2130. doi: 10.1007/s10531-013-0531-3.
- 491 Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in european beech forests – a review with recommendations for
492 sustainable forest management. *Ecol. Bull.* 53, 77-94.
- 493 Chao, A., 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Stat.* 11, 265-270.
- 494 Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather
495 than size. *Ecology* 93, 2533-2547.
- 496 Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison A.M., 2014. Rarefaction and
497 extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol.*
498 *Monogr.* 84, 45-67. DOI: 10.1890/13-0133.1.
- 499 Dufrière, M. & Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical
500 approach. *Ecol. Monogr.* 67, 345-366.
- 501 Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki,
502 J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. Can retention forestry help save
503 biodiversity? A meta-analysis. *J. Appl. Ecol.* 51, 1669-1679
- 504 Fermon, H., Waltert, M., Vane-Wright, R.I., Mühlenberg, M., 2003. Forest use and vertical stratification in fruit-feeding
505 butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodivers. Conserv.* 14, 333-350.
- 506 Fierro, A., Grez, A.A., Vergara, P.M., Ramírez-Hernández, A., Micó, E., 2017. How does the replacement of native
507 forest by exotic forest plantations affect the diversity, abundance and trophic structure of saproxylic beetle
508 assemblage? *Forest Ecol. Manag.* 405, 246-256.
- 509 Floren A., Mueller T., Dittrich M., Weiss M., Linsenmair K.E., 2014. The influence of tree species, stratum and forest
510 management on beetle assemblages responding to dead wood enrichment. *Forest Ecol. Manag.* 323, 57-64.
511 doi:10.1016/j.foreco.2014.03.028.
- 512 Franc, N., Götmark, F., Okland, B., Norden, B., Paltto, H., 2007. Factors and scales potentially important for saproxylic
513 beetles in temperate mixed oak forest. *Biol. Conserv.* 135, 86–98.
- 514 Fridman, J., Walheim, M., 1999. Amount, structure and dynamics of dead wood on managed forestland in sweden.
515 *Forest Ecol. Manag.* 131, 23-36.

- 516 Götmark, F., 2013. Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis
517 and implications. *Forest Ecol. Manag.* 131, 292-307
- 518 Green, P., Peterken, G.F., 1997. Variation in the amount of dead wood in the woodlands of the lower Wye Valley, UK in
519 relation to the intensity of the management. *Forest Ecol. Manag.* 98, 229-238.
- 520 Grimbacher, P.S., Stork, N.E., 2009. Seasonality of a diverse beetle assemblage inhabiting lowland tropical rainforest in
521 Australia. *Biotropica* 41, 328-337.
- 522 Grove, S.J., Stork, N.E., 1999. The conservation of saproxylic insects in tropical forests: a research agenda. *J. Insect*
523 *Conserv.* 3, 67-74.
- 524 Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests, in: Futuyama, D.J. (Ed.),
525 *Annu. Rev. Ecol. Evol. S.* 33, 1-23.
- 526 Hassan, R. M., Scholes, R., Ash, N. (Eds.), 2005. *Ecosystems and human well-being: current state and trends:*
527 *findings of the Condition and Trends Working Group.* Millennium Ecosystem Assessment Series, volume 1.
528 Island Press, Washington, D.C., USA.
- 529 Harrison, X.A., 2014. Using observation-level random effects to model overdispersion in count data in ecology and
530 evolution. *PeerJ* 2:e616DOI 10.7717/peerj.616
- 531 Homeier, J., Breckle, S.W., Günter, S., Rollenbeck, R.T., Leuschner, C., 2010. Tree diversity, forest structure and
532 productivity along altitudinal and topographical gradients in a species-rich ecuadorian montane rain forest.
533 *Biotropica* 42, 140-148.
- 534 Hsieh, T. C., Ma, K. H., Chao, A., 2016. iNEXT: Interpolation and Extrapolation for species diversity. R package
535 version 2.0.12 URL: <http://chao.stat.nthu.edu.tw/blog/software-download/>
- 536 Intachat, J., Holloway, J.D., 2000. Is there stratification in diversity or preferred flight height of geometroid moths in
537 Malaysian lowland tropical forest? *Biodivers. Conserv.* 9, 1417-1439.
- 538 Janik, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., Horal, D., 2013. Spatiotemporal differences in
539 tree spatial patterns between alluvial hardwood and mountain beech-fir forests: do characteristic patterns exist?
540 *J. Veg. Sci.* 24, 1141-1153. doi: 10.1111/jvs.12018.
- 541 Johansson, T., Hjältén, J., de Jong, J., von Stedingk, H., 2013. Environmental considerations from legislation and
542 certification in managed forest stands: A review of their importance for biodiversity. *Forest Ecol. Manag.* 303,
543 98-112
- 544 Jonsson, B.G., Ekström, M., Esseen, P.A., Grafström, A., Ståhl, G., Westerlund, B., 2016. Dead wood availability in
545 managed swedish forests – Policy outcomes and implications for biodiversity. *Forest Ecol. Manag.* 376, 174-

