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1 **Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case**  
2 **study in unfragmented montane forests**

3

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20 **Abstract**

21 Understanding the processes that shape biodiversity patterns is essential for ecosystem management and  
22 conservation. Local environmental conditions are often good predictors of species distribution and variations in  
23 habitat quality usually positively correlate to species richness. However, beside habitat limitation, species  
24 presence-absence may be constrained by dispersal limitation. We tested the relative importance of both  
25 limitations on saproxylic beetle diversity, using forest continuity as a surrogate for dispersal limitation and  
26 stand maturity as a surrogate for habitat limitation. Forest continuity relies on the maintenance of a forest  
27 cover over time, while stand maturity results in the presence of old-growth habitat features. Forty montane  
28 beech-fir forests in the French pre-Alps were sampled, under a balanced sampling design in which forest  
29 continuity and stand maturity were crossed. A total of 307 saproxylic beetle species were captured using flight-  
30 interception traps and Winkler-Berlese extractors. We explored the response of low- versus high-dispersal  
31 species groups to forest continuity and stand maturity. Saproxylic beetle diversity increased significantly with  
32 stand maturity and was mostly influenced by variables related to deadwood diversity at the stand scale and  
33 suitable habitat availability at the landscape scale. Surprisingly, no evidence of dispersal limitation was found,  
34 as diversity patterns were not influenced by forest continuity and associated variables, even for low-dispersal  
35 species. Our study demonstrates that in an unfragmented forest landscape, saproxylic beetles are able to  
36 colonize recent forests, as long as local deadwood resources are sufficiently diversified (e.g. tree species,  
37 position, diameter and/or decay stage).

38

39 **Keywords:** biodiversity patterns, forest continuity, stand maturity, saproxylic beetles.

40

41 **Introduction**

42           Understanding the processes that shape local species composition and diversity is a fundamental  
43 question in ecology (Sutherland et al. 2013). Variability in local species diversity is usually assumed to reflect  
44 differences in environmental conditions. This assumption relies both on the island biogeography theory  
45 (MacArthur and Wilson 1967) and the ecological niche theory (Hutchinson 1957), where species-rich sites  
46 result from species coexistence through habitat availability and heterogeneity, two complementary qualities  
47 usually correlated. However, beside habitat limitation, variability in local species diversity may result from  
48 dispersal limitations that constrain species movements toward suitable habitats (Pulliam 2000). Understanding  
49 the relative influence of dispersal versus habitat limitations has implications for biodiversity conservation and  
50 the management of ecosystems (Hodgson et al. 2011).

51           Species dispersal plays several fundamental roles in communities dynamics through the colonization of  
52 newly available habitats and genetic flow (Clobert et al. 2012). Dispersal is closely related to spatio-temporal  
53 variations in resource availability, given that species tend to move from poor-quality to high-quality habitats  
54 (Lowe 2009). However, dispersal abilities vary within and among species groups, which can be defined  
55 according to species traits such as flight ability for animals. Depending on dispersal abilities and distance to  
56 habitat source, colonization of newly available habitats may take more or less time and explain the absence of  
57 species from suitable habitats (Pulliam 2000).

58           Even for high-dispersal species, the ability to successfully establish a population in new habitat patches  
59 remains dependent on species-specific requirements. Species niche breadth shows the ability of a given  
60 individual species to perform as a function of resource availability (Devictor et al. 2010). Furthermore, habitat  
61 quality may contribute to species presence-absence patterns (Pulliam 2000). Indeed, habitats that include both  
62 a large amount and a diversity of resources may support a greater diversity of species, including specialists  
63 which are able to perform thanks to very specific resources. Variations in habitat quality therefore provide a  
64 practical framework in which to study patterns of species diversity.

65           In forest ecosystems, forest continuity and stand maturity have contrasting effects on biodiversity.  
66 Forest continuity is related to the maintenance of forest cover over time, regardless of stand maturity and  
67 management type. Ancient forests have been in continuous existence for at least 200 years while recent forests  
68 are mainly agricultural areas afforested during the last 200 years (Hermý and Verheyen 2007). Experimental

69 studies testing the role of forest continuity in shaping community structure have largely focused on plants  
70 (Hermy and Verheyen 2007). Results have shown that plant species closely related to ancient forests were  
71 usually more adapted to forest interior conditions (e.g. shade tolerant) and have short-distance dispersal  
72 abilities (e.g. myrmecochory) (Verheyen et al. 2003; Sciama et al. 2009). However, the influence of forest  
73 continuity on other taxa remained unclear since very few studies have been conducted to date (e.g. Assmann  
74 1999; Gossner et al. 2008; Buse 2012). Stand maturity is usually related to old-growth habitat features.  
75 Compared to mature stands, overmature stands are characterized by a greater proportion of very large trees  
76 (e.g. Whitman and Hagan 2007), and a larger abundance and diversity of deadwood (e.g. Meyer and Schmidt  
77 2011) and tree-related microhabitats (e.g. Winter and Möller 2008). By enhancing habitat quality, overmature  
78 stands may improve species coexistence, especially for saproxylic species depending on specific deadwood  
79 resources (e.g. Stenbacka et al. 2010; Lassauce et al. 2012). Finally, overmature stands may highlight the effect  
80 of habitat limitation on biodiversity patterns.

81           Using forest continuity as a surrogate for dispersal limitation and stand maturity as a surrogate for  
82 habitat limitation, we evaluated the relative importance of both limitations on saproxylic beetle diversity  
83 patterns. Saproxylic beetles are a rich group of specialized species that depend on deadwood for at least a part  
84 of their lifecycle (Speight 1989). They are among the first organisms to colonize dying trees and, consequently,  
85 play a fundamental role in wood decomposition and nutrient recycling (Speight 1989; Siitonen 2001). Previous  
86 works have shown that saproxylic beetle diversity is closely linked to deadwood quantity (Lassauce et al. 2011;  
87 Lachat et al. 2012; Bouget et al. 2014) and that many species are more closely linked to specific deadwood  
88 qualities such as tree species, diameter, stage of decay and microhabitat presence (Jonsell et al. 2007; Brin et  
89 al. 2011; Bouget et al. 2013). Saproxylic beetle diversity may therefore respond to stand maturity. Moreover,  
90 dispersal abilities vary greatly among saproxylic species, i.e. between flightless and flying beetles. Since  
91 probability of colonization is a function of patch isolation in space and time (Clobert et al. 2012), response of  
92 saproxylic beetles to forest continuity may depend on their dispersal abilities. This suggests that low- and high-  
93 dispersal species may have different response patterns to both environmental conditions (Lassau et al. 2005;  
94 Janssen et al. 2009) and distance to sources (Irmiler et al. 2010; Bouget et al. 2015).

95           Based upon a sampling design crossing forest continuity and stand maturity, we quantified the relative  
96 contribution of dispersal and habitat limitation on saproxylic beetle richness and abundance. We used

97 information on flight ability to build species groups, i.e. flightless beetles (brachypterous and apterous) were  
98 considered as low-dispersal species and flying beetles (macropterous) were considered as high-dispersal  
99 species. We then studied the response of (i) total species, (ii) low-dispersal species and (iii) high-dispersal  
100 species to forest continuity and stand maturity. Specifically, we explored the following two hypotheses:

101 (1) Forest continuity induces dispersal limitation from habitat sources, i.e. ancient forests, to newly  
102 available habitats, i.e. recent forests. This limitation should influence low-dispersal species more than high-  
103 dispersal species, and may be a function of isolation from habitat sources. Regardless of stand maturity, we  
104 hypothesized that the richness and abundance of low-dispersal saproxylic beetle species would increase from  
105 recent to ancient forests, and that the proportion of ancient forests in the surrounding landscape and the  
106 distance at which they are found would be key parameters explaining diversity patterns.

107 (2) Stand maturity induces habitat limitation between structurally homogeneous habitats, i.e. mature  
108 stands, and structurally heterogeneous habitats, i.e. overmature stands. This limitation may influence  
109 specialized species, such as saproxylic beetles, and may be driven above all by resource availability. Regardless  
110 of forest continuity, we hypothesized that the richness and abundance of low- and high-dispersal saproxylic  
111 beetle species would increase from mature to overmature stands. We further hypothesized that deadwood  
112 quantity and quality would be key parameters explaining diversity patterns.

113

## 114 **Materials and methods**

### 115 **Study area and sampling design**

116 The study was carried out in the French pre-Alps, west of the Northern Alps Mountains (Fig. 1). The  
117 area encompasses the Vercors, Chartreuse and Bauges ranges (three Regional Natural Parks) characterized by a  
118 limestone substratum and a temperate climate. Landscapes are mainly covered by forests (63%) among which  
119 beech-fir stands are the most widespread. Owing to topographic and social constraints, forest management has  
120 been quite extensive and certain forest stands have not been managed for decades.

121 In 2014, we sampled 40 sites located in montane beech-fir forests at an altitude of 800 – 1500 m. The  
122 dominant tree species are European beech *Fagus sylvatica*, silver fir *Abies alba* and Norway spruce *Picea abies*.  
123 Our stratified and balanced sampling design crossed forest continuity and stand maturity. Forest continuity was  
124 characterized using 1:40 000 État-Major maps of France (Cateau et al. 2015), charted in the middle of the 19<sup>th</sup>

125 century, and 1:10 000 up-to-date vegetation maps. Forest cover overlapping in both maps was considered to  
126 indicate ancient forests (AF, n=20), while current forest cover overlapping with crops or meadows in the État-  
127 Major maps was considered to indicate recent forests (RF, n=20). Stand maturity was *a priori* approached by  
128 forest prospections and confirmed after stand attribute measurements were taken. Among a larger sampling  
129 design of 70 stands, we selected 20 mature (AF=10, RF=10) and 20 overmature stands (AF=10, RF=10). To  
130 improve the independence of our observations and avoid edge influence, all sampling sites were established  
131 >1.2 km away from any other site, were located in ancient or recent forest stands >5 ha in area, and were >68  
132 m from the nearest stand edge.

### 133 **Insect sampling**

134 Insects were collected using two sampling methods: flight-interception traps efficient at capturing  
135 flying beetles and Winkler-Berlese extractors of litter samples efficient at capturing flightless soil-dwelling  
136 beetles. From May to August 2014, three replicates of flight-interception traps were installed in each stand  
137 approximately 30 m apart and 1.5 m above the ground, for a total of 120 traps. Each trap consisted of two  
138 perpendicularly intercepting transparent plastic panes (40–60 cm), for a cumulative panel area of 1 m<sup>2</sup>, with a  
139 funnel below leading to collecting vials filled with a mixture of 50% propylene glycol, 50% water and detergent  
140 to kill and preserve the insects. Flight-interception traps were emptied monthly. Flightless soil-dwelling beetles  
141 were sampled by sifting litter through 0.5 cm-mesh Winkler bags. In each stand, a total of six liters of litter  
142 samples was collected at the base of the six largest living trees: two beech, two fir and two spruce trees. Litter  
143 sifting was conducted in October 2014 and insects were extracted at the laboratory with Berlese funnels for  
144 one month (Cateau et al. 2016). Except for Staphylinidae beetles (excl. Pselaphinae and Dasycerinae), most  
145 saproxylic beetles were identified to the species or genus level, depending on the information available in the  
146 literature, by the authors and independent experts. Staphylinidae is one of the most diversified beetle families,  
147 and its identification is quite difficult and time-consuming. Moreover, saproxylic species richness and  
148 composition, with or without staphylinidea, respond similarly to stand and landscape gradients (Parmain et al.  
149 2015).

### 150 **Characterization of sampling sites**

151 At the stand scale, each plot was characterized using a 10-m-radius and a 20-m-radius subplot. Within  
152 the 10-m-radius subplot (area: 314 m<sup>2</sup>), we recorded all standing trees with a diameter at breast height (DBH) ≥

153 7.5 cm and all lying trunks with a diameter  $\geq 7.5$  cm at the base and  $\geq 1$  m in length. Within the 20-m-radius  
154 subplot (area: 1 256 m<sup>2</sup>), we recorded all standing trees with a DBH  $\geq 30$  cm and all lying trunks with a diameter  
155  $\geq 30$  cm at the base and  $\geq 1$  m in length. For each standing tree and lying trunk, tree species, decay stage and  
156 tree microhabitats (cavities, sporophores of saproxylic fungi, ivy, sap runs, missing bark, cracks and shelter  
157 bark) were recorded whenever possible. For lying trunk, the diameter at both ends and in the middle section as  
158 well as length was recorded (only the portion located inside the plots was considered). Five decay stages were  
159 estimated based on resistance to tree caliper penetration: (I) hard wood, (II) caliper penetration  $< 1/4$  of the  
160 tree diameter, (III) caliper penetration  $< 1/2$  but  $> 1/4$  of the tree diameter, (IV) caliper penetration  $< 3/4$  but  $>$   
161  $1/2$  of the tree diameter, (V) caliper penetration  $> 3/4$  of the tree diameter.

