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1 **Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic**  
2 **beetles**

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22 **ABSTRACT**

23 Long temporal continuity in forests has been shown to influence biodiversity through dispersal and  
24 recruitment limitations. However, for motile taxa that depend on stand maturity attributes, these limitations  
25 may be less relevant. Moreover, while certain habitats may be created rapidly, the development of other  
26 habitats may take a long time. Forest continuity and stand maturity may therefore have additive effects on  
27 biodiversity. Understanding their relative influence on biodiversity is crucial for conservation. We explored the  
28 response of species and functional trait composition of saproxylic beetle assemblages using a balanced  
29 sampling design in which we crossed forest continuity (ancient vs recent) and stand maturity (mature vs  
30 overmature). We established forty plots in montane forests where we sampled beetles. Stand maturity, related  
31 to deadwood resources, induced a strong environmental filtering on both species and functional trait  
32 composition. Regardless of forest continuity, species preferring large wood of late decay stages were more  
33 abundant in overmature stands. Moreover, overmature stands enhanced the co-occurrence of different  
34 saproxylic beetles with contrasting resource requirements. Forest continuity interacting with stand maturity  
35 induced taxonomic and functional changes in communities. Compared to other forest types, overmature stands  
36 in ancient forests hosted assemblages with many more characteristic species, with a larger average body size  
37 and species that prefer large deadwood pieces. Finally, a greater diversity of body sizes was found in these  
38 forests. Saproxylic species conservation should therefore benefit from strategies that favor setting-aside  
39 overmature stands in ancient forests, promoting sites with higher amounts and heterogeneity of deadwood.

40

41 Keywords: assemblage structure, biodiversity conservation, functional composition, habitat continuity, habitat  
42 quality.

43

44 **1. INTRODUCTION**

45 Forest cover has consistently increased since the mid-nineteenth century in western Europe and the  
46 eastern United States (Hermy and Verheyen, 2007), despite a worldwide trend toward loss of forest cover  
47 (Hansen et al., 2010). This afforestation has mainly occurred on abandoned agricultural land, both by  
48 spontaneous growth and by deliberate replantation. Two types of forests have resulted: ancient forests, which  
49 have existed for centuries, and recent forests, which result from afforestation after a certain threshold date  
50 (Hermy and Verheyen, 2007). Forest continuity is thus defined as a minimum residence time of the wooded  
51 state since a threshold date, which differs between countries in northwestern Europe due to the complex land  
52 use history and availability of historical maps (e.g. 1600 or 1700 in GB; 1750 or 1800 in Germany; 1770-1800 in  
53 Belgium & Denmark; 1820 in Sweden; 1820-1850 in France & Netherlands; Hermy and Verheyen, 2007). In a  
54 context of ongoing global biodiversity loss, forecasting the relative importance of ancient versus recent forests  
55 for conservation is of primary importance.

56 Plant assemblages, for instance, have been shown to be driven by forest continuity (Flinn and Vellend,  
57 2005; Hermy and Verheyen, 2007). Two processes have been highlighted: dispersal limitations due to poor  
58 ability of ancient-forest plant species to colonize recent forests (e.g. Verheyen and Hermy, 2004), and  
59 recruitment limitations due to modifications in soil properties and competitive interactions (e.g. Baeten et al.,  
60 2009). However, these limitations may be less relevant for motile taxa that depend on stand structural  
61 properties (Nordén and Appelqvist, 2001; Rolstad et al., 2002). Indeed, the diversity of many forest taxa  
62 increases with stand maturity, i.e. the continuous process of tree and stand ageing, depending on the lifespan,  
63 the traditional harvest age of the dominant tree species and the type of forest management. These taxa are  
64 associated to the availability of stand structural attributes, e.g. deadwood and tree-related microhabitats  
65 (Bouget et al., 2014), that may accumulate with time in both ancient and recent forests. This raises the  
66 question of the relative contribution of forest continuity versus stand maturity for biodiversity conservation.  
67 Moreover, while certain microhabitats may develop rapidly, e.g. broken twigs, other microhabitats, e.g. tree  
68 cavities with mould, may take decades or even centuries to develop (Müller et al., 2014). It should be kept in  
69 our memory that the oldest stands in recent forests are at most 200 years of age. Past deforestation and  
70 temporary lack of deadwood may also have cause local extinctions of species which could experience difficulty  
71 in recolonizing the recent forests. Therefore, the long-term past habitat continuity and the iteration of several

72 forest cycles has only occurred in ancient forests. This may suggest an additive effect of forest continuity on  
73 stand maturity, indicating that overmature stands in ancient forests may be of greater value for conservation  
74 than overmature stands in recent forests.

75 We aimed to study the effect of forest continuity and stand maturity on species and functional trait  
76 composition of saproxylic beetle assemblages. Saproxylic beetles belong to a rich group of species that depend  
77 on deadwood for at least a part of their lifecycle (Stokland et al., 2012). They are among the first organisms to  
78 colonize dying trees and, consequently, play a functionally important role in wood decomposition (Stokland et  
79 al., 2012). Previous studies have shown that saproxylic diversity is closely linked to stand maturity parameters  
80 such as deadwood volume and heterogeneity (e.g. Brin et al., 2011; Lassauce et al., 2011). Among studies  
81 about the effects of forest continuity on saproxylic beetles, several reported that recent forests were species-  
82 poor sites (Gossner et al., 2008; Irmeler et al., 2010). However, most of these studies were carried out in  
83 fragmented landscapes, where recent forests were disconnected from ancient forests. Since isolated forest  
84 fragments are less prone to be colonized by low-dispersal species (Jamoneau et al., 2012), it makes it difficult  
85 to disentangle the effect of forest continuity from the effect of spatio-temporal isolation. Moreover most  
86 studies did not control for stand maturity parameters between ancient and recent forests, making it difficult to  
87 distinguish the effect of stand maturity from the effect of forest continuity per se (Nordén et al., 2014).

88 Unlike classical measures of species diversity, the range and distribution of functional trait values in a  
89 community are useful measures in unraveling complex patterns linking environmental change, assemblage  
90 structures and ecosystem processes (Lavorel et al., 2008). Strategies that combine measures of the mean and  
91 the dispersion of traits, within a given species assemblage, have been showed to describe two complementary  
92 aspects of the relationship between community structure and ecosystem functioning (de Bello et al., 2013;  
93 Ricotta and Moretti, 2011): (i) shifts in trait values due to environmental selection and (ii) patterns of trait  
94 convergence or divergence due to niche differentiation. For European saproxylic beetles, data are now  
95 available concerning niche position traits (preferred canopy cover and diameter and decay stage of deadwood  
96 in which larvae develop) and morphological traits (mean body size) (Gossner et al., 2013). The mean trait values  
97 of a species determine its niche position along environmental gradients, referring to some dimensions of the  
98 distribution of resources which a population responds to (Violle and Jiang, 2009). Deadwood diameter and  
99 decay stage are especially useful to evaluate the effects of habitat change (e.g. Gossner *et al.* 2013) because (i)  
100 they are closely related to the resource required by saproxylic beetles and (ii) their distribution is strongly

101 affected by forest management practices such as selective harvest of large-diameter wood. For example, an  
102 increase in large-deadwood availability may lead to an increase in the mean and dispersion of the diameter  
103 niche (Gossner *et al.* 2013). Among the morphological traits, body size correlates well with many life-history  
104 traits – foraging capacity, duration of larval development... – and thus captures a significant proportion of the  
105 ecologically relevant characteristics of the ecosystem (Woodward *et al.*, 2005). As such, an increase in mean  
106 body size, which usually depends on the duration of larval development, may indicate an increase in habitat  
107 stability, and thus in the availability of long-lasting habitats (Brin *et al.*, 2011). The use of these traits may give  
108 new insights into the potential effects of habitat changes (deadwood profile, stand openness...) induced by  
109 forest continuity and stand maturity on saproxylic beetles.