- 546 182
- 547 Kappes, H., Topp, W., 2004. Emergence of coleoptera from deadwood in a managed broadleaved forest in central
548 europe. *Biodivers. Conserv.* 13, 1905-1925.
- 549 Legendre, P., & De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and
550 partitioning. *Ecol. Lett.* 16, 951-963.
- 551 Leidinger, J., Seibold, S., Weisser, W.W., Lange, M., Schall, P., Türke, M., Gossner, M.M., 2019. Effects of forest
552 management on herbivorous insects in temperate Europe. *Forest Ecol. Manag.* 437, 232-245.
- 553 Leksono, A.S., Takada, K., Shinsaku, K., Nobukazu, N., Anggraeni, T., Nakamura, K., 2005. Vertical and seasonal
554 distribution of flying beetles in a suburban deciduous temperate forest collected by water pan traps. *Insect Sci.*
555 12, 199-206. doi: 10.1111/j.1744-7917.2005.00025.x.
- 556 Leschen, R.A.B., Beutel, R.G., Lawrence, J.F., 2010. Coleoptera, Beetles, in: Kristensen NP, Beutel RG, (Eds.),
557 *Handbook of Zoology, Arthropoda: Insecta*. De Gruyter, Berlin/New York.
- 558 Lieberman, D., Lieberman, M., Peralta, R., Hartshorn, G.S., 1996. Tropical forest structure and composition on a large-
559 scale altitudinal gradient in Costa Rica. *J. Ecol.* 84, 137-152.
- 560 Maguire, D.Y., Robert, K., Brochu, K., Larrivé, M., Buddle, C.M., Wheeler, T.A., 2014 Vertical stratification of beetles
561 (Coleoptera) and flies (Diptera) in temperate forest canopies. *Environ. Entomol.* 43, 9-17. doi:
562 10.1603/EN13056.
- 563 Martikainen, P., 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on
564 clearcut areas. *Ecol. Bull.* 49, 205-218. doi: 10.2307/20113277.
- 565 Martius, C., Bandeira, A.C., 1998. Wood litter stock in tropical moist forests in central Amazonia. *Ecotropica* 4, 115-
566 118.
- 567 Mazerolle, M.J., 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package
568 version 2.1-1. <https://cran.r-project.org/package=AICcmodavg>.
- 569 Meier, C.L., Rapp, J., Bowers, R.M., Silman, M., Fierer, N., 2010. Fungal growth on a common wood substrate across a
570 tropical elevation gradient: Temperature sensitivity, community composition, and potential above-ground
571 decomposition. *Soil Biol. Biochem.* 42, 1083-1090.
- 572 Müller, J., Bussler, H., Gossner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle *Ips typographus*
573 in a national park: from pest to keystone species. *Biodivers. Conserv.* 17, 2979-3001. doi: 10.1007/s10531-008-
574 9409-1.
- 575 Nadkarni, N.M., Longino, J.T., 1990. Invertebrates in canopy and ground organic matter in a neotropical montane