162 At the landscape scale, a Geographic Information System managed with ArcGIS 10.1 (Environmental  
163 Systems Research Inst., Redlands, CA, USA) was used to characterize the geographic context within a 500-m-  
164 radius around each sampling site. We used local scale vegetation maps provided by Regional Natural Parks to  
165 describe forest stand types and landscape composition around each plot.

#### 166 **Environmental variables**

167 At the stand scale, latitude, longitude, altitude, exposure and slope were recorded at the center of the  
168 plots. The number of diameter classes was calculated using 2-cm-diameter classes. Deadwood diversity was  
169 estimated as the number of combinations formed by position (snags versus logs), species, decay class and 2-  
170 cm-diameter classes (Table 1).

171 At the landscape scale, variables based on spatial composition and configuration were computed.  
172 Landscape composition refers to the relative proportion of forests, beech-fir stands and ancient forests within a  
173 500-m-radius around each sampling site, while landscape configuration refers to the spatial arrangement of  
174 patches within the landscape, i.e. perimeter-area ratio, distance to the nearest forest edge and distance to the  
175 nearest ancient/recent forest edge.

#### 176 **Statistical analysis**

177 All statistical analyses were performed with R version 3.1.2 (R Core Team 2014).

178 Based upon data exploration (Zuur et al. 2010), independent variables with a skewness  $>1$  were log or  
179 log+1 transformed to approximate normal distribution (see also correlation matrix, Online Resource Fig. 1 & 2).



180 We then test the significance of each environmental variable to forest continuity, stand maturity and the  
181 interaction term using two-ways ANOVA with Tukey's post-hoc tests (Table 1).

182 At regional scale ( $\gamma$  diversity), we estimated the performance of our sampling design by comparing the  
183 total number of species collected with the extrapolated species richness using incidence-based Chao estimator  
184 (vegan package). We then used rarefaction curves to compare accumulated species richness between ancient  
185 and recent forests, mature and overmature stands, ancient mature and ancient overmature stands, recent  
186 mature and recent overmature stands (BiodiversityR package).

187 At local scale ( $\alpha$  diversity), we used two-ways ANOVA with Tukey's post-hoc tests to determine  
188 whether diversity patterns were influenced by forest continuity, stand maturity and their interaction. We then  
189 investigated whether saproxylic beetle richness and abundance were predicted by habitat and landscape  
190 features, using 30 *a priori* biologically plausible candidate linear models (Online Resource Table 2). Because,  
191 richness and abundance may not be independent, we furthermore assessed models performance with  
192 standardized richness as dependent variable, by including abundance as a covariate. To avoid biasing estimates  
193 toward forest continuity or stand maturity, ten models included variables describing forest continuity only, ten  
194 models included variables describing stand maturity only, and ten models included both types of variables. We  
195 used either Poisson or negative binomial regressions depending on the overdispersion of the count data and  
196 controlled for multicollinearity among explanatory variables with variance inflation factors (car package), *i.e.*  
197 only models with VIF <3 were considered (Zuur et al. 2010). To assess spatial autocorrelation, we used Moran's  
198 correlogram in the model residuals among sampling sites (ncf package). The significance of Moran's  
199 coefficient at each distance class was evaluated with 999 permutations while the overall significance of the  
200 correlogram was tested with Bonferroni's correction (Legendre and Legendre 1998). To identify the most  
201 parsimonious regression model, we used Akaike's information criterion corrected for small sample sizes  
202 (Burnham and Anderson 2002). Moreover, as recommended by Burnham and Anderson (2002), we used model  
203 averaging to estimate parameter and associated unconditional standard errors based on the subset of top  
204 ranking models for which the sum of AIC<sub>c</sub> weights reached  $\geq 0.95$  (MuMIn package). To determine the relative  
205 importance of forest continuity versus stand maturity for saproxylic beetles, we compared the sum of AIC<sub>c</sub>  
206 weights for the three categories of models: forest continuity variables only, stand maturity variables only, and  
207 both types of variables (Burnham and Anderson 2002).

208

## 209 **Results**

### 210 **Forest continuity and stand maturity**

211 Compared to recent forest sites, ancient forest sites were included in a matrix that contained more  
212 forests ( $p = 0.028$ ), more beech-fir stands ( $p = 0.025$ ) and more ancient forests ( $p < 0.001$ ) (Table 1). Ancient  
213 forest sites were also located at a greater distance from the forest edge ( $p = 0.021$ ) and in patches with less  
214 complex shapes ( $p = 0.005$ ) than recent forest sites.

215 Compared to mature stands, overmature stands were poorer in beech ( $p = 0.033$ ) but richer in fir ( $p <$   
216  $0.001$ ) (Table 1). Overmature stands were also more heterogeneous ( $p = 0.002$ ), with a greater number of very  
217 large trees ( $p < 0.001$ ), a smaller number of stems ( $p < 0.001$ ) and a higher diversity of tree microhabitats ( $p <$   
218  $0.001$ ). The deadwood compartment was more diversified ( $p < 0.001$ ) and more abundant (volume of large  
219 logs,  $p < 0.001$ ; number of large snags,  $p < 0.001$ ) in overmature than in mature stands.

220 Finally, except for the perimeter-area ratio of forest cover ( $p = 0.043$ ) and the volume of large logs ( $p =$   
221  $0.049$ ), all of the environmental variables were not influenced by the interaction term. Tukey HSD tests showed  
222 that the perimeter-area ratio of forest cover was more important in recent-mature stands than in ancient-  
223 mature stands ( $p = 0.005$ ) and ancient-overmature stands ( $p = 0.011$ ), and that the volume of large logs was  
224 more important in ancient-overmature stands than in ancient-mature stands ( $p < 0.001$ ) and recent-mature  
225 stands ( $p = 0.001$ ).

### 226 **Diversity patterns of saproxylic beetles**

227 A total of 307 saproxylic beetle species (18 729 individuals) belonging to 53 families were captured at  
228 the 40 sites (flight-intercept traps: 284 species, 16 884 individuals; Winkler-Berlese extractors: 52 species, 1  
229 845 individuals). High-dispersal beetles encompassed 275 species (17 032) from 48 families, while low-dispersal  
230 beetles encompassed 27 species (1 666 individuals) from 5 families (Online Resource Table 1). Extrapolated  
231 species richness (Chao) indicated that species pool may encompass 385 (SD  $\pm 149$ ) species, meaning that 80% of  
232 the saproxylic beetle diversity in the area was sampled.