110 In order to assess the influence of forest continuity on saproxylic beetle species and functional  
111 composition, we developed a balanced sampling design in which we controlled for effects of stand maturity  
112 and spatial isolation between ancient and recent forests. Assuming that saproxylic communities are mostly  
113 shaped by habitat features related to maturity, we tackled the following questions. First, how do structural  
114 features differ between mature and overmature stands, as well as between recent and ancient forests? For  
115 instance, higher amount and diversity of deadwood are expected in overmature than in mature stands,  
116 regardless of forest continuity. Secondly, how do maturity or continuity affect beetle assemblages, specifically  
117 species composition, mean and diversity of single trait values? Regarding this second part, we made three basic  
118 assumptions:

119 (1) Stand maturity induces a filtering related to the availability of deadwood, independently of forest  
120 continuity. In mature stands, a lower amount and more homogeneous deadwood supply is expected to cause  
121 environmental filtering on the regional species pool. Due to high resource variability (in quantity and quality),  
122 species or traits adapted to specific resources, e.g. specialist species dependent on large deadwood or on  
123 advanced decay stages, may be favored in overmature stands. Species and trait diversity of saproxylic beetles is  
124 therefore expected to be higher, i.e. rather overdispersed and less filtered, in overmature than in mature  
125 stands. This should induce (1.1) a shift in saproxylic beetle species composition due to nestedness; (1.2) a shift  
126 in mean trait values due to environmental selection for certain traits (deadwood of large diameter and in  
127 advanced decay stages); and (1.3) an increase in the dispersion of traits related to specific deadwood resources  
128 (diameter and decay) from mature to overmature stands.

129 (2) Forest continuity induces filtering related to differences in the dispersal abilities of species,  
130 independently of stand maturity. As compared to ancient forests, species may be absent in recent forests, even  
131 at a comparable level of stand maturity, due to contrasting time for colonization. This should induce (2.1) a  
132 shift in saproxylic beetle species composition due to turnover; but should not influence (2.2) the mean and  
133 (2.3) the dispersion of body size and niche position traits.

134 (3) Forest continuity, in interaction with stand maturity, makes unique long-lasting habitat features  
135 available, thus increasing niche differentiation within stands. In ancient overmature stands, the availability of  
136 these unique resources (e.g. large decayed wood) may allow the habitat requirements of certain specialized  
137 species (i.e. characteristic species) to be better fulfilled, which may result in an increase in their abundance or  
138 occurrence. Moreover, niche differentiation may enhance local resource heterogeneity, which in turn may  
139 promote functional divergence in the assemblage. This should lead to (3.1) an increase in the number of  
140 characteristic species; and (3.2) an increase in the dispersion of traits related to cryptic differences in habitat  
141 quality (i.e. body size) from recent to ancient forests, at a comparable level of stand maturity.

142

## 143 **2. MATERIALS and METHODS**

### 144 **2.1. Study area and experimental design**

145 The study was carried out in the French pre-Alps, in the Vercors, Chartreuse and Bauges ranges (see  
146 Appendix A); these areas are characterized by a limestone substratum and a temperate climate. The landscapes  
147 are mostly covered by unfragmented forests (63% of landscape cover of the three areas) and afforestation has  
148 mainly occurred above and below the persistent forest belt, as elsewhere in European mountain areas (e.g.  
149 Gellrich et al., 2007). Moreover, due to physical constraints and the lack of logging roads, mountain forests has  
150 hitherto been less intensively managed than lowland forests (Paillet et al., 2015). Therefore, compared to  
151 recent lowland forests, recent montane forests in the Northern Alps, i.e. forest that have established after  
152 1864, are mostly adjacent to ancient forests and have the potential to develop towards stand structures similar  
153 to those found in ancient forests.

154 In 2014, we selected 40 sites, among a larger sampling design ( $n = 70$ ), that perfectly cross forest  
155 continuity (ancient forests = 20; recent forests = 20) with stand maturity (mature stands = 20; overmature  
156 stands = 20). Forest continuity was characterized using historical maps and stand maturity was a priori

157 approached by forest inspections and confirmed after stand attribute measurements were taken. This  
158 sampling scheme was located in montane beech-fir forests (800 – 1500 m in altitude). The dominant tree  
159 species were European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and Norway spruce (*Picea abies*) (see  
160 structural and compositional variations between treatments in Appendix C & D). To improve the independence  
161 among our observations and avoid edge influence, all sampling sites were established > 1.2 km away from any  
162 other site, were located in ancient or recent forests > 5 ha in area, and were > 68 m from the nearest stand  
163 edge.

## 164 **2.2. Insect sampling**

165 We used two complementary sampling methods to characterize saproxylic beetle communities: flight-  
166 interception traps efficient at capturing flying beetles and Winkler-Berlese litter sample extractors efficient at  
167 capturing flightless soil-dwelling beetles. From May to August 2014, three flight-interception traps were  
168 installed at each site, approximately 30 m apart and 1.5 m above the ground (total = 120 traps). Each trap  
169 consisted of two perpendicularly intercepting transparent plastic panes (40–60 cm) with a funnel below leading  
170 to collecting vials filled with a killing and preservative mixture of 50% propylene glycol and 50% water with  
171 detergent. The flight-interception traps were emptied monthly. Soil-dwelling beetles were sampled by sifting  
172 litter through 0.5 cm-mesh Winkler bags. At each site, 1 liter of litter was collected at the base of the six largest  
173 living trees (for a total volume of 6 liters of litter per site). Litter sifting was conducted in September 2014 and  
174 insects were extracted at the laboratory through Berlese funnels for one month (Cateau et al., 2016). All  
175 saproxylic beetles were identified to the species or genus level, including Pselaphinae and Dasycerinae, but  
176 excluding the other Staphylinidae subfamilies.

## 177 **2.3. Species traits**

178 We estimated four quantitative ecological traits describing crucial dimensions of ecological  
179 requirements (abiotic conditions, quality of deadwood substrate) of each species: i) mean body size, ii)  
180 diameter and iii) decay stage of the deadwood in which the species was recorded, and iv) canopy cover of  
181 forests in which the species is known to occur. The traits were extracted from Gossner *et al.* (2013) and  
182 completed for missing values (Appendix B), using the ecological information stored in the Frisbee database  
183 (Bouget et al., 2008). For niche position traits, these authors used the frequency of occurrence (0.5 = very rare;  
184 1 = rare; 2 = common; 3 = preferred) of each species in ordered classes – diameter: < 15, 15 - 35, 35 - 70, > 70

185 cm; decay stage: alive, freshly dead, initiated decomposition, advanced decomposition, extremely  
186 decomposed; canopy cover: open, semi-open, closed – and calculated a weighted score for each niche value.  
187 We computed community-weighted means (CWM) and functional dispersion (FDis) for each trait value (dbFD  
188 function, FD package, Laliberté and Legendre, 2010). CWM is defined as the mean of trait values weighted by  
189 the relative abundance of each species bearing each value (Lavorel et al., 2008). FDis is defined as the mean  
190 distance of individual species to the weighted centroid of all species in the assemblage and is unaffected by  
191 species richness (Laliberté and Legendre, 2010). Since we knew that stand maturity influenced richness of  
192 saproxylic beetles (Janssen et al. 2016), this multidimensional index was preferred over other potential  
193 functional dispersion measures. To reduce the influence of very abundant species (10 species > 50% of the  
194 cumulative abundance), log-transformation was applied before CWM and FDis were calculated. This  
195 transformation does not affect the robustness of these indices and their interpretation (Májeková et al., 2016).

#### 196 **2.4. Forest continuity and stand maturity characterization**

197 We characterized forest continuity by crossing digitized 1:40 000 État-Major maps of France charted in  
198 the middle of the 19<sup>th</sup> century with 1:10 000 recently updated vegetation maps in a Geographic Information  
199 System managed using ArcGIS 10.1 (Environmental Systems Research Inst., Redlands, CA, USA). Forest cover  
200 overlapping in both maps was considered to indicate ancient forests, while current forest cover overlapping  
201 with crops or meadows in the État-Major maps was considered to indicate recent forests. We then  
202 characterized landscape composition (i.e. proportion of forests, beech-fir stands and ancient forests) and  
203 spatial configuration (i.e. perimeter-area ratio, distance to the nearest forest edge and distance to nearest  
204 ancient/recent forest edge) variables within a 500-m radius around each sampling site, and tested for the  
205 effect of forest continuity on these variables (Appendix C).