- 576 forest, Costa Rica. *Biotropica* 22, 286-289.
- 577 Novotný, V., Basset, Y., 2000. Rare species in communities of tropical insect herbivores: pondering the mysteries of
578 singletons. *OIKOS* 89, 564-572.
- 579 Ødegaard, F., 2000. The relative importance of trees versus lianas hosts for phytophagous beetles (Coleoptera) in
580 tropical forests. *J. Biogeogr.* 27, 283-296.
- 581 Ødegaard, F., 2003. Taxonomic composition and host specificity of phytophagous beetles in a dry forest in Panama, in:
582 Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), *Arthropods of Tropical Forests*. Cambridge
583 University Press. pp. 220-236.
- 584 Ødegaard, F., 2004. Species richness of phytophagous beetles in the tropical tree *Brosimum utile* (Moraceae): the
585 effects of sampling strategy and the problem of tourists. *Ecol. Entomol.* 29, 76-88.
- 586 Parker, G.G., 1995. Structure and microclimate of forest canopies, in: Lowman, M.D., Nadkarni, N.M.. (Eds.), *Forest*
587 *Canopies*. Academic Press, San Diego, pp 431-455.
- 588 Pinheiro J., Bates D., DebRoy S., Sarkar D. & R Core Team (2016). nlme: Linear and Nonlinear Mixed Effects Models.
589 R package version 3.1-128, URL: <http://CRAN.R-project.org/package=nlme>.
- 590 Price, P. W., Diniz, I. R., Morais, H. C., Marques, E. S. A, 1995. The abundance of insect herbivore species in the
591 tropics: the high local richness of rare species. *Biotropica* 27, 468-478.
- 592 Procházka, J., Schlaghamerský, J., Cizek, L., 2015. Vertical stratification of scolytine beetles in temperate forests.
593 *Insect Conserv. Diver.* <https://doi.org/10.1111/icad.12301>
- 594 R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing,
595 Vienna, Austria. URL <http://www.R-project.org/>.
- 596 Roberts, D. W., 2016. labdsv: Ordination and Multivariate Analysis for Ecology. R package version 1.8-0.
597 <https://CRAN.R-project.org/package=labdsv>.
- 598 Roisin, Y., Dejean, A., Corbara, B., Orivel, J., Samaniego, M., Leponce, M., 2006. Vertical stratification of the termite
599 assemblage in a neotropical rainforest. *Oecologia* 149, 301-311. doi: 10.1007/s00442-006-0449-5.
- 600 Rozkošný, R. & Vaňhara, J., 1996. Terrestrial Invertebrates of the Pálava Biosphere Reserve of UNESCO, I-III. *Folia*
601 *Facultatis scientiarum naturalium Universitatis Masarykianae Brunensis*, *Biologia* 92, 1-208, 93, 209-408,
602 94, 409-630.
- 603 Schlaghamerský, J., 2000. The saproxylic beetles (Coleoptera) and ants (Formicidae) of central European hardwood
604 floodplain forests. *Folia Facultatis scientiarum naturalium Universitatis Masarykianae Brunensis*, *Biologia*
605 103, 1-168.

- 606 Schulze, C.H., Linsenmair, K.E., Fiedler, K., 2001. Understorey versus canopy: patterns of vertical stratification and
607 diversity among Lepidoptera in a Bornean rain forest. *Plant Ecol.* 153, 133-152.
- 608 Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose,
609 O., Velle, L. & Bouget, C., 2012. A test for assessment of saproxylic beetle biodiversity using subsets of
610 “monitoring species”. *Ecol. Indic.* 20, 304-315.
- 611 Sebek, P., Bace, R., Bartos, M., Benes, J., Chlumska, Z., Dolezal, J., Dvorsky, M., Kovar, J., Machac, O., Mikatova, B.,
612 Perlik, M., Platek, M., Polakova, S., Skorpik, M., Stejskal, R., Svoboda, M., Trnka, F., Vlasin, M., Zapletal,
613 M., Cizek, L., 2015. Does a minimal intervention approach threaten the biodiversity of protected areas? A
614 multi-taxa short-term response to intervention in temperate oak-dominated forests. *Forest Ecol. Manag.* 358,
615 80-89
- 616 Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature
617 managed and old-growth boreal mesic forests in southern Finland. *Forest Ecol. Manag.* 128, 211–225. doi:
618 10.1016/S0378-1127(99)00148-6.
- 619 Smith, A.P., 1973. Stratification of temperate and tropical forests. *Am. Nat.* 107, 671-683.
- 620 Stokland, J.N., Tomter, S.M., Söderberg, G.U. Development of dead wood indicators for biodiversity monitoring:
621 experiences from Scandinavia, in: Marchetti, M. (Ed.), *Monitoring and indicators of forest biodiversity in*
622 *Europe – from ideas to operationality*. European Forest Institute, EFI Proceedings 51; 2004. pp. 207-226.
- 623 Stokland, J.N., Siitonen, J., Jonsson, B.G. Biodiversity in dead wood. Cambridge University Press, Cambridge; 2012.
624 521 pp.
- 625 Stork, N.E., 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* 35, 321-337.
- 626 Tanabe, S., 2002. Between-forest variation in vertical stratification of drosophilid populations. *Ecol. Entomol.* 27, 720-
627 731. doi: 10.1046/j.1365-2311.2002.00469.x.
- 628 Tavakilian, G., Berkov, A., Meurer-Grimes, B., Mori, S., 1997. Neotropical tree species and their faunas of
629 xylophagous longicorns (Coleoptera: Cerambycidae) in French Guiana. *Bot. Rev.* 63, 303–355.
- 630 Terborgh, J., 1985. The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.* 126,
631 760-776.
- 632 Tykarski, P., 2006. Beetles associated with scolytids (Coleoptera, Scolytidae) and the elevational gradient: Diversity
633 and dynamics in the Tatra National Park, Poland. *Forest Ecol. Manag.* 225, 146-159. doi:
634 10.1016/j.foreco.2005.12.034.
- 635 Ulyshen M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation

- 636 oriented management. *Forest Ecol. Manag.* 261, 1479-1489. doi:10.1016/j.foreco.2011.01.033.
- 637 Ulyshen M.D., 2016. Wood decomposition as influenced by invertebrates. *Biol. Rev.* 91, 70-85
- 638 Vávra, J.C., Stanovský, J. Brouci (Coleoptera), in: Roháček, J., Ševčík, J., Vlk, P. (Eds.), Příroda Slezska. Slezské
639 zemské muzeum [Nature of Silesia. Silesian State Museum]. Opava; 2013. 480 pp.
- 640 Vítková, L., Baček, R., Kjučukov, P., Svoboda, M., 2018. Deadwood management in central european forests: Key
641 considerations for practical implementation. *Forest Ecol. Manag.* 429, 394-405
- 642 Vodka, Š., Cizek, L., 2013. The effects of edge interior and understorey-canopy gradients on the distribution of
643 saproxylic beetle beetles in a temperate lowland forest. *Forest Ecol. Manag.* 304, 33-41.
- 644 Wardhaugh, C.W., 2014. The spatial and temporal distributions of arthropods in forest canopies: uniting disparate
645 patterns with hypotheses for specialisation. *Biol. Rev.* 89, 1021-1041.
- 646 Weaver, P.L. & Bauer, G.P.. The San Lorenzo Protected Area: A Summary of Cultural and Natural Resources.
647 International Institute of Tropical Forestry, San Juan, PR.; 2004. 68 pp.
- 648 Weiss, M., Procházka, J., Schlaghamerský J., Cizek, L., 2016. Fine-scale vertical stratification of saproxylic beetles in
649 lowland and montane forests: Similar patterns despite low faunal overlap. *PLoS ONE* 11 e0149506.
- 650 Wermelinger, B., 2004. Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent
651 research. *Forest Ecol. Manag.* 202, 67-82.
- 652 Wermelinger, B., Flückiger, P.F., Obrist, M.K., Duelli, P., 2007. Horizontal and vertical distribution of saproxylic
653 beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *J. Appl. Entomol.* 131,
654 104–114. doi: 10.1111/j.1439-0418.2006.01128

655

656 **Tables:**

657 **Table 1: Vertical stratification of beetle species richness in three forest types.** Results of a generalised linear mixed
658 effects model (GLMM) showing the influence of sample abundance, trap height (by its 2nd degree polynomials; L =
659 linear component, Q = quadratic component), forest type (TeL = temperate lowland forest, TeM = temperate montane
660 forest) and the interaction between these factors on the number of saproxylic beetle species per sample. SE = Standard
661 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

662

663

664 **Table 2: Dissimilarity in beetle species composition along vertical gradients in three forest types.** Results of a linear
665 mixed effects model (LMM) showing the influence of trap height, forest type (TeL = temperate lowland forest, TeM =
666 temperate montane forest) and the interaction between these factors on the species dissimilarity of saproxylic beetle
667 communities to the average ground-level community at the same site ($Diss_{Rel}$). SE = Standard error of the model
668 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

669

670 **Table 3: Distribution of beetle species associated with certain heights (indicator species) along the vertical gradient**
 671 **in three forest types.** Results of a generalised linear mixed effects model (GLMM) showing the influence of trap height,
 672 forest type (TeL = temperate lowland forest, TeM = temperate montane forest) and the interaction between these factors
 673 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