233 The species pool of saproxylic beetles was much more influenced by stand maturity than by forest  
234 continuity (Online Resource Fig. 3). From sample-based rarefaction curves, overmature stands encompassed a  
235 pool of 281 (SD $\pm 5.56$ ) species versus 239 (SD $\pm 5.04$ ) species in mature stands, while ancient forests

236 encompassed a pool of 267 (SD±5.34) versus 249 (SD±5.06) species in recent forests. Interaction between  
237 forest continuity and stand maturity confirmed previous patterns: ancient overmature stands were more  
238 diversified than ancient mature stands, with 235 (SD±5.37) and 196 (SD±5.03) species respectively. Recent  
239 overmature stands were also more diversified than recent mature stands, with 216 (SD±5.02) and 192  
240 (SD±4.96) species respectively.

241 At local scale, diversity patterns were influenced by stand maturity but not by forest continuity or  
242 interaction term (Table 2). Total richness ( $p = 0.012$ ) and abundance ( $p = 0.003$ ), and high-dispersal richness ( $p$   
243  $= 0.014$ ) and abundance ( $p = 0.004$ ) all increased from mature to overmature stands.

#### 244 **Key parameters driving saproxylic beetle richness and abundance**

245 Observed Moran's  $I$  in model residuals were non-significant for all of the dependent variables,  
246 indicating that spatial patterns were accounted for by forest continuity and stand maturity variables (Online  
247 Resource Fig. 4).

#### 248 **Model ranking**

249 Overall, stand maturity models were far more powerful than forest continuity models in explaining  
250 diversity patterns (Table 3). Total and high-dispersal richness were best predicted by stand maturity model #1  
251 (pseudo- $R^2$  range from 37% to 38%), while total and high-dispersal abundance were best predicted by forest  
252 continuity and stand maturity model #21 (pseudo- $R^2 = 29\%$ ). Low-dispersal richness and abundance were best  
253 explained by the null model. When accounting for abundance in models, standardized richness was best  
254 predicted by the same best model as total richness (i.e. model # 1) but model performance increased  
255 substantially (pseudo- $R^2 = 68\%$ ). Although some of these models show quite a strong support to explain  
256 diversity patterns, model selection uncertainty remains since associated  $AIC_c$  weight and evidence ratio were  
257 relatively low. We therefore used model averaging, ranging from the 5 to the 20 best models, to draw  
258 inferences about the variables influencing saproxylic beetles.

#### 259 **Model parameters**

260 Forest continuity-associated variables mostly influenced abundance patterns (Table 4 & 5). Total and  
261 high-dispersal abundance increased with the proportion of beech-fir stands in the surrounding landscape but  
262 decreased with increasing distance to forest edge. Stand maturity-associated variables positively influenced  
263 both saproxylic beetle abundance and richness (Table 4 & 5). Standardized richness, total and high-dispersal

264 richness and abundance increased with the diversity of deadwood types. Moreover, high-dispersal richness  
265 increased with the number of large snags, while standardized richness increased with the total abundance of  
266 saproxylic beetles but decreased with the number of very large trees. The other forest continuity- and stand  
267 maturity-associated variables we tested had little influence and none of them significantly influenced low-  
268 dispersal saproxylic beetles (Table 4 & 5).

269 Relative influence of forest continuity and stand maturity on saproxylic beetles

270 Judging from the sum of  $AIC_c$  weights for the models, richness patterns were mostly influenced by  
271 stand maturity (Fig. 2). For Total, standardized richness and high-dispersal richness, the cumulative  $AIC_c$  weight  
272 of stand maturity models was  $> 0.80$ . Indeed, six of the top ten models included only stand maturity variables.  
273 Remaining top ten models included both stand maturity and forest continuity variables. In contrast to richness  
274 patterns, abundance patterns were more heterogeneous. For total and high-dispersal abundance, the relative  
275 influence of stand maturity was lower (from 0.49 to 0.51) and models combining both stand maturity and  
276 forest continuity variables gained in importance (from 0.41 to 0.43). For these dependent variables, the  
277 cumulative  $AIC_c$  weight of forest continuity models was  $< 0.07$ . Finally, because low-dispersal richness and  
278 abundance were best explained by the null model, none of the models and associated metrics (i.e.  $AIC_c$  weight)  
279 is of any inferential value.

280

## 281 Discussion

282 Our results clearly show that saproxylic beetle diversity patterns were shaped by habitat limitation. No  
283 evidence of dispersal limitation was found. As indicators of habitat limitation, stand maturity models and  
284 associated variables performed much better than did forest continuity models and associated variables in  
285 explaining richness and abundance patterns of saproxylic beetles. In unfragmented montane forests, key  
286 parameters related to deadwood diversity at the stand scale and suitable habitat availability at the landscape  
287 scale appeared to be major drivers of saproxylic beetle diversity.

288 Dispersal limitation

289 Contrary to our first hypothesis, no evidence of dispersal limitation was found, i.e. diversity patterns  
290 were not influenced by forest continuity. This indicates that saproxylic beetles, even low-dispersal species,  
291 were able to successfully disperse and colonize newly available habitats. Previous studies have reported a

292 significant effect of forest continuity on plants (e.g. Sciama et al. 2009), epiphytic bryophytes and lichens (e.g.  
293 Fritz and Brunet 2010), and carabids (e.g. Assmann 1999). For saproxylic beetles, the few existing studies have  
294 reported that recent forests were species poor sites (Gossner et al. 2008; Irmiler et al. 2010; Buse 2012). In our  
295 study, forest continuity had no significant effect on saproxylic beetles richness and abundance; species  
296 accumulation curves simply indicated that ancient forests encompassed a larger species pool than recent  
297 forests. Given that most previous studies were conducted in fragmented landscapes, these apparently  
298 contradictory results may indicate confounding effects between forest continuity and fragmentation, as  
299 previously showed for plants (Jamoneau et al. 2012). In the Northern Alps, landscapes are dominated by  
300 unfragmented forests and recent forests have colonized agricultural areas next to ancient forest areas.  
301 Afforestation adjacent to ancient forests reduces the distance to habitat source and limits dispersal barriers  
302 within the habitat matrix (Honnay et al. 2002). This may have facilitated the colonization of recent forests by  
303 saproxylic beetles. Moreover, the assumption that flightless saproxylic beetles are dispersal-limited species is  
304 questionable. In our study, four of the six flightless saproxylic weevils (Curculionidae) presented as ancient  
305 forest relict species (Buse 2012) were recorded – *Acalles lemur*, *Kyklioacalles navieresi*, *Echinodera hypocrita*,  
306 *Trachodes hispidus* – and all of them were evenly present in both ancient and recent forests. In accordance  
307 with Horák et al. (2013), we believe that the dispersal ability of these flightless saproxylic species has probably  
308 been underestimated.