206 In each selected plots, stand maturity was characterized based on two concentric subplots: (a) a 10-m-  
207 radius subplot, where all living and dead trees as well as lying trunks ( $\geq 7.5$  cm in DBH or basis diameter;  $\geq 1$  m  
208 in length) were recorded, and (b) a 20-m-radius plot, where all large living and dead trees and lying trunks ( $\geq 30$   
209 cm in DBH or basis diameter;  $\geq 1$  m in length) were recorded (for further details, see Janssen et al., 2016). For  
210 each tree and lying trunk, tree species, decay stage and tree-related microhabitats (cavities, sporophores of  
211 saproxylic fungi, ivy, sap runs, missing bark, cracks and shelter bark) were recorded. Diameters at both ends  
212 and at the middle section as well as the length of the portion of each lying trunk located inside the plot were  
213 recorded. We estimated decay stage by crossing five classes of inner wood hardness (based on resistance to

214 tree caliper penetration) and four classes of remaining bark cover. Deadwood heterogeneity was estimated as  
215 the number of combinations formed by position (snags versus logs), species, decay class and 2-cm-diameter  
216 classes. We estimated canopy openness with a spherical densiometer by taking readings from four points in the  
217 cardinal directions, 10 m from the plot center. We used hierarchical cluster analysis (Ward method) based on  
218 the first three axes of a principal component analysis (cumulative projected inertia = 88.30%) to distinguish  
219 between mature and overmature stands (dudi.pca and hclust function, ade4 package, Dray and Dufour, 2007)  
220 (Appendix A). PCA was conducted considering four environmental variables closely related to stand maturity:  
221 volume of large logs, number of large snags, number of very large living trees and microhabitat heterogeneity  
222 (i.e. the number of microhabitat types). The effect of stand maturity on stand attributes was then tested using  
223 simple two-way ANOVA in order to confirm the validity of the classification (Appendix C).

## 224 **2.5. Statistical analysis**

225 Analyses were performed with R 3.1.2 (R Core Team, 2015).

226 To determine if saproxylic beetle assemblages were influenced by forest continuity and/or stand  
227 maturity, we performed PERMANOVA (adonis function) and PERMDISP (betadisper function) analyses  
228 (Anderson and Walsh, 2013) based on a Bray-Curtis distance, with 999 permutations (vegan package, Oksanen  
229 et al., 2013). Non-metric multidimensional scaling (NMDS) provided a graphical representation of dissimilarity  
230 (metaMDS function, vegan package). Since dissimilarity may be related to differences in richness, we quantified  
231 the nestedness pattern in a presence/absence matrix using the NODF metric (nestednodf function, vegan  
232 package, Almeida-Neto et al., 2008) and compared observed patterns with those resulting from a fixed-fixed  
233 null model (999 permutations, oecosimu function, vegan package) (Ulrich et al., 2009).

234 To determine the relative contribution of variables associated with forest continuity and stand  
235 maturity on saproxylic beetle assemblage variations, we used canonical analysis of principal coordinates (CAP,  
236 Anderson and Willis, 2003) based on a Bray-Curtis distance, with 999 permutations (capscale function, vegan  
237 package) (Appendix E). As we knew that differences in richness were driving variations in saproxylic beetles  
238 assemblages, we added the species richness as a condition in the CAP in order to remove its effect from the  
239 analysis. Then, we calculated the marginal contribution of eight uncorrelated and *a priori* biologically important  
240 variables indicative of stand structure (n = 4) and deadwood (n = 4) features and of three variables indicatives

241 of landscape composition and configuration to total constrained inertia (with all other variables accounted for  
242 in the model) and tested for their individual significance (after all other variables were partialled out).

243 To determine the individual species response to forest continuity and/or stand maturity, we used  
244 indicator species analysis (multipatt function, indicpecies package, De Cáceres and Legendre, 2009), based on  
245 the indicator values index (IndVal), actually combining two features, i.e. the concentration of abundance within  
246 a particular cluster of sites (exclusivity), and the relative frequency of species within this group (fidelity). Low-  
247 frequency and low-abundance species (occupied sites < 10%, < 10 individuals in total) were discarded (n = 184).  
248 We used the IndVal index to investigate the preferences of individual species for ancient overmature, ancient  
249 mature, recent overmature and recent mature plots, and a permutation test (n = 9999) to test for the statistical  
250 significance of indicator species (called “characteristic species” hereafter).

251 To determine whether functional composition was influenced by forest continuity and/or stand  
252 maturity, we used two-way ANOVAs. We tested the response of the CWM and FDis of each individual trait to  
253 both factors individually and to their interaction. We also conducted pairwise comparisons of the individual  
254 effect of forest continuity (controlling for stand maturity) and of stand maturity (controlling for forest  
255 continuity) using one-way ANOVAs (alpha = 0.025 after Bonferroni correction).

256 To determine whether functional composition was influenced by variation in stand attributes between  
257 ancient and recent forests, we used linear models (family = Gaussian). We developed 16 a priori models plus  
258 null model that tested the main effect and the interaction effect of forest continuity factor with eight variables  
259 indicative of stand structure (n = 4) and deadwood (n = 4) features (see correlation matrix in appendix F), on  
260 the CWM and FDis of saproxylic beetle traits. The most parsimonious model was identified using Akaike’s  
261 information criterion corrected for small sample sizes (Burnham and Anderson, 2002) and model averaging was  
262 used to estimate parameter and associated unconditional standard errors (model.sel and model.avg functions,  
263 MuMIn package, Barton, 2015).

264 To determine whether traits mediate differences in abundance across saproxylic beetle species and  
265 forest continuity and/or stand maturity, i.e. measured through the interaction terms between factors and trait  
266 variables, we used community assembly via trait selection (CATS) regression (Warton et al., 2015). This  
267 multisite extension of CATS is closely related to recent model-based solutions to the fourth-corner problem  
268 (e.g. Brown et al., 2014). Based on a generalized linear modeling framework, extended CATS is better able to  
269 handle the strong mean-variance relationship in abundance data. Models were fitted using negative binomial

270 distribution and the significance of the interaction terms was calculated using PIT-trap methods with 999  
271 bootstrap resamples (manyglm function, mvabund package, Wang et al., 2012). PIT-trap is a new method  
272 which bootstraps probability integral transform residuals, and which have been found to give the most reliable  
273 Type I error rates. Finally, in order to understand the relative importance of species traits in explaining  
274 differences in abundance across environmental factors, we extracted and plotted the related interactions'  
275 standardized coefficients.

276

### 277 **3. RESULTS**

#### 278 **3.1. Variations in stand-maturity- and forest-continuity-associated variables**

279 Two-way ANOVAs showed that the variation in stand-maturity- and forest-continuity-associated  
280 variables was consistent with the classification of the two categorical variables used (Appendix C). Indeed,  
281 nearly all of the variables related to stand structural complexity, deadwood quantity and heterogeneity, and  
282 tree-related microhabitat diversity increased from mature to overmature stands. The landscape pattern around  
283 each site varied accordingly: the ancient forest sites were included in a landscape matrix that contained more  
284 forests, more beech-fir stands and more ancient forests; and were located at a greater distance from the forest  
285 edge and in patches with less complex shapes than the recent forest sites.

286 The interaction term between forest continuity and stand maturity was only significant for the  
287 perimeter-area ratio of forest cover and for the volume of large logs (Appendix D). All other environmental  
288 variables varied consistently between ancient and recent forests, at a comparable maturity level.

#### 289 **3.2. Assemblage structure and individual species response to forest continuity and stand maturity**

290 A total of 307 saproxylic beetle species (18 729 individuals) were captured at the 40 sites: 284 species  
291 (16 884 individuals) with flight intercept traps, among which 255 species were exclusives, and 52 species (1 845  
292 individuals) with Winkler-Berlese extractors, among which 23 species were exclusives. Data per site were  
293 pooled before analysis.

294 Saproxylic beetle assemblage composition was not influenced by forest continuity (Fig. 1) or maturity-  
295 continuity interaction, but significantly differed between mature and overmature stands (PERMANOVA pseudo-  
296  $F_{1,38} = 2.409$ ,  $p = 0.003$ ). Since PERMDISP revealed no significant difference in the average within-group  
297 distances, we conclude that variation in assemblage structures revealed by PERMANOVA was clearly related to

298 location effect (Anderson and Walsh, 2013), i.e. to differences between mature and overmature stands. The  
299 nestedness metric for all species-by-site matrix was significantly different from the simulated mean under the  
300 null model (NODF = 41.14,  $p = 0.019$ ), indicating that species-poor sites were a subset of species-rich sites.  
301 Therefore, the observed shift in species composition revealed by PERMANOVA between mature and  
302 overmature stands should probably be viewed as a result of nestedness rather than of species turnover.

303 CAP ordination revealed that 29.6 % ( $p = 0.004$ ) of the variation in species composition was explained  
304 by environmental variables (see Appendix E for elementary contributions of variables to inertia), after that the  
305 effect of species richness was removed from the analysis. The first CAP axis was positively related to distance to  
306 forest edge (11.2 %) but negatively related to the basal area of living trees (9.7 %) and to lesser extent to the  
307 number of diameter classes of standing trees (9.3 %). The second CAP axis was positively related to canopy  
308 openness (11.8 %) and the number of large snags (9.2 %). All other variables slightly influenced saproxylic  
309 beetle assemblages.

310 Indicator species analysis (Fig. 2 & Appendix G) showed that, among the 123 species considered, only a  
311 few species were influenced by forest continuity and/or stand maturity: two were characteristic of ancient  
312 forests, two of recent forests, one was characteristic of mature stands and 13 of overmature stands. No species  
313 were characteristic of ancient-mature stands, ten species were characteristic of ancient-overmature stands, no  
314 species were characteristic of recent-mature stands and one species was characteristic of recent-overmature  
315 stands.

### 316 **3.3. Responses of individual traits in mean and dispersion to forest continuity and stand maturity**

317 Two-way ANOVAs showed that the mean trait value for decay preference (mean decay niche) ( $p =$   
318  $0.012$ ) increased from mature to overmature stands (Table 1); however, mean body size ( $p = 0.016$ ) and the  
319 mean trait value for diameter preference (mean diameter niche) ( $p = 0.014$ ) increased differently in ancient  
320 and recent forests (Table 2). The mean trait value for canopy preference (mean canopy niche) was influenced  
321 neither by stand maturity nor forest continuity. Pairwise comparison revealed that mean body size ( $p = 0.007$ )  
322 and mean diameter niche ( $p < 0.001$ ) increased between ancient-mature and ancient-overmature stands, and  
323 that mean decay niche ( $p = 0.013$ ) increased between recent-mature and recent-overmature stands. For trait  
324 dispersion, two-way ANOVAs showed that the diversity of decay ( $p = 0.030$ ) and canopy cover ( $p = 0.043$ )  
325 preferences increased from mature to overmature stands (Table 1); however, trait dispersion for body size ( $p =$   
326  $0.015$ ) increased differently in ancient and recent forests (Table 2). Trait dispersion for diameter preference

327 was influenced neither by stand maturity nor forest continuity. Pairwise comparison revealed that only body  
328 size dispersion ( $p = 0.015$ ) increased between ancient-mature and ancient-overmature stands.

329 Model results showed that none of the competing models best predicted the mean and dispersion of  
330 individual trait values, since associated delta  $AIC_c$  and  $AIC_c$  weight were relatively low (Appendix H). Model  
331 averaging revealed that mean body size increased more in ancient forests with the number of very large trees,  
332 the diversity of tree diameter classes, the volume of large logs and deadwood heterogeneity (Table 3).  
333 Moreover, regardless of forest continuity, mean body size increased with the availability of large snags. For  
334 niche traits, mean diameter increased more in ancient forests with the number of very large trees. Moreover,  
335 regardless of forest continuity, mean diameter and decay niche increased with the availability of snags and  
336 logs, and the diversity in microhabitats. Mean decay niche increased also with the heterogeneity of deadwood.  
337 For trait dispersion, model averaging revealed that body size dispersion increased more in ancient forests with  
338 the number of very large trees and deadwood heterogeneity (Table 4). For niche traits, the dispersion of trait  
339 values for diameter preferences increased more in ancient forests with the number of very large trees, while  
340 the dispersion of trait values for decay preference increased with the diversity of microhabitats in both ancient  
341 and recent forests.

#### 342 **3.4. How traits mediate abundance patterns across forest continuity and stand maturity**

343 The CATS regression showed that the interaction term between stand maturity and trait variables was  
344 significant (log-likelihood ratio = 17.6,  $p = 0.001$ ). Differences in mean beetle abundance between mature and  
345 overmature stands was therefore mediated by traits, especially deadwood diameter. This pattern was more  
346 specifically related to ancient-overmature stands, as shown by the interaction term between the continuity-  
347 maturity combination and trait variables (log-likelihood ratio = 27.1,  $p = 0.034$ ). Compared to other interaction  
348 terms, deadwood diameter niche was the trait that best explained variations across species in their response to  
349 stand maturity and to the continuity-maturity combination (Fig. 3). Difference in deadwood diameter niche was  
350 especially marked between mature and overmature stands in ancient forests, as compared to recent forests,  
351 indicating that saproxylic beetles that had preferences for large deadwood pieces were more abundant in  
352 ancient-overmature stands.

353

#### 354 **4. DISCUSSION**

355 Our results show that stand maturity was more important than forest continuity in shaping the  
356 assemblage structure and the functional composition of saproxylic beetles. Moreover, beyond the effect of  
357 stand maturity per se, the additive effect of forest continuity on stand maturity induces several habitat changes  
358 which, although not directly measurable considering the resolution of the forest descriptors used, influenced  
359 the functional composition of saproxylic beetle assemblages. We here demonstrated that stand maturity acts  
360 congruently with forest continuity in providing valuable resources for both saproxylic beetle assemblages and  
361 functional composition. Specifically, we highlighted the fact that the functional structure of saproxylic beetle  
362 assemblages is shaped by the quantity of large deadwood and by the heterogeneity of resources available (i.e.  
363 deadwood and light microsites).

#### 364 **4.1. Stand maturity rather than forest continuity shapes saproxylic beetles assemblage and functional** 365 **composition**

366 In accordance with our first hypothesis, we found a strong influence of stand maturity on assemblage  
367 structure. However, forest continuity had no effect on assemblage structure. The nestedness analysis reveals  
368 that dissimilarity in assemblages was related to differences in species richness, indicating that saproxylic beetle  
369 diversity in mature stands was generally a subset of the diversity in overmature stands. Thus, in accordance  
370 with numerous previous studies (e.g. Janssen et al., 2016; Martikainen et al., 2000; Stenbacka et al., 2010), our  
371 results report a positive relationship between stand maturity and saproxylic diversity. Moreover, far more  
372 species were characteristic of overmature stands than mature stands and several of these species have clear  
373 preferences for large deadwood (trait values >3 for diameter) and decayed wood (trait values >3 for decay  
374 stages). By improving habitat conditions for saproxylic beetles, i.e. deadwood availability, stand maturity acts  
375 by decreasing the environmental filter on the regional species pool, i.e. by opening selection to a larger  
376 diversity of species, notably those dependent on more specific deadwood attributes. However, contrary to a  
377 previous study by Buse (2012), we found very few characteristic species for ancient forests, and none of these  
378 were flightless species. No methodological argument could be advanced to explain this trend, since we actually  
379 set up complementary protocols to sample both flying and flightless species with a standardized effort in each  
380 plot. This may confirm that, in unfragmented forests, flightless beetles are able to disperse and successfully  
381 colonize recent forests (e.g. Janssen et al., 2016; Marcus et al., 2015), and thus that habitat limitation is of  
382 more importance than dispersal limitation in shaping assemblage structure.