674

675 **Table 4: Vertical stratification of beetle feeding guilds from three forest types.** Results of a generalised linear mixed
 676 effects model (GLMM) showing the influence of trap height (by its 2nd degree polynomials; L = linear component, Q =
 677 quadratic component), forest type (TeL = temperate lowland forest, TeM = temperate montane forest, reference state =
 678 tropical forest), feeding guild (M = mycetophagous, X = xylophagous, S = saprophagous, Z = zoophagous) and the
 679 interaction between these factors on the frequency of saproxylic beetle individuals. SE = Standard error of the model
 680 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

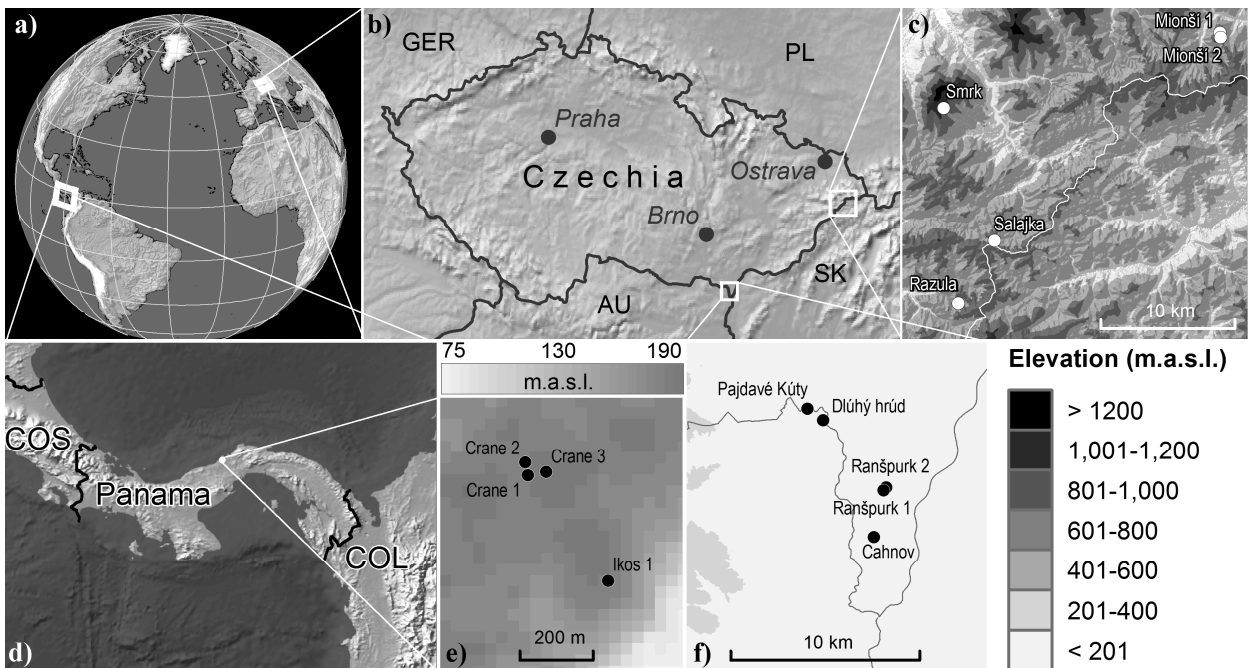
Trap Height: L	0.82	0.19	< 0.001
Trap Height: Q	- 0.63	0.28	< 0.05
Forest Type: TeL	0.69	0.15	< 0.001
Forest Type: TeM	- 0.07	0.17	0.6840
Guild M × Trap Height: L	- 0.64	0.20	< 0.01
Guild S × Trap Height: L	- 0.05	0.25	0.8264
Guild X × Trap Height: L	- 0.05	0.21	0.7985
Guild M × Trap Height: Q	0.57	0.29	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