309         Beside dispersal limitation, it has been argued that forest continuity influences biodiversity patterns  
310 through habitat limitation (Hermy and Verheyen 2007). Even for highly connected patches, differences in  
311 habitat characteristics between ancient and recent forests may persist for centuries, especially for soil  
312 properties (Dupouey et al. 2002). These differences in habitat quality can limit species establishment in newly  
313 available forests by recruitment limitation (Honnay et al. 2002). Such long-lasting effects act directly on plant  
314 communities (Baeten et al. 2009) and indirectly on plant consumers (Gossner et al. 2008). Saproxylic beetles,  
315 however, should be more influenced by stand structural attributes than by understory vegetation and soil  
316 properties. If stand maturity parameters are not controlled for between ancient and recent forests (e.g. Irmiler  
317 et al. 2010; Buse 2012), it may be hazardous to infer that the differences observed in biodiversity patterns are  
318 related to dispersal limitation (Nordén et al. 2014). Our sampling design was designed to disentangle the  
319 relative effect of dispersal limitation from habitat limitation and our results show that stand maturity was

320 indeed independent from forest continuity. Habitat quality can therefore be regarded as homogeneous  
321 between ancient and recent forests. Although forest continuity may have acted on soil properties and  
322 associated plant communities, no effects were observed for saproxylic beetles. This indicates that, in  
323 unfragmented montane forests, dispersal limitation is not a major driver in shaping saproxylic beetle diversity  
324 patterns.

#### 325 Habitat limitation

326 Habitat limitation was powerful to explain variation in species diversity. In accordance with our second  
327 hypothesis, the richness and abundance of saproxylic beetles increased with stand maturity, in both ancient  
328 and recent forests, from the regional species pool scale to the local diversity scale. This indicates that species  
329 requirements were best supported in overmature stands and that stand maturity allowed greater species  
330 coexistence regardless of forest continuity. This pattern may be related to a diversification in resource  
331 availability, given that habitat heterogeneity usually positively correlates to stand maturity (McElhinny et al.  
332 2005). In our sampling design, structural attributes such as the number of diameter classes of standing trees,  
333 the number of very large living trees or the diversity of deadwood types, strongly increased with stand  
334 maturity. Stand maturity may therefore be viewed as a surrogate for habitat heterogeneity, which is known to  
335 have significant effects on biodiversity patterns, e.g. for wood-inhabiting fungi (Junninen et al. 2006), epiphytic  
336 bryophytes (Dittrich et al. 2013) and birds (Poulsen 2002). For saproxylic beetles, numerous studies have also  
337 reported a positive relationship between stand maturity and diversity patterns (e.g. Martikainen et al. 2000;  
338 Stenbacka et al. 2010; Lassauce et al. 2012). Our results are therefore consistent with knowledge related to the  
339 ecological niche theory and highlight the significance of habitat limitation as a major driver in shaping  
340 biodiversity patterns. However, low-dispersal saproxylic beetles were not influenced by stand maturity. This  
341 finding may indicate that, in our study, the variation in habitat quality between mature and overmature stands  
342 was not strong enough. Indeed, flightless saproxylic weevils depend on twigs for their development (Heijerman  
343 2004), which are not a limiting resource in mountain forests (Barbati et al. 2014). Flightless saproxylic beetles,  
344 on the other hand, may be more dependent on environmental factors related to litter depth, soil moisture  
345 (Sroka and Finch 2006), altitude (Horák et al. 2013), climate and topography (Buse 2012).

#### 346 Key parameters at stand scale

347           At the stand scale, parameters related to stand maturity, especially those linked to deadwood quality,  
348 provided relevant explanatory variables for species richness and abundance variation patterns. Although stand  
349 structural attributes have been pointed out as key parameters for saproxylic beetles (Ranius and Jansson 2000;  
350 Grove 2002), in our study, the diversity of deadwood types was by far the most powerful explanatory variable  
351 for diversity patterns. Deadwood diversity is related to habitat diversity and allows a larger range of species,  
352 including specialists, to coexist through an increase in the heterogeneity of the resource supply. The  
353 importance of deadwood diversity for saproxylic beetles has already been pointed out in boreal (Økland et al.  
354 1996; Similä et al. 2003) and temperate forests (Brin et al. 2011; Bouget et al. 2013). However, contrary to our  
355 expectations, deadwood quantity was not as powerful as deadwood diversity in explaining diversity patterns.  
356 While richness of high-dispersal species was significantly influenced by large snag density, large log volume had  
357 no significant effect on saproxylic beetles. Large log volume has been pointed out as a key parameter for  
358 saproxylic species (e.g. Økland et al. 1996; Lachat et al. 2012; Bouget et al. 2014) and is a commonly used  
359 indicator for sustainable forest management (Forest Europe, UNECE and FAO 2011). Müller and Bütler (2010)  
360 stated that the amount and diversity of deadwood are usually correlated and, consequently, that it may be  
361 difficult to disentangle their relative influence. In our montane mixed forests, as in others forests (Grove 2002;  
362 Similä et al. 2003; Bouget et al. 2013), the total amount and diversity of deadwood were correlated ( $R = 0.75$ ).  
363 Nevertheless, our deadwood diversity models consistently performed better than our deadwood amount  
364 models in explaining richness patterns of saproxylic beetles, even when controlling for species abundance. In  
365 line with Lassauce et al.'s meta-analysis (2011), our results confirm that deadwood diversity is of more  
366 importance than deadwood amount in shaping saproxylic diversity patterns in forest ecosystems.

#### 367 Key parameters at landscape scale

368           At the landscape scale, parameters related to forest continuity had contrasting effects on saproxylic  
369 beetles but were found to be relevant in explaining abundance patterns. The proportion of beech-fir stands in  
370 the surrounding landscape increased the abundance of all dependent variables, except for low-dispersal  
371 species, while the proportion of forests and ancient forests had no effect. As previously demonstrated for plant  
372 species recovery in recent forests (De Frenne et al. 2011), our results underlines the importance for saproxylic  
373 beetles of suitable habitat availability at a larger scale. The abundance of many saproxylic species has been  
374 shown to increase with the proportion of suitable habitat at landscape scale in boreal forests (Gibb et al. 2006;

375 Laaksonen et al. 2008). These findings may indicate that larger source populations are available for colonization  
376 in stands surrounded by a larger proportion of suitable habitat (Gibb et al. 2006). This may be viewed as an  
377 additive effect of habitat limitation versus dispersal limitation at the landscape scale. However, total and high-  
378 dispersal species abundance decreased with distance to forest edge. This may be related to the attractiveness  
379 of the sunny conditions found along forest edges (Vodka and Cizek 2013). Moreover, several adult forms of  
380 saproxylic beetles are floricolous. The likelihood of them being captured increases with the availability of  
381 flowering plants, i.e. with the proximity to forest edge. This response pattern may be linked to edge effect,  
382 rather than to a negative effect of forest continuity. Our overall results highlight the relevance of considering  
383 multiple spatial scales to better characterize diversity patterns, in accordance with previous studies (e.g.  
384 Økland et al. 1996; Janssen et al. 2009).

385

## 386 **Conclusion**

387 We found that habitat limitation was the main ecological mechanism explaining saproxylic beetle  
388 diversity patterns in unfragmented montane forests. Habitat limitation was primarily driven by variations in  
389 deadwood diversity at the stand scale and by availability of suitable habitat at the landscape scale. In the  
390 ecological context of the Northern Alps, i.e. unfragmented forests, our results clearly show that dispersal  
391 limitation was not a causative factor for saproxylic beetle diversity. This suggests that biodiversity responses to  
392 forest continuity may depend on species groups and/or on the regional setting. Indeed, caution must be used  
393 in studies based on a limited group of taxa when generalizing the ecological mechanisms resulting from  
394 complex ecosystem modifications such as land use change. Saproxylic beetle conservation would benefit from  
395 forestry practices that maintain a diversity of deadwood types within stands, e.g. snags and logs of various  
396 diameters and in different stages of decay, and a high availability of overmature stands in the surrounding  
397 landscape.

398

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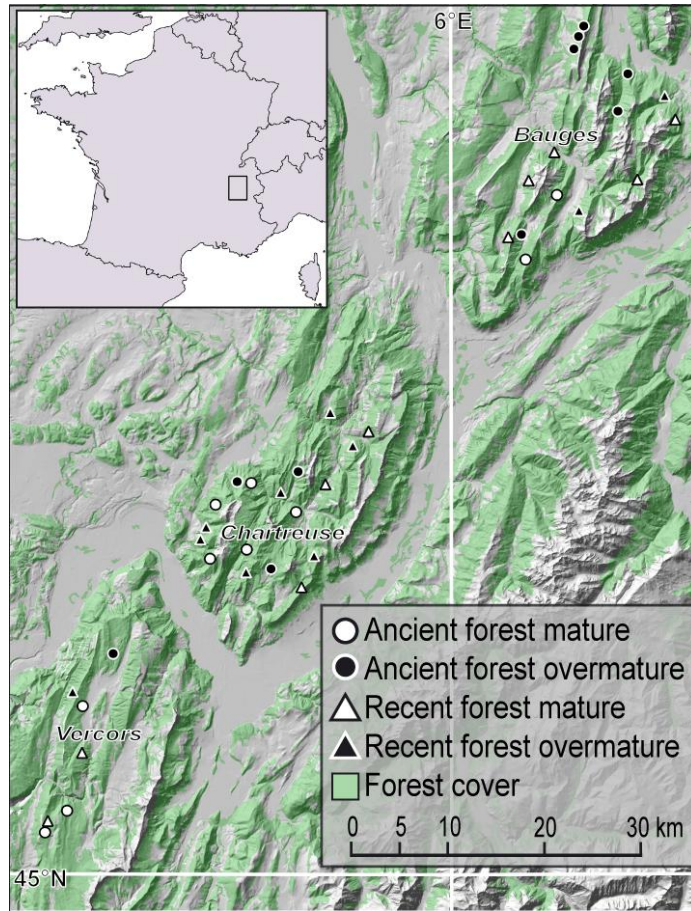
533 **Figure captions**

534

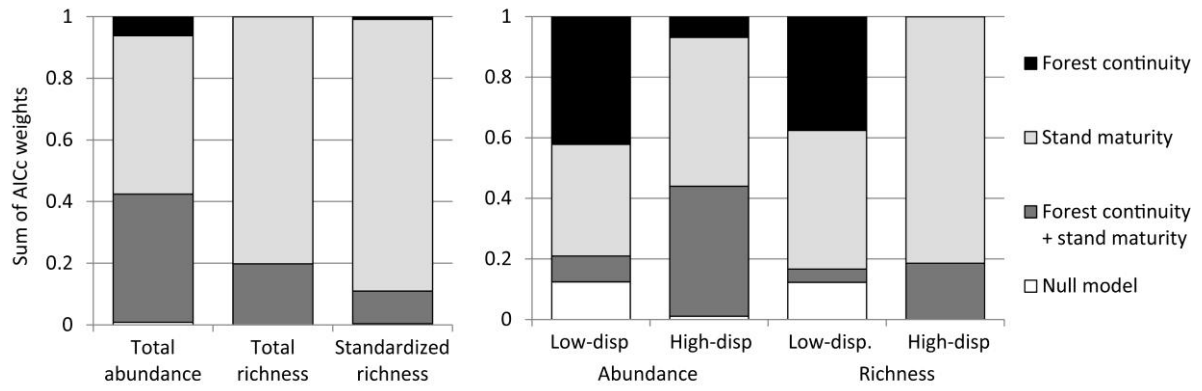
535 **Fig. 1** Study area and distribution of sampling sites among ancient and recent forests and mature and  
536 overmature stands in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France

537

538 **Fig. 2** Influence of parameters related to forest continuity and/or stand maturity on saproxylic beetle richness  
539 and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France. Sums of  $AIC_c$  weights are  
540 provided for models based exclusively on forest continuity variables (10 models), on stand maturity variables  
541 (10 models) or on both types of variables (10 models) plus the null model; Low-disp. = Low-dispersal, High-disp.  
542 = High-dispersal



543 **Fig. 1**



544 **Fig. 2**



545 **Table 1** Variation in forest continuity and stand maturity variables used to model saproxylic beetle richness and abundance in the Vercors, Chartreuse and Bauges ranges,  
 546 Northern Alps, France (BD = basal diameter, DBH = diameter at breast height, p-value based on two-ways ANOVA)

Variables	Description	Ancient	Recent	p-value	Mature	Overmature	p-value
		Mean ( $\pm$ SD)	Mean ( $\pm$ SD)		Mean ( $\pm$ SD)	Mean ( $\pm$ SD)	
lati	Latitude in decimal degrees	45.44 ( $\pm$ 0.25)	45.42 ( $\pm$ 0.21)	0.7777	45.38 ( $\pm$ 0.23)	45.48 ( $\pm$ 0.22)	0.1551
long	Longitude in decimal degrees	5.86 ( $\pm$ 0.27)	5.88 ( $\pm$ 0.26)	0.8203	5.84 ( $\pm$ 0.27)	5.91 ( $\pm$ 0.25)	0.3856
alti	Altitude in meters	1172 ( $\pm$ 156.1)	1137 ( $\pm$ 159.5)	0.5008	1171 ( $\pm$ 160.0)	1137 ( $\pm$ 155.7)	0.5070
slope	Slope in percentage	22.20 ( $\pm$ 7.22)	25.63 ( $\pm$ 7.21)	0.1409	24.02 ( $\pm$ 7.76)	23.82 ( $\pm$ 7.08)	0.9323
expo	Exposure in degrees	216.3 ( $\pm$ 103.7)	226.0 ( $\pm$ 113.7)	0.7841	206.1 ( $\pm$ 108.1)	236.2 ( $\pm$ 107.5)	0.3941
Stand maturity variables measured at stand scale							
G_beech	Beech basal area in m <sup>2</sup>	1.42 ( $\pm$ 0.85)	1.53 ( $\pm$ 1.07)	0.7123	1.80 ( $\pm$ 0.80)	1.15 ( $\pm$ 1.01)	0.0334
G_fir	Fir basal area in m <sup>2</sup>	3.30 ( $\pm$ 2.28)	2.97 ( $\pm$ 2.21)	0.5594	1.79 ( $\pm$ 1.15)	4.48 ( $\pm$ 2.24)	0.0000
G_spruce	Spruce basal area in m <sup>2</sup>	1.07 ( $\pm$ 1.04)	1.49 ( $\pm$ 1.27)	0.3093	1.50 ( $\pm$ 1.28)	1.05 ( $\pm$ 1.01)	0.3345
N_trees_classes	Number of diameter classes of standing trees	21.55 ( $\pm$ 3.05)	21.60 ( $\pm$ 3.10)	0.9542	20.15 ( $\pm$ 2.35)	23.00 ( $\pm$ 3.03)	0.0022
N_trees	Number of living trees per hectare	93.8 ( $\pm$ 40.66)	108.1 ( $\pm$ 48.32)	0.2476	124.5 ( $\pm$ 46.94)	77.4 ( $\pm$ 26.92)	0.0004
N_large_trees	Number of very large living trees (DBH > 62.5 cm)	3.35 ( $\pm$ 4.15)	3.45 ( $\pm$ 3.36)	0.9001	0.60 ( $\pm$ 0.88)	6.20 ( $\pm$ 3.35)	0.0000
Vol_large_cwd	Volume of large logs (BD > 30 cm) in m <sup>3</sup>	2.47 ( $\pm$ 3.65)	1.20 ( $\pm$ 1.82)	0.0986	0.31 ( $\pm$ 0.61)	3.36 ( $\pm$ 3.49)	0.0002

N_large_snags	Number of large snags (DBH > 30 cm)	1.95 (±2.39)	1.25 (±1.89)	0.2090	0.35 (±0.59)	2.85 (±2.43)	0.0000
Alpha_cwd	Diversity of deadwood types	13.30 (±9.70)	10.05 (±5.33)	0.1174	7.30 (±4.46)	16.05 (±8.23)	0.0001
Alpha_mh	Diversity of tree microhabitats	2.20 (±2.07)	2.60 (±1.76)	0.4211	1.25 (±1.02)	3.55 (±1.90)	0.0000
Forest continuity variables measured at landscape scale							
Prop_Forest	Forest proportion within a 500-m-radius (%)	93.72 (±7.85)	86.73 (±11.62)	0.0289	88.06 (±12.90)	92.39 (±6.78)	0.1666
Prop_BF	Beech-fir proportion within a 500-m-radius (%)	84.99 (±16.18)	72.61 (±17.04)	0.0252	77.13 (±17.32)	80.48 (±18.08)	0.5311
Prop_Ancient	Ancient forest proportion within a 500-m-radius (%)	86.06 (±10.71)	39.35 (±25.65)	1.1158	62.90 (±32.09)	62.51 (±29.86)	0.9507
Complex_Forest	Perimeter-area ratio of forest cover	0.005 (±0.001)	0.008 (±0.004)	0.0054	0.007 (±0.004)	0.006 (±0.002)	0.1011
Dist_Forest	Distance to the nearest forest edge in meters	367.3 (±243.4)	216.8 (±125.2)	0.0212	312.5 (±234.8)	271.6 (±175.5)	0.5165
Dist_Past_Edge	Distance to the nearest ancient/recent edge in meters	386.1 (±320.7)	249.7 (±320.3)	0.1940	335.2 (±329.8)	300.5 (±325.3)	0.7382

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547 **Table 2** Mean ( $\pm$ SD) of dependent variables in relation to forest continuity and stand maturity in the Vercors,  
 548 Chartreuse and Bauges ranges, Northern Alps, France (p-value based on two-ways ANOVA)

Dependent variable	Forest continuity			Stand maturity		
	Ancient	Recent	p-value	Mature	Overmature	p-value
Total richness	75.1 ( $\pm$ 19.95)	72.8 ( $\pm$ 17.44)	0.6887	66.6 ( $\pm$ 15.44)	81.3 ( $\pm$ 18.79)	0.0125
Total abundance	457.8 ( $\pm$ 207.05)	478.6 ( $\pm$ 182.94)	0.7128	379.8 ( $\pm$ 152.23)	556.6 ( $\pm$ 192.18)	0.0033
Low-dispersal richness	8.3 ( $\pm$ 1.90)	9.0 ( $\pm$ 2.44)	0.3103	8.3 ( $\pm$ 2.16)	9.0 ( $\pm$ 2.21)	0.3103
Low-dispersal abundance	38.4 ( $\pm$ 16.75)	44.9 ( $\pm$ 16.41)	0.2282	39.6 ( $\pm$ 16.22)	43.6 ( $\pm$ 17.33)	0.4555
High-dispersal richness	66.4 ( $\pm$ 19.81)	63.0 ( $\pm$ 16.04)	0.5372	57.8 ( $\pm$ 14.77)	71.6 ( $\pm$ 18.38)	0.0149
High-dispersal abundance	419.1 ( $\pm$ 209.29)	432.5 ( $\pm$ 177.96)	0.8114	339.6 ( $\pm$ 156.13)	512.0 ( $\pm$ 188.55)	0.0040

549

550

551 **Table 3** Top-ranking models among 31 models predicting saproxylic beetle richness and abundance in the  
 552 Vercors, Chartreuse and Bauges ranges, Northern Alps, France, as assessed with Akaike’s information criterion  
 553 corrected for small sample size ( $AIC_c$ ). Dependent variable, model number, related group model (continuity,  
 554 maturity or both), number of estimated parameters including the intercept (k),  $AIC_c$ ,  $AIC_c$  weight (W), adjusted  
 555  $R^2$  and evidence ratio (ER), i.e. Akaike weight of best model/Akaike weight of second best model, are provided

Dependent variable	Top-ranking	Type	k	$AIC_c$	W	$R^2$	ER
Total richness	1	Maturity	2	332.7	0.546	0.38	3.4
Total abundance	21	Continuity + Maturity	4	534.2	0.211	0.29	1.4
Standardized richness	1	Maturity	3	311.5	0.380	0.65	1.3
Low-dispersal richness	31	Null	1	184.1	0.122	0.00	1.0
Low-dispersal abundance	31	Null	1	339.3	0.124	0.00	1.3
High-dispersal richness	1	Maturity	2	329.5	0.525	0.37	3.4
High-dispersal abundance	21	Continuity + Maturity	4	534.9	0.239	0.29	1.4

556

557 **Table 4** Average coefficients (AC) and confidence intervals (CI) for each variable of the top ranking models (i.e.  
558 sum of AIC<sub>c</sub> weights ≥0.95) predicting total saproxylic beetles richness and abundance in the Vercors,  
559 Chartreuse and Bauges ranges, Northern Alps, France. The 95% confidence interval of coefficients in bold  
560 excluded 0, NA = not available

Parameter	Total abundance		Total richness		Standardized richness	
	AC	CI	AC	CI	AC	CI
<b>(Intercept)</b>	<b>6.000</b>	<b>(4.012; 7.988)</b>	<b>3.821</b>	<b>(3.408; 4.234)</b>	<b>3.620</b>	<b>(3.319; 3.923)</b>
<b>Abundance</b>	NA	NA	NA	NA	<b>0.001</b>	<b>(0.001; 0.001)</b>
N_tree_classes	0.041	(-0.007; 0.089)	0.001	(-0.022; 0.024)	-0.009	(-0.026; 0.008)
<b>N_large_trees</b>	0.160	(-0.015; 0.336)	-0.029	(-0.114; 0.056)	<b>-0.069</b>	<b>(-0.133; -0.007)</b>
Vol_large_cwd	0.110	(-0.103; 0.323)				
N_large_snags	0.193	(-0.010; 0.397)				
<b>Alpha_cwd</b>	<b>0.281</b>	<b>(0.082; 0.480)</b>	<b>0.225</b>	<b>(0.130; 0.319)</b>	<b>0.148</b>	<b>(0.066; 0.230)</b>
Alpha_mh	-0.016	(-0.098; 0.066)	0.012	(-0.026; 0.050)	0.012	(-0.014; 0.039)
Prop_Forest	0.003	(-0.013; 0.020)	-0.003	(-0.011; 0.006)	-0.004	(-0.010; 0.002)
<b>Prop_BF</b>	<b>0.010</b>	<b>(0.002; 0.019)</b>				
Prop_Ancient	-0.001	(-0.005; 0.003)	0.000	(-0.002; 0.002)	-0.0001	(-0.002; 0.002)
Complex_Forest	0.160	(-0.282; 0.602)				
<b>Dist_Forest</b>	<b>-0.282</b>	<b>(-0.556; -0.007)</b>	-0.010	(-0.148; 0.128)	0.073	(-0.034; 0.180)
Dist_Past_Edge	-0.130	(-0.276; 0.015)	-0.051	(-0.121; 0.019)	-0.008	(-0.065; 0.049)

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562

563 **Table 5** Average coefficients (AC) and confidence intervals (CI) for each variable of the top ranking models (i.e.  
564 sum of AIC<sub>c</sub> weights ≥0.95) predicting low-dispersal (Low-disp.) and high-dispersal (High-disp) saproxylic beetles  
565 richness and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France. The 95%  
566 confidence interval of coefficients in bold excluded 0, NA = not available

Parameter	Low-disp. abundance		Low-disp. richness		High-disp. abundance		High-disp. richness	
	AC	CI	AC	CI	AC	CI	AC	CI
<b>(Intercept)</b>	<b>3.761</b>	<b>(2.644; 4.878)</b>	<b>2.175</b>	<b>(1.090; 3.259)</b>	<b>5.932</b>	<b>(3.800; 8.065)</b>	<b>3.669</b>	<b>(3.210; 4.128)</b>
Abundance	NA	NA	NA	NA	NA	NA	NA	NA
N_tree_classes	0.030	(-0.014; 0.074)	0.027	(-0.011; 0.065)	0.043	(-0.012; 0.097)	-0.001	(-0.026; 0.024)
N_large_trees	0.057	(-0.089; 0.202)	0.007	(-0.115; 0.130)	0.169	(-0.035; 0.372)	-0.027	(-0.121; 0.067)
Vol_large_cwd	-0.013	(-0.178; 0.152)	-0.092	(-0.259; 0.076)	0.126	(-0.113; 0.366)		
<b>N_large_snags</b>	-0.028	(-0.206; 0.151)	0.018	(-0.154; 0.190)	0.222	(-0.010; 0.453)	<b>0.205</b>	<b>(0.105; 0.306)</b>
<b>Alpha_cwd</b>	-0.044	(-0.240; 0.152)	0.039	(-0.130; 0.208)	<b>0.325</b>	<b>(0.104; 0.547)</b>	<b>0.245</b>	<b>(0.141; 0.349)</b>
Alpha_mh	0.033	(-0.036; 0.102)	0.023	(-0.034; 0.080)	-0.026	(-0.117; 0.065)	0.010	(-0.031; 0.052)
Prop_Forest	-0.011	(-0.028; 0.006)	-0.003	(-0.015; 0.009)	0.005	(-0.014; 0.024)	-0.003	(-0.012; 0.007)
<b>Prop_BF</b>	-0.001	(-0.008; 0.007)	0.003	(-0.005; 0.011)	<b>0.011</b>	<b>(0.001; 0.021)</b>		
Prop_Ancient	-0.003	(-0.007; 0.001)	-0.001	(-0.004; 0.003)	-0.001	(-0.006; 0.004)	0.000	(-0.002; 0.002)
Complex_Forest	0.165	(-0.145; 0.475)	0.179	(-0.125; 0.482)	0.134	(-0.377; 0.645)		
<b>Dist_Forest</b>	0.126	(-0.185; 0.436)	-0.048	(-0.261; 0.165)	<b>-0.333</b>	<b>(-0.645; -0.021)</b>	-0.004	(-0.157; 0.148)
Dist_Past_Edge	0.015	(-0.129; 0.158)	-0.011	(-0.134; 0.111)	-0.150	(-0.317; 0.016)	-0.056	(-0.133; 0.022)

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