383 The functional structure of saproxylic beetle assemblages was significantly influenced by stand  
384 maturity but not by forest continuity. Variations in mean trait values confirm that the abundance of species  
385 that prefer large deadwood and/or deadwood in advanced stages of decay increase with stand maturity. This  
386 shift in trait values was mostly due to an increase in both deadwood amount and heterogeneity, from mature  
387 to overmature stands, confirming previous results (Gossner et al., 2013). Moreover, probably due to the larger  
388 habitat heterogeneity, overmature stands seemingly allowed a higher co-occurrence among saproxylic beetles  
389 with contrasting resource requirements. Indeed, divergence in trait related to decay stage of deadwood in  
390 which larvae develop and preferred canopy cover increased with stand maturity. Several studies have pointed  
391 out the turnover of saproxylic beetles during the decaying process (e.g. Saint-Germain et al., 2007). Our results  
392 confirmed that, as maturity increases, the co-occurrence of species associated with fresh and decayed wood  
393 also increases. This highlights the importance of supplying different deadwood types, which, as demonstrated  
394 by recent studies (Gossner et al., 2016; Seibold et al., 2016), give indirect support for the importance of  
395 deadwood heterogeneity. Likewise, the increase in saproxylic beetle species light tolerances with stand  
396 maturity may be due to the fact that, during forest succession, changes in the canopy - gap structure lead to an  
397 increase in light heterogeneity on the forest floor (Vieilledent et al., 2010). Opening conditions influence  
398 saproxylic beetles in different ways, through microclimatic effects directly stimulating adult activity or larval  
399 development, or through complementation effects based on increased flower availability used by adults (e.g.  
400 Bouget et al., 2013). Thus, light heterogeneity may promote a diversity of microsites that benefits a larger  
401 diversity of species with contrasting light requirements. Overall and in accordance with recent studies (Gossner  
402 et al., 2013; Müller et al., 2014), our results show that not only the species richness of saproxylic beetles  
403 (Janssen et al., 2016) but also the functional trait composition, in mean (decay and diameter preference) and  
404 in dispersion (decay and canopy preference), benefits from habitat heterogeneity.

#### 405 **4.2. Forest continuity in interaction with stand maturity structures the species and trait composition of** 406 **saproxylic beetle assemblages**

407 In accordance with our third hypothesis, the individual species response of saproxylic beetles was  
408 largely influenced by the additive effect of forest continuity on stand maturity, with almost all characteristic  
409 species being associated to ancient-overmature stands. Those species are quite diverse in terms of body size  
410 and niche preferences, though some species appear more specifically associated to large-diameter decayed  
411 wood, as in the case of *Melanotus castanipes* and *Rhizophagus cribratus*. Considering that, in our study area,

412 recent-overmature stands are at best 200 years old, unique habitat resources such as tree cavities with mould  
413 or large-diameter decayed wood could only have developed in ancient-overmature stands. The importance of  
414 long-term continuous availability of suitable habitat has been pointed out as a key factor for the conservation  
415 of several saproxylic beetle species (e.g. Müller et al., 2005; Siitonen and Saaristo, 2000). Our results pointed  
416 out that the additive effect of forest continuity on stand maturity provides better ecological conditions for  
417 saproxylic beetles, with higher niche differentiation in ancient-overmature stands. This indicates that recent  
418 forests, even at an advanced stage of maturity, still do not fulfill the requirements of certain specialist species.  
419 However, since forest cover in the surrounding landscape was actually higher for ancient (ca. 94%) than recent  
420 forests (ca. 87%) (Appendix C), it cannot be ruled out that habitat amount could be a driver behind this  
421 observed additive effect (e.g. Sverdrup-Thygeson and Lindenmayer, 2003).

422           The functional structure of saproxylic beetle assemblages was significantly influenced by the  
423 interaction between forest continuity and stand maturity. As compared to recent forests and even mature-  
424 ancient forests, the mean trait values for deadwood diameter and beetle body size increased most in ancient-  
425 overmature stands. The CATS regression confirmed that saproxylic beetles which develop in large-diameter  
426 deadwood were more abundant in ancient-overmature stands. This shift in trait value was mostly due to an  
427 increase in the availability of very large trees as well as an increase in both deadwood amount and  
428 heterogeneity. Larger insects are generally associated with a long larval development phase and require stable  
429 and long-lasting habitats (Stokland et al., 2012). Large deadwood provides long-lasting habitats, stable  
430 microclimatic conditions and a large diversity of available resources (Stokland et al., 2012). Hence, large  
431 saproxylic beetles are often associated with large deadwood pieces (Brin et al., 2011). Several studies have  
432 pointed out the importance of large deadwood for saproxylic beetle diversity (e.g. Bouget et al., 2014); our  
433 results emphasize that this specific stand attribute not only impacts the diversity (Janssen et al., 2016) but also  
434 induces a shift in the mean body size and the mean deadwood diameter preferred by saproxylic beetles.  
435 Beyond a shift in body size, the additive effect of forest continuity on stand maturity also induces trait  
436 divergence, with an increase in small and large species co-occurrence in ancient-overmature stands. This  
437 increase in body size dispersion was closely related to an increase in deadwood heterogeneity and in the  
438 availability of very large trees within stands. In beech forests, Gossner *et al.* (2013) found that the increase in  
439 body size diversity was linked to an increase in deadwood amount. Deadwood amount and heterogeneity are  
440 usually correlated (Müller and Bütler, 2010), as they were in our montane mixed forests. Since body size is a

441 morphological trait that correlated well with many life-history traits (Woodward et al., 2005), changes in the  
442 mean and the dispersion of this trait may indicate the existence of cryptic differences in niches occupied by  
443 saproxylic beetles, between overmature stands in ancient or recent forests. We therefore suspect that body  
444 size diversity was linked to a higher diversity of deadwood pieces in ancient than in recent forests.

445

## 446 **5. CONCLUSION**

447 Silvicultural practices, by truncating the late developmental phases of forest dynamics, remove  
448 overmature forest attributes, which may contribute to biodiversity loss among associated taxa (Stokland et al.,  
449 2012). Here, we have shown that habitat conditions promoted by forest continuity also influence the functional  
450 composition of saproxylic beetles. The need to disentangle interactions among deadwood factors is of  
451 importance and improved knowledge of these interactions could increase the efficiency of conservation  
452 strategies (Seibold et al., 2015a). In line with recent studies (Gossner et al., 2013; Müller et al., 2014; Seibold et  
453 al., 2015b), our results confirm that not only the species composition but also the functional composition of  
454 saproxylic beetle assemblages is shaped by resource quantity and heterogeneity. Even in a quite extensive  
455 montane forest context (Paillet et al., 2015), saproxylic species conservation would benefit from strategies that  
456 not only promote higher amounts of deadwood in stands, but also ones that favor the diversity of deadwood  
457 substrates, especially in terms of diameter and decay stage. From our results, not only deadwood  
458 heterogeneity, but also the volume of large logs and the density of very large trees fostered the dispersion of  
459 several trait values. Silvicultural practices raising these noteworthy stand metrics, through selective cutting and  
460 extended rotations and habitat tree and deadwood active retention, should be encouraged in mature and  
461 recent forests. Since large-bodied saproxylic beetles and those species that rely on large deadwood run a  
462 higher risk of extinction (Seibold et al., 2015b), set-aside conservation strategies should primarily focus on  
463 overmature stands in ancient forests, secondly on overmature stands regardless of forest continuity.

464

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471

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607

608

609 Table 1. Variation in individual traits, measured by CWM and FDis, related to forest continuity and stand  
 610 maturity (p-value based on two-way ANOVAs).

Variable	Ancient forest	Recent forest	p-value	Mature stand	Overmature stand	p-value
	Mean ( $\pm$ SD)	Mean ( $\pm$ SD)		Mean ( $\pm$ SD)	Mean ( $\pm$ SD)	
CWM Body size	3.69 ( $\pm$ 0.43)	3.71 ( $\pm$ 0.34)	0.8901	3.60 ( $\pm$ 0.37)	3.80 ( $\pm$ 0.38)	0.0969
CWM Diameter	2.03 ( $\pm$ 0.09)	2.01 ( $\pm$ 0.05)	0.3680	1.99 ( $\pm$ 0.05)	2.05 ( $\pm$ 0.07)	0.0024
CWM Decay stage	2.54 ( $\pm$ 0.12)	2.50 ( $\pm$ 0.08)	0.1684	2.48 ( $\pm$ 0.09)	2.56 ( $\pm$ 0.10)	0.0124
CWM Canopy cover	1.78 ( $\pm$ 0.05)	1.77 ( $\pm$ 0.04)	0.7366	1.77 ( $\pm$ 0.04)	1.78 ( $\pm$ 0.05)	0.3252
FDis Body size	0.54 ( $\pm$ 0.10)	0.55 ( $\pm$ 0.10)	0.7572	0.53 ( $\pm$ 0.10)	0.56 ( $\pm$ 0.09)	0.3825
FDis Diameter	0.73 ( $\pm$ 0.05)	0.73 ( $\pm$ 0.07)	0.9530	0.72 ( $\pm$ 0.06)	0.74 ( $\pm$ 0.07)	0.2710
FDis Decay stage	0.79 ( $\pm$ 0.06)	0.80 ( $\pm$ 0.04)	0.7208	0.78 ( $\pm$ 0.05)	0.81 ( $\pm$ 0.04)	0.0281
FDis Canopy cover	0.78 ( $\pm$ 0.06)	0.77 ( $\pm$ 0.08)	0.6743	0.75 ( $\pm$ 0.06)	0.80 ( $\pm$ 0.07)	0.0429

611

612

613 Table 2. Variation in individual traits, measured by CWM and FDis, related to the interaction between forest  
 614 continuity and stand maturity (p-value based on two-way ANOVAs).

Variable	Ancient mature	Ancient overmature	Recent mature	Recent overmature	p-value
	Mean ( $\pm$ SD)				
CWM Body size	3.45 ( $\pm$ 0.35)	3.93 ( $\pm$ 0.37)	3.75 ( $\pm$ 0.34)	3.67 ( $\pm$ 0.34)	0.0159
CWM Diameter	1.97 ( $\pm$ 0.04)	2.09 ( $\pm$ 0.08)	2.00 ( $\pm$ 0.06)	2.02 ( $\pm$ 0.05)	0.0142
CWM Decay stage	2.51 ( $\pm$ 0.11)	2.58 ( $\pm$ 0.13)	2.46 ( $\pm$ 0.07)	2.55 ( $\pm$ 0.08)	0.7907
CWM Canopy cover	1.77 ( $\pm$ 0.05)	1.79 ( $\pm$ 0.06)	1.77 ( $\pm$ 0.04)	1.78 ( $\pm$ 0.04)	0.9096
FDis Body size	0.49 ( $\pm$ 0.09)	0.59 ( $\pm$ 0.08)	0.57 ( $\pm$ 0.10)	0.53 ( $\pm$ 0.09)	0.0144
FDis Diameter	0.74 ( $\pm$ 0.05)	0.72 ( $\pm$ 0.06)	0.70 ( $\pm$ 0.06)	0.76 ( $\pm$ 0.07)	0.0676
FDis Decay stage	0.78 ( $\pm$ 0.06)	0.81 ( $\pm$ 0.05)	0.78 ( $\pm$ 0.04)	0.81 ( $\pm$ 0.03)	0.9122
FDis Canopy cover	0.77 ( $\pm$ 0.06)	0.79 ( $\pm$ 0.06)	0.74 ( $\pm$ 0.07)	0.80 ( $\pm$ 0.08)	0.3408

615

616 Table 3. Average coefficients (Estimate), standard error ( $\pm$ SE) and confidence intervals (95% CI) for each variable predicting the mean of individual trait values of saproxylic  
617 beetles in the French pre-Alps. The 95% confidence interval of coefficients in bold excluded 0 [FC: forest continuity; Canop: canopy openness; Gtrees: tree basal area; Nvlt:  
618 number of very large living trees ( $\emptyset > 62.5$  cm); Ndiam: number of diameter classes of standing trees; Nlsnags: number of large snags ( $\emptyset > 30$  cm); Vllogs: volume of large  
619 logs ( $\emptyset > 30$  cm) in m<sup>3</sup>; Dcwd: deadwood heterogeneity; Dmicro: diversity of tree-related microhabitats].

Variable	CWM Body size		CWM Canopy cover		CWM Decay stage		CWM Diameter	
	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Canop	-0.001 ( $\pm$ 0.151)	(-0.306; 0.306)	0.008 ( $\pm$ 0.019)	(-0.030; 0.045)	-0.027 ( $\pm$ 0.048)	(-0.123; 0.069)	0.044 ( $\pm$ 0.027)	(-0.009; 0.097)
Gtrees	0.055 ( $\pm$ 0.046)	(-0.037; 0.145)	-0.002 ( $\pm$ 0.005)	(-0.010; 0.008)	0.007 ( $\pm$ 0.009)	(-0.012; 0.025)	0.004 ( $\pm$ 0.007)	(-0.010; 0.017)
Nvlt	<b>0.244 (<math>\pm</math> 0.092)</b>	<b>(0.060; 0.428)</b>	0.006 ( $\pm$ 0.01)	(-0.014; 0.026)	0.034 ( $\pm$ 0.020)	(-0.006; 0.074)	<b>0.045 (<math>\pm</math> 0.017)</b>	<b>(0.011; 0.079)</b>
Ndiam	0.039 ( $\pm$ 0.033)	(-0.027; 0.103)	-0.001 ( $\pm$ 0.004)	(-0.007; 0.006)	0.005 ( $\pm$ 0.007)	(-0.008; 0.017)	0.002 ( $\pm$ 0.005)	(-0.008; 0.010)
Nlsnags	<b>0.207 (<math>\pm</math> 0.088)</b>	<b>(0.029; 0.385)</b>	0.005 ( $\pm$ 0.012)	(-0.020; 0.028)	<b>0.064 (<math>\pm</math> 0.023)</b>	<b>(0.018; 0.110)</b>	<b>0.059 (<math>\pm</math> 0.020)</b>	<b>(0.019; 0.098)</b>
Vllogs	<b>0.267 (<math>\pm</math> 0.096)</b>	<b>(0.075; 0.459)</b>	0.005 ( $\pm$ 0.011)	(-0.018; 0.027)	<b>0.050 (<math>\pm</math> 0.022)</b>	<b>(0.006; 0.094)</b>	<b>0.038 (<math>\pm</math> 0.018)</b>	<b>(0.003; 0.072)</b>
Dcwd	<b>0.294 (<math>\pm</math> 0.114)</b>	<b>(0.065; 0.522)</b>	0.007 ( $\pm$ 0.014)	(-0.021; 0.035)	<b>0.075 (<math>\pm</math> 0.023)</b>	<b>(0.029; 0.120)</b>	0.039 ( $\pm$ 0.021)	(-0.002; 0.080)
Dmicro	0.232 ( $\pm$ 0.118)	(-0.006; 0.468)	0.023 ( $\pm$ 0.014)	(-0.005; 0.050)	<b>0.071 (<math>\pm</math> 0.028)</b>	<b>(0.015; 0.127)</b>	<b>0.057 (<math>\pm</math> 0.020)</b>	<b>(0.019; 0.096)</b>
FC	0.469 ( $\pm$ 0.528)	(-0.575; 1.511)	-0.015 ( $\pm$ 0.037)	(-0.087; 0.059)	-0.030 ( $\pm$ 0.052)	(-0.134; 0.074)	0.004 ( $\pm$ 0.038)	(-0.071; 0.079)
FC*Canop	0.169 ( $\pm$ 0.284)	(-0.408; 0.745)	0.019 ( $\pm$ 0.035)	(-0.052; 0.089)	0.118 ( $\pm$ 0.074)	(-0.031; 0.267)	0.014 ( $\pm$ 0.051)	(-0.088; 0.116)
FC*Gtrees	-0.109 ( $\pm$ 0.059)	(-0.228; 0.010)	0.002 ( $\pm$ 0.008)	(-0.014; 0.017)	0.005 ( $\pm$ 0.017)	(-0.029; 0.038)	-0.006 ( $\pm$ 0.012)	(-0.029; 0.017)
FC*Nvlt	<b>-0.337 (<math>\pm</math> 0.128)</b>	<b>(-0.595; -0.079)</b>	0.013 ( $\pm$ 0.018)	(-0.023; 0.048)	0.013 ( $\pm$ 0.037)	(-0.062; 0.087)	<b>-0.049 (<math>\pm</math> 0.024)</b>	<b>(-0.096; -0.002)</b>

FC*Ndiam	<b>-0.089 (± 0.040)</b>	<b>(-0.169; -0.010)</b>	0.005 (± 0.006)	(-0.006; 0.015)	0.004 (± 0.012)	(-0.020; 0.026)	-0.001 (± 0.008)	(-0.017; 0.015)
FC*Nlsnags	-0.044 (± 0.166)	(-0.379; 0.291)	0.011 (± 0.022)	(-0.033; 0.055)	0.018 (± 0.042)	(-0.068; 0.104)	-0.050 (± 0.028)	(-0.107; 0.007)
FC*Vllogs	<b>-0.353 (± 0.154)</b>	<b>(-0.664; -0.042)</b>	0.019 (± 0.022)	(-0.024; 0.062)	-0.030 (± 0.044)	(-0.118; 0.059)	-0.047 (± 0.030)	(-0.107; 0.014)
FC*Dcwd	<b>-0.502 (± 0.159)</b>	<b>(-0.824; -0.180)</b>	0.027 (± 0.022)	(-0.017; 0.070)	-0.008 (± 0.042)	(-0.092; 0.077)	-0.042 (± 0.031)	(-0.104; 0.022)
FC*Dmicro	-0.273 (± 0.226)	(-0.730; 0.184)	-0.004 (± 0.029)	(-0.061; 0.055)	0.014 (± 0.059)	(-0.105; 0.133)	-0.026 (± 0.040)	(-0.106; 0.055)

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620

621 Table 4. Average coefficients (Estimate), standard error ( $\pm$ SE) and confidence intervals (95% CI) for each variable predicting the dispersion of individual trait values of  
622 saproxylic beetles in the French pre-Alps. The 95% confidence interval of coefficients in bold excluded 0 [FC: forest continuity; Canop: canopy openness; Gtrees: tree basal  
623 area; Nvlt: number of very large living trees ( $\varnothing > 62.5$  cm); Ndiam: number of diameter classes of standing trees; Nlsnags: number of large snags ( $\varnothing > 30$  cm); Vllogs: volume  
624 of large logs ( $\varnothing > 30$  cm) in  $m^3$ ; Dcwd: deadwood heterogeneity; Dmicro: diversity of tree-related microhabitats].

Variable	FDis Body size		FDis Canopy cover		FDis Decay stage		FDis Diameter	
	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)	Estimate ( $\pm$ SE)	(95% CI)
Canop	0.003 ( $\pm$ 0.039)	(-0.075; 0.080)	0.030 ( $\pm$ 0.030)	(-0.030; 0.090)	-0.010 ( $\pm$ 0.021)	(-0.051; 0.033)	-0.007 ( $\pm$ 0.026)	(-0.058; 0.046)
Gtrees	0.003 ( $\pm$ 0.012)	(-0.021; 0.026)	-0.001 ( $\pm$ 0.008)	(-0.016; 0.016)	0.001 ( $\pm$ 0.005)	(-0.008; 0.010)	0.004 ( $\pm$ 0.007)	(-0.010; 0.018)
Nvlt	<b>0.050 (<math>\pm</math> 0.024)</b>	<b>(0.003; 0.097)</b>	0.015 ( $\pm$ 0.017)	(-0.021; 0.049)	0.016 ( $\pm$ 0.010)	(-0.004; 0.034)	-0.011 ( $\pm$ 0.016)	(-0.043; 0.022)
Ndiam	0.002 ( $\pm$ 0.009)	(-0.015; 0.019)	0.001 ( $\pm$ 0.006)	(-0.010; 0.012)	-0.001 ( $\pm$ 0.004)	(-0.007; 0.006)	0.004 ( $\pm$ 0.004)	(-0.005; 0.012)
Nlsnags	0.042 ( $\pm$ 0.023)	(-0.005; 0.089)	0.021 ( $\pm$ 0.018)	(-0.016; 0.057)	0.017 ( $\pm$ 0.012)	(-0.008; 0.040)	-0.003 ( $\pm$ 0.021)	(-0.043; 0.039)
Vllogs	0.038 ( $\pm$ 0.025)	(-0.012; 0.088)	0.031 ( $\pm$ 0.017)	(-0.002; 0.064)	0.020 ( $\pm$ 0.010)	(-0.001; 0.041)	0.010 ( $\pm$ 0.016)	(-0.022; 0.040)
Dcwd	0.054 ( $\pm$ 0.030)	(-0.007; 0.113)	0.007 ( $\pm$ 0.023)	(-0.040; 0.053)	0.023 ( $\pm$ 0.012)	(-0.001; 0.046)	0.007 ( $\pm$ 0.020)	(-0.034; 0.047)
Dmicro	0.054 ( $\pm$ 0.031)	(-0.008; 0.115)	0.041 ( $\pm$ 0.022)	(-0.003; 0.084)	<b>0.037 (<math>\pm</math> 0.013)</b>	<b>(0.011; 0.062)</b>	0.019 ( $\pm$ 0.020)	(-0.022; 0.059)
FC	0.163 ( $\pm$ 0.155)	(-0.143; 0.468)	-0.037 ( $\pm$ 0.057)	(-0.150; 0.077)	-0.001 ( $\pm$ 0.024)	(-0.048; 0.048)	-0.040 ( $\pm$ 0.056)	(-0.151; 0.071)
FC*Canop	0.039 ( $\pm$ 0.073)	(-0.108; 0.185)	0.062 ( $\pm$ 0.050)	(-0.040; 0.162)	0.045 ( $\pm$ 0.035)	(-0.026; 0.114)	0.034 ( $\pm$ 0.047)	(-0.062; 0.130)
FC*Gtrees	-0.029 ( $\pm$ 0.015)	(-0.059; 0.002)	0.017 ( $\pm$ 0.011)	(-0.006; 0.039)	0.002 ( $\pm$ 0.008)	(-0.015; 0.017)	0.014 ( $\pm$ 0.010)	(-0.006; 0.034)
FC*Nvlt	<b>-0.092 (<math>\pm</math> 0.033)</b>	<b>(-0.159; -0.025)</b>	0.045 ( $\pm$ 0.024)	(-0.005; 0.093)	-0.006 ( $\pm$ 0.017)	(-0.041; 0.029)	<b>0.056 (<math>\pm</math> 0.022)</b>	<b>(0.012; 0.100)</b>

FC*Ndiam	-0.020 (± 0.011)	(-0.040; 0.002)	0.012 (± 0.008)	(-0.004; 0.027)	0.005 (± 0.006)	(-0.007; 0.015)	0.005 (± 0.007)	(-0.010; 0.019)
FC*Nlsnags	-0.006 (± 0.044)	(-0.094; 0.082)	0.026 (± 0.032)	(-0.039; 0.090)	0.014 (± 0.022)	(-0.030; 0.056)	0.052 (± 0.029)	(-0.006; 0.109)
FC*Vllogs	-0.068 (± 0.043)	(-0.153; 0.019)	0.040 (± 0.029)	(-0.019; 0.099)	-0.006 (± 0.021)	(-0.047; 0.037)	0.033 (± 0.029)	(-0.025; 0.091)
FC*Dcwd	<b>-0.126 (± 0.041)</b>	<b>(-0.209; -0.044)</b>	0.056 (± 0.032)	(-0.007; 0.119)	0.009 (± 0.021)	(-0.034; 0.051)	0.046 (± 0.029)	(-0.013; 0.103)
FC*Dmicro	-0.071 (± 0.058)	(-0.188; 0.047)	0.056 (± 0.040)	(-0.025; 0.136)	-0.005 (± 0.027)	(-0.059; 0.050)	0.046 (± 0.039)	(-0.033; 0.124)

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625

626 **FIGURE LEGENDS**

627

628 Fig. 1. Nonmetric multidimensional scaling ordination plot of the Bray – Curtis dissimilarity matrix of recent vs  
629 ancient forest or mature vs overmature stand samples. The two axes with highest correlation to forest  
630 continuity and stand maturity factors are represented (NMDS stress = 0.211) and centroid are displayed to help  
631 visualizing the difference between treatments. PERMANOVA analysis of similarities (1000 permutations) tested  
632 the difference of assemblages.

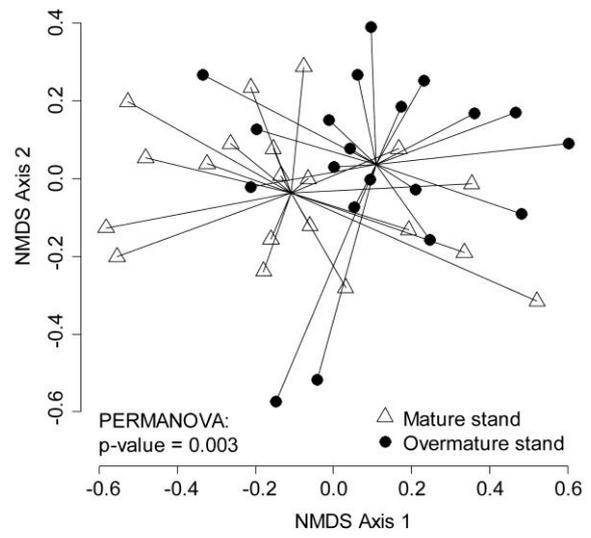
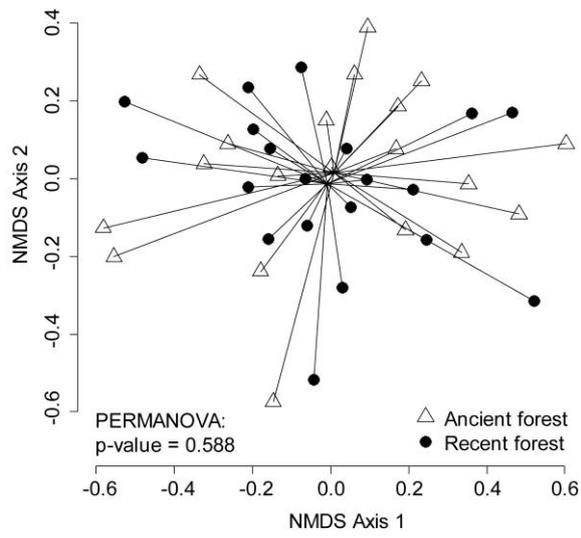
633

634 Fig. 2. Characteristic species, abundance (N), correlation values (IndVal) and p-value for saproxylic beetles  
635 related to forest continuity (Anc = ancient, Rec = recent), stand maturity (Mat = mature, Over = overmature)  
636 and interaction. Mean trait values of each characteristic species are provided (Body = body size in mm, Diam =  
637 preferred deadwood diameter, Decay = preferred deadwood decay stage, Canop = preferred canopy cover).

638

639 Fig. 3. Interaction standardized coefficients estimated under the sum-to-zero constraint from community  
640 assembly via trait selection (CATS) regressions testing the relationship between morphological and niche  
641 position traits and environmental factors, accounting for saproxylic beetles abundance. Red represents a  
642 positive association, blue represents a negative association; the relative tone of color indicates the strength of  
643 the association.

644



645

646 Fig. 1.

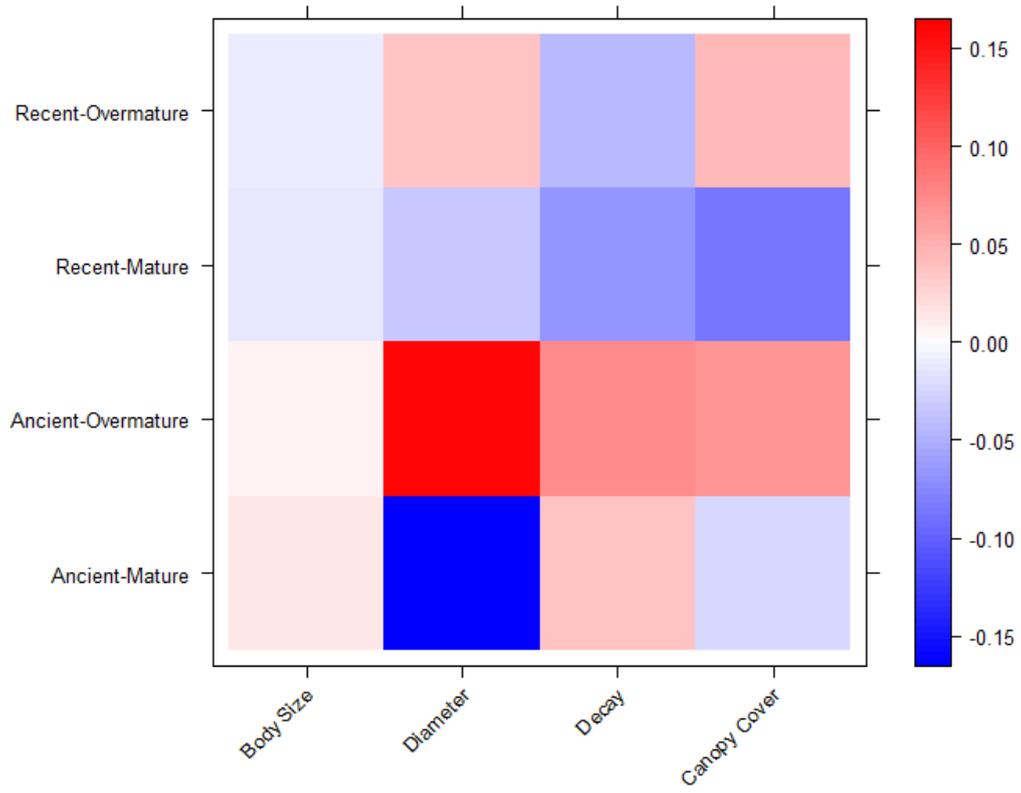
Factor	Species	N	IndVal	p-value	Body	Diam	Decay	Canop
Mat	Rhizophagus dispar	22	0.652	0.034	3	2.50	2.50	1.60
	Cis bidentatus	13	0.588	0.030	2	3.00	3.40	2.50
Over	Xylechinus pilosus	428	0.810	0.033	2	2.17	2.00	1.40
	Trimium brevicorne	20	0.618	0.036	1	1.80	2.00	2.00
	Phloeotribus spinulosus	33	0.688	0.020	2	1.50	1.30	1.20
	Melanotus castanipes	280	0.839	0.001	17	3.00	3.67	2.40
	Ampedus erythrogonus	128	0.835	0.001	6	3.50	3.86	2.50
	Grynobius planus	206	0.818	0.012	5	2.29	3.00	1.50
	Ptilinus pectinicornis	165	0.799	0.030	4	2.50	3.00	1.50
	Pediacus dermestoides	140	0.799	0.004	4	2.50	2.00	1.00
	Enicmus testaceus	347	0.797	0.019	1	1.67	3.00	2.25
	Hallomenus binotatus	61	0.774	0.014	4	2.50	3.40	2.00
	Denticollis rubens	27	0.760	0.001	13	2.29	3.40	2.60
	Melasis buprestoides	88	0.715	0.031	7	2.29	3.00	1.40
	Pityophagus ferrugineus	33	0.661	0.032	5	2.50	2.00	1.50
	Rhizophagus bipustulatus	19	0.613	0.041	2	2.50	2.50	1.60
	Thanasimus formicarius	18	0.612	0.026	8	2.29	2.25	1.50
	Aulonothroscus brevicollis	74	0.588	0.023	2	1.50	3.50	2.50

Factor	Species	N	IndVal	p-value	Body	Diam	Decay	Canop
Mat	Pediacus dermestoides	140	0.632	0.041	4	2.50	2.00	1.00
Over	Glischrochilus quadripunctatus	21	0.753	0.001	4	2.29	2.00	1.50
	Dryocoetes autographus	502	0.684	0.015	3	2.40	2.00	1.60
	Pityophagus ferrugineus	33	0.635	0.026	5	2.50	2.00	1.50
	Melanotus castanipes	280	0.624	0.038	17	3.00	3.67	2.40
	Denticollis rubens	27	0.624	0.017	13	2.29	3.40	2.60
	Rhizophagus ferrugineus	12	0.612	0.023	3	2.50	2.00	2.00
	Thanasimus formicarius	18	0.606	0.021	8	2.29	2.25	1.50
	Crypturgus pusillus	14	0.598	0.018	1	1.20	2.00	1.00
	Rhizophagus cribratus	13	0.582	0.014	3	3.00	2.71	2.40
	Orchesia minor	14	0.567	0.031	3	1.00	3.40	2.00

647

648 Fig. 2.



649 Fig. 3.