681

682

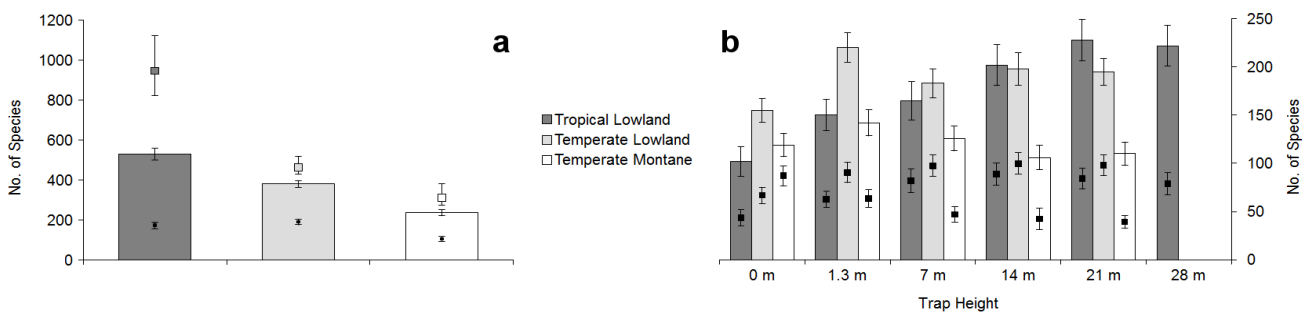
683 **Figures:**



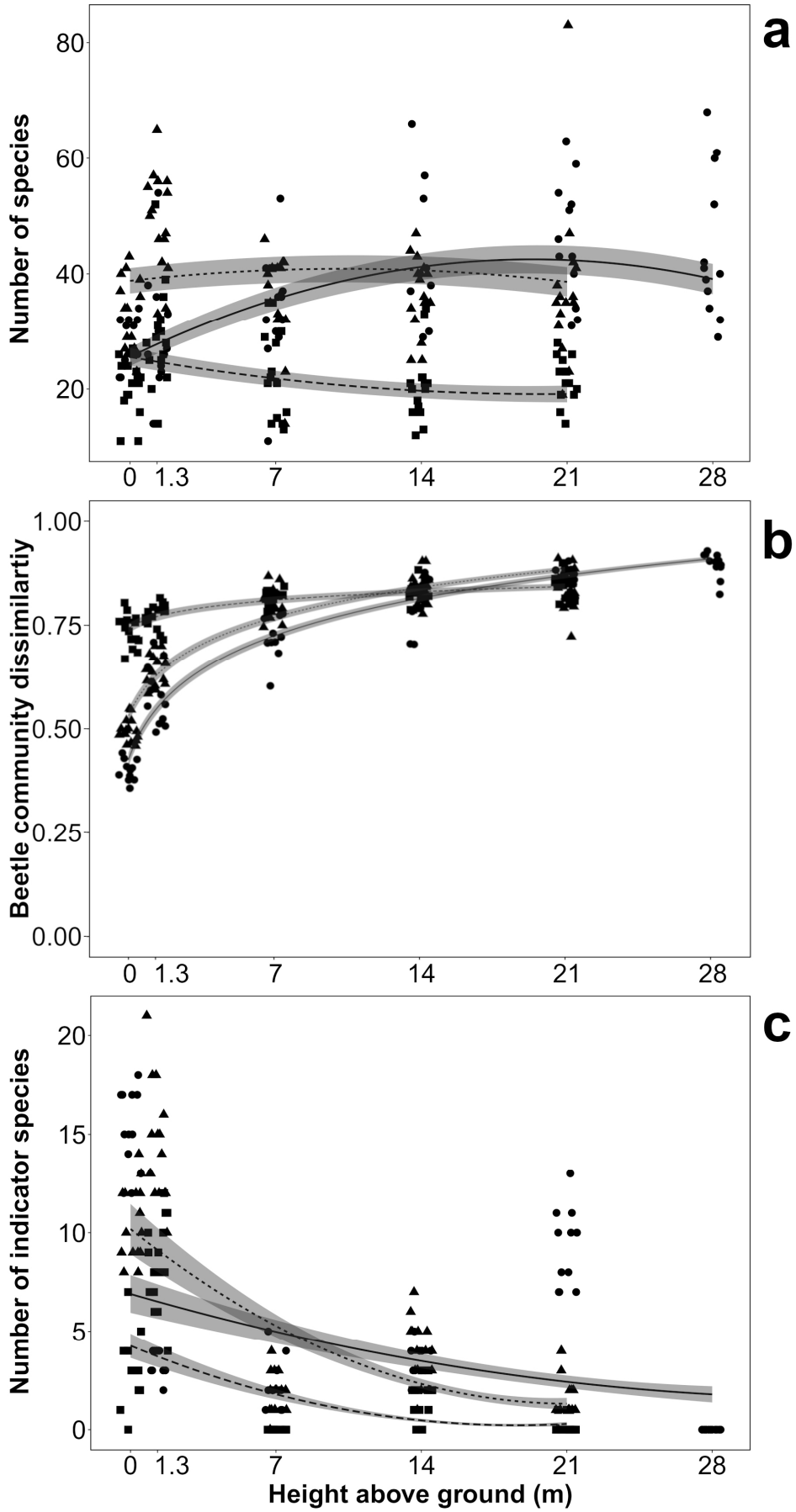
684

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

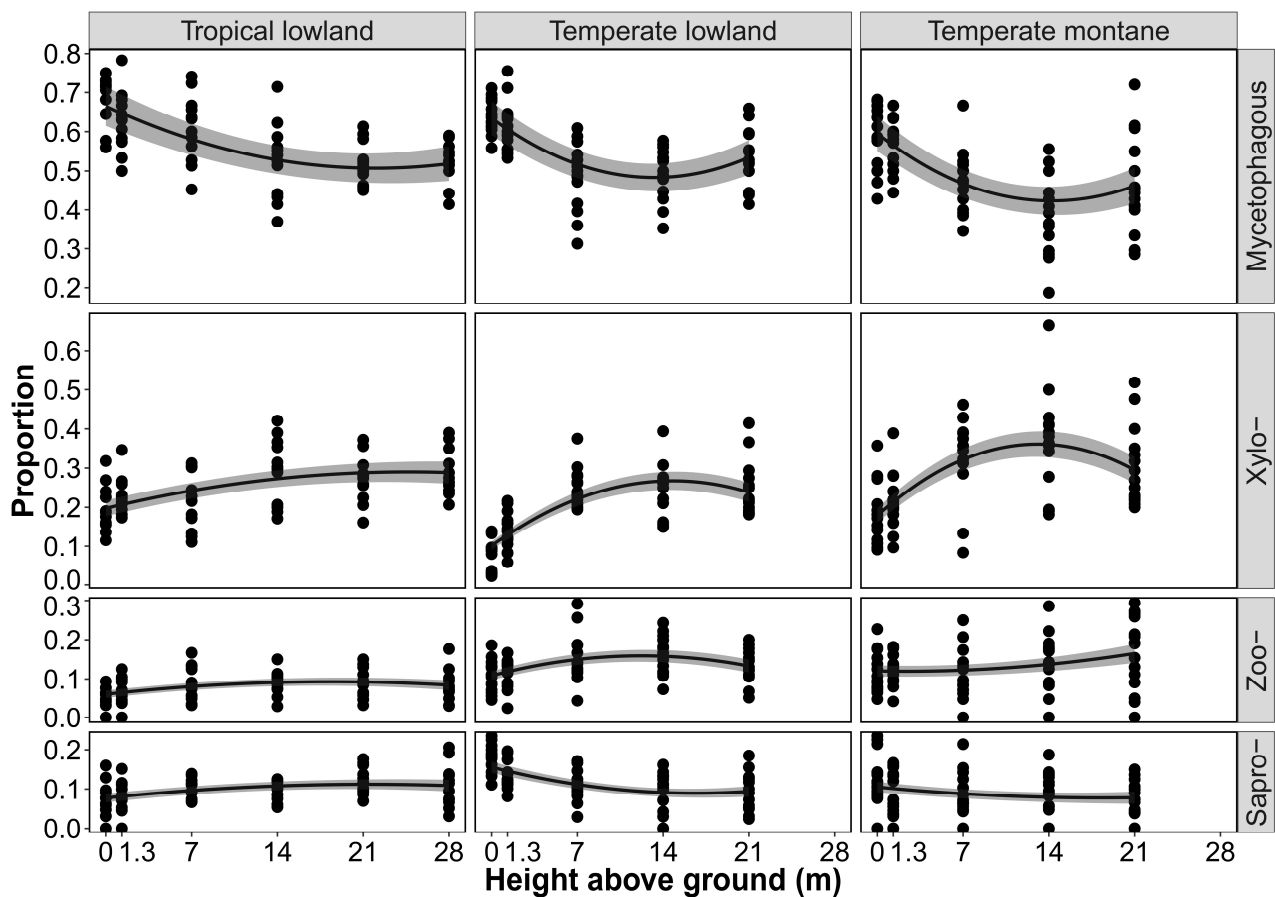
688



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



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



703

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