

1 **Current “near-to-nature” forest management affects functional**  
2 **trait composition of saproxylic beetles in beech forests**

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24 **Running head:** Functional diversity of beetles

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29 **Abstract**

30 With the aim of wood production with negligible negative effects on biodiversity and  
31 ecosystem processes, a silvicultural practice of felling single trees has been implemented in  
32 European beech forests (*Fagus sylvatica*) during the last decades. Despite this “near-to-  
33 nature” strategy, species richness decreased compared to unmanaged forests. To develop  
34 guidelines to eliminate the fundamental weaknesses in the current practice, we used an  
35 approach that links functional traits of species to ecosystem characteristics. Using data from  
36 eight European countries and from one large forest in southern Germany and forest stand  
37 variables that represent a gradient of forest-use intensity, we evaluated the effect of current  
38 near-to-nature management strategies on the functional diversity of saproxylic beetles. We  
39 found no effect of habitat variables on the overall functional diversity, but clear effects on  
40 single functional traits. With increasing amount of dead wood we found an increase in large  
41 species but also in small species with a preference for dead wood of large diameter and  
42 advanced decay stage. For most species, the mean amount of dead wood across plots in which  
43 they occurred was between 20 and 60 m<sup>3</sup> ha<sup>-1</sup>. Species occurring in plots with a mean amount  
44 > 60 m<sup>3</sup> ha<sup>-1</sup> were consistently those inhabiting dead wood of large diameters and late decay  
45 stages. To make the current wood production practice in beech forests throughout Europe  
46 more conservation oriented, we recommend (1) increasing the amount of dead wood to > 20  
47 m<sup>3</sup> ha<sup>-1</sup>, (2) not removing particularly dead wood of large diameter (50 cm) and allow more  
48 dead wood in advanced stages of decomposition to develop, and (3) conserving strict forest  
49 reserves with their exceptionally high amounts of dead wood as an insurance, refuge, and  
50 source pool for habitat specialists.

## 51 **Introduction**

52 In Europe, modern forestry has significantly changed the species and age composition of  
53 forest fragments during the last centuries, with documented losses of forest species (Speight  
54 1989). To protect and promote biodiversity and ecosystem functions, forest authorities in  
55 Europe developed “near-to-nature” strategies to mitigate negative effects of logging, and  
56 these strategies have been used worldwide since then (Duchiron 2000). One such strategy was  
57 established in the 1980s for the naturally most important habitat type in Europe, the beech  
58 (*Fagus sylvatica*) forests. This concept entails selective cutting, promoting native tree  
59 communities, and allowing for natural regeneration (Boncina 2011; Johann 2006).

60 Forests managed based on the felling of single trees are presumed to mimic the  
61 regeneration process of an old-growth beech forest, with its shade-tolerant trees retaining the  
62 stand structure. Despite such a “near-to-nature” concept, forest authorities still must focus on  
63 wood production. Therefore, they regularly remove old and senescent trees (so-called veteran  
64 trees), significantly reduce the amount of dead wood and plant economically valuable conifers  
65 (Bauhus et al. 2009; Brunet et al. 2010; Fig. 1). Furthermore, logging reduces the canopy  
66 cover and changes soil properties (Christensen et al. 2005; Durak 2010; Fig. 1). This  
67 influences ecological important structural characteristics as well as ecological key processes  
68 in these beech forests (Merino et al. 2008; Meyer & Schmidt 2011). In fact, variables such as  
69 the amount of dead wood and the occurrence and age of old trees are effective measures of  
70 forest-use intensity, which is more than a simple measure of the amount of wood removed  
71 (Bauhus et al. 2009; Fig. 1).

72 The recycling of detritus is one of the key processes in forest ecosystems driving  
73 element cycling and productivity. The quantity and quality of detritus affect the diversity of  
74 decomposers and decomposition (Moore et al. 2004). Thus, besides the amount, also the  
75 structural diversity of dead wood is important to understand the effects of forest use on wood

76 decomposition. However, it is difficult to measure the complex diversity of dead wood. In  
77 addition to fungi, saproxylic beetles are reliable indicators for aspects of dead-wood ecology  
78 (Stokland et al. 2012). These beetles promote decomposition through mutualisms with fungi  
79 or microorganisms and by creating entry ports (Stokland et al. 2012). As bioengineers, some  
80 of them generate resources for other organisms and thus promote biodiversity and influence  
81 ecosystem functions (Buse et al. 2008; Müller et al. 2008a; Zhou et al. 2006). However, most  
82 studies to date have ignored the rich biology of saproxylic beetles and have investigated only  
83 species richness correlated to forest-use intensity.

84         If the focus is moved from the single species to assemblages, diversity becomes the  
85 parameter to evaluate (Pielou 1966). And beyond species richness, functional diversity is a  
86 component of diversity that has been used to understand the functional role of assemblages,  
87 functional redundancy, and the consequences of species loss in ecosystems (Petchey &  
88 Gaston 2006). Functional diversity is linked to the phenotype and therefore the traits of  
89 species (Tilman 2001). Most traits do not vary randomly across species but are correlated to  
90 evolutionary relatedness; therefore, phylogenetic diversity is often used as a surrogate of  
91 functional diversity (Ding et al. 2012). One can analyze the change in functional diversity  
92 along climate or land-use gradients and correlate functional diversity to ecosystem processes  
93 (Cadotte et al. 2011; Ding et al. 2012). In the context of exploring the effects of land use, the  
94 analysis of functional diversity may provide a valuable tool for bioindication, a possibility  
95 almost unexplored in the existing literature.

96         In managed beech forests, various taxonomical groups, particularly saproxylics,  
97 decrease in species richness and diversity and undergo a considerable species turnover  
98 compared to species in unmanaged forests (Brunet et al. 2010; Lassauce et al. 2011; Müller et  
99 al. 2008b). As mentioned above, even the current near-to-nature practice in beech forests  
100 reduces the amount and diameter of dead wood, the amount of dead wood in later stages of

101 decay, and the number of veteran trees (Fig. 1). This should lead to shifts in the trait  
102 composition of species assemblages, in particular those traits describing the preferred  
103 diameter and decay stage of the dead wood. These traits are linked to the feeding strategies,  
104 life cycle duration, and contribution to the recycling process of wood of the assemblages  
105 (Stokland et al. 2012). The reduced habitat availability and diversity should both decrease the  
106 mean trait composition of assemblages toward species that prefer dead wood of smaller  
107 diameter and earlier decay stages and reduce single trait diversity. Another important and  
108 functionally meaningful trait is body size. Species with a large body size rely on large pieces  
109 of dead wood as stable habitats to complete their longer larval development (Foit 2010).  
110 Overall, a reduced structural diversity of dead wood with increasing forest-use intensity  
111 should lead to a decrease of functional and phylogenetic diversity (Bishop et al. 2009).

112 We investigated the influence of forest-use intensity on the occurrence of saproxylic  
113 beetle species and the composition of their assemblages with respect to their traits. We used  
114 data from both a continental and a regional scale to test the predictions that a decreasing  
115 intensity of forest use results in increasing phylogenetic diversity; increasing functional  
116 diversity, increasing mean body size and body size diversity; a higher occurrence of species  
117 preferring dead wood of large diameter, advanced stages of decomposition, and closed  
118 canopies; and a higher single trait diversity with regard to habitat preferences (Fig. 1).

119

## 120 **Material and Methods**

### 121 *Study areas and sites*

122 Our study is based on two data sets: a Europe-wide data set of standardized trap samples (for  
123 details, see Müller et al. 2012) and a regional data set based on a more intensive sampling  
124 within one beech forest of the Steigerwald in southern Germany. This latter data set was  
125 collected across only 15 km, but with a steep gradient from intensively managed forests to

126 strict forest reserves (Müller et al. 2008b; Table 1). The Europe-wide data set across eight  
127 countries covers 75% of the distributional range of European Beech; from the Carpathians in  
128 the east to the Pyrenees in the west, and north up to Sweden. For the present analyses, we  
129 expanded the data set described by Müller et al. (2012) by 17 stands (41 traps) in the  
130 Schwäbische Alb, in the Hainich-Dün, and in the Schorfheide-Chorin in Germany.

131

### 132 *Beetle assemblage data*

133 Beetles were sampled using flight-interception traps placed at 1.5 m above the ground during  
134 the whole vegetation period (mountains: May–September, lowlands; April–October; Müller et  
135 al. 2012). The Europe-wide data set consists of samples of 1,156 traps from 242 forest stands  
136 distributed in 79 forest sites. The regional data were sampled on 69 circular plots of 0.1 ha  
137 that were separated by at least 100 m. In addition to trap sampling, an entomologist sampled  
138 beetles using beating, sieving, bark peeling, and visual inspection of trees and inflorescences  
139 in each sampling plot. This additional sampling was performed during visits in spring,  
140 summer, and fall, each within two weeks and for one hour on each plot. All sampled  
141 individuals of both data sets were identified to the species level, except Staphylinidae and  
142 Pselaphidae from France. These two families were therefore omitted from analyses on the  
143 European scale. We classified beetles as saproxylic following reference lists from Germany  
144 (Müller et al. 2012).

145

### 146 *Environmental data*

147 Based on the differences in the structure of the two data sets, it was not always possible to  
148 extract the same variables for subsequent analysis. Nevertheless, we attempted to extract  
149 variables that have at least the same ecological meaning. For the Europe-wide data set, we  
150 used variables characterizing geography, landscape, local climate, and forest stands as

151 predictors for certain characteristics of the beetle assemblages (Table 1). For the regional data  
152 set, only variables of forest stands were used because the climate and landscape were similar  
153 for all plots.

154 The forest stand variables were selected to represent a gradient of forest-use intensity  
155 (Fig. 1). As a descriptor of the protection status on the Europe-wide scale, we used the time  
156 since protection because the protected areas were set aside up to 80 years ago. On the regional  
157 scale, all protected areas were set aside about 40 years ago, and thus protection was  
158 considered on a nominal scale (yes/no). On the Europe-wide scale, the variable ‘veteran trees’  
159 describes the presence/absence of trees older than 250 years. On the regional scale, we were  
160 able to use the age of the oldest tree occurring in a particular stand. The amount of dead wood  
161 was classified in three categories on the Europe-wide scale and continuously on the regional  
162 scale. On both scales, tree diversity was measured as the number of tree genera occurring in a  
163 particular stand. Data on the proportion of conifers was not available for all forests. We  
164 therefore used the presence/absence of conifers as a categorical variable on the Europe-wide  
165 scale, but the percentage of conifers on the regional scale (Table 1).

166 Latitude and longitude were used as geographic variables. We estimated landscape  
167 characteristics (3 km radius around the center of each stand) using mainly the data provided  
168 by CORINE (<http://www.corine.dfd.dlr.de>), a Europe-wide project mapping land use across  
169 most European countries. Climate variables were extracted from WorldClim with a resolution  
170 of 30 seconds and calculated as a mean value within a 1 km radius to minimize the bias  
171 introduced by rough terrains.

172

173 *Trait characterization*



174 We were able to compile information for four ecological traits for each species (Table S3-1):  
175 (1) the mean *body size*; (2) the *diameter* of dead wood in which a species was recorded; (3)  
176 the *decay stage* of the dead wood; and (4) the *canopy cover* of forests in which the species is  
177 known to occur. In his compilation, Möller (2009) provides semiquantitative information of  
178 *diameter*, *decay stage* and *canopy cover* across categories. We first extracted the occurrence of  
179 species across these categories: *diameter*: < 15 cm, 15–35 cm, > 35 cm, and > 70 cm; *decay*  
180 *stage*: 0, alive; 1, freshly dead (1–2 years); 2, initiated decomposition (loose bark, tough  
181 sapwood); 3, advanced decomposition (soft sapwood, partly tough hardwood); and 4/5,  
182 extremely decomposed and moldered; *canopy cover*: open, semi-open, and closed. Then, we  
183 estimated niche positions for each species along these three axes based on the occurrence of  
184 species across these categories and by using weighting scores (0.5, very rarely used; 1, rarely  
185 used; 2, commonly used; 3, preferred; for an example, see S3).

186

### 187 *Phylogeny*

188 We constructed an approximate phylogeny of all sampled beetles to control for the  
189 relationship between species in trait–environment correlations and to calculate phylogenetic  
190 diversity of assemblages. The current phylogeny of beetles is still under debate (Lawrence et  
191 al. 2011). Therefore, we decided to use the genetic phylogeny provided by Hunt et al. (2007)  
192 as our back-bone topology. We expanded this tree by using the phylogenetic relationships of  
193 several subgroups and additional information from taxonomic classifications (for more details,  
194 see S4 and Fig. S4-1) to construct the tree topology. The final tree was calibrated with 24  
195 calibration points from fossil records (Table S4-1) using the function *bladj* in the program  
196 *phylocom*, resulting in branch lengths of millions of years (Webb et al. 2008).

197

### 198 *Data analysis*

199 To visualize the occurrence of saproxylic beetle species along gradients characterizing forest-  
200 use intensity in beech forests, we considered the first two axes of a canonical correspondence  
201 analysis (CCA) with the variables veteran trees, dead wood, tree diversity, and conifers  
202 available for both data sets. All these variables characterize aspects of forest-use intensity (Fig.  
203 1). To evaluate which particular trait makes species susceptible to forest-use intensity, we  
204 modeled the positions of species along the axes versus their traits *body size*, *diameter*, *decay*  
205 *stage*, and *canopy cover*. However, in such an analysis, data points (species) might not be  
206 independent, which inflates the degrees of freedom (Garland et al. 1992). Therefore, we  
207 calculated a linear model using generalized least squares (GLS) with a correlation structure  
208 derived from our phylogenetic tree using Pagel's  $\lambda$  (Pagel 1999). Pagel's  $\lambda$  is the degree of  
209 phylogenetic constraints from 0 (not constrained) to 1 (fully constrained) and was estimated  
210 by maximizing the likelihood of the model (Freckleton et al. 2002).

211 In a second approach, we characterized assemblages of saproxylic beetles to test our  
212 predictions (see Fig 1). We calculated the following characteristics using presence/absence  
213 data because the mass occurrence of a single species in some traps might bias the results. The  
214 phylogenetic diversity based on the patristic distances extracted from the phylogeny was  
215 calculated as the effect size of the mean phylogenetic distance between co-occurring  
216 saproxylic species within each assemblage using the function *ses.mpd* in the add-on package  
217 *picante*. The effect size was calculated based on a null model with 999 randomizations by  
218 reshuffling the tip labels to achieve independence from species numbers (Webb et al. 2002).  
219 This null model retains the structure of the assemblage matrix of beetles and tests whether the  
220 phylogenetic composition of species within assemblages is random with respect to the  
221 phylogeny. Values above zero indicate over-dispersion; values below zero indicate clumping  
222 (Pausas & Verdu 2010). Following the same procedure, we calculated the functional diversity  
223 as effect size based on a Euclidian distances matrix created with standardized values of the

224 four selected ecological traits. Additionally, we calculated the diversity values for each of  
225 these traits (for simplicity named henceforth *body size diversity*, *diameter diversity*, *decay*  
226 *diversity*, and *canopy diversity*) and the mean values of all four traits of the assemblages (for  
227 simplicity named henceforth *mean body size* and so on). The latter characterize the average of  
228 the trait space of the assemblages; the former characterize the dispersion around the average.

229 To test for effects of environmental variables on characteristics of saproxylic beetle  
230 assemblages, we used generalized linear mixed effect models (lmer) with forest stand as a  
231 random factor to account for pseudoreplications on the Europe-wide scale. On the regional  
232 scale, the residuals of multiple linear models were tested for spatial independency (see S1).

233

## 234 **Results**

235 Across both data sets, we recorded 752 saproxylic species. The Europe-wide data set  
236 comprised 456,638 individuals of 709 saproxylic beetle species (excluding Staphylinidae and  
237 Pselaphidae), with a range of 1 to 111 species per trap. The regional data set comprised 9,303  
238 individuals of 284 saproxylic beetle species, with species richness ranging from 11 to 48  
239 species per plot in the sampled beech forests.

240 In both data sets, the composition of the saproxylic beetle assemblages revealed the  
241 same two main gradients: a ‘conifer gradient’ and ‘dead wood/veteran tree gradient’ (Fig. 2).  
242 We modeled the position of species along these two gradients. On the Europe-wide scale, the  
243 dead-wood diameter niche was significantly correlated with both ordination axes ( $\lambda$  between  
244 0.1 and 0.2; Table 2). On the regional scale, decay niche was significantly correlated with the  
245 ‘dead wood/veteran tree’ axis. In both models, the phylogenetic constraint was low (Table 2).  
246 Even if not significant in our GLS, diameter niche was also correlated in univariate models  
247 with the dead-wood axis on the regional scale (Fig. S5-1). Furthermore, diameter niche and  
248 decay niche were significantly correlated (GLS;  $\lambda = 0.83$ ,  $p < 0.001$ ,  $R^2 = 0.246$ ).

249 The importance of dead wood was further illustrated by focusing on the traits of species  
250 that were positively correlated with the 'dead wood/veteran tree' axis of the CCA on both  
251 scales (especially those of diameter and decay niches; Fig. S5-1). Furthermore, for the  
252 regional data set, we plotted species traits against the mean amount of dead wood (measured  
253 with a high resolution), averaged across plots in which each species was recorded (Fig. 3).  
254 Three important findings emerged: 1) for none of the species was the mean amount of dead  
255 wood across plots in which it occurred  $< 10 \text{ m}^3 \text{ ha}^{-1}$ , although plots with such a low amount  
256 of dead wood were sampled; 2) the majority of species occurred in plots with a mean amount  
257 of dead wood of 20 to  $60 \text{ m}^3 \text{ ha}^{-1}$ ; and 3) most species occurring on plots with a mean amount  
258 of dead wood  $> 60 \text{ m}^3 \text{ ha}^{-1}$  required dead wood of large diameter ( $\approx 50 \text{ cm}$ , Fig. 3) and late  
259 decay stages. Interestingly, these species were not necessarily large.

260 When we tested our predictions using the characteristics of the assemblage (Fig. 1), we  
261 found clear effects of variables characterizing geography, landscape, and local climate on the  
262 Europe-wide scale (see symbols outside the gray confidence band in Fig. 4; Tables S6-1 and  
263 S6-2). When we controlled for these variables and compared the Europe-wide results with the  
264 regional results, we found no support for our predictions that a decreasing intensity of forest  
265 use as represented by the stand variables resulted in increasing phylogenetic and functional  
266 diversity (Fig. 4; Table S6-1).

267 In contrast, the analyses of single traits (Tables S6-1 to S6-4) revealed the amount of  
268 dead wood as the forest stand variable of major importance for functional composition  
269 independent of species richness, and the patterns for the two data sets were highly consistent.  
270 In line with our predictions, *mean body size* (which did not increase with sample size; Fig. S7-  
271 1), *body size diversity*, and *mean diameter* increased significantly with the amount of dead  
272 wood on both scales, and the *mean decay* increased significantly with the amount of dead  
273 wood on the regional scale. In contrast to our predictions, the *diameter diversity* decreased

274 with an increasing amount of dead wood on both scales (Fig. 4; Table S6-1). The increase in  
275 *mean body size*, *body size diversity*, and *mean diameter* indicated that both large and small  
276 species preferring dead wood of large diameter occurred on plots with a large amount of dead  
277 wood (Fig. S9-1). Thus, along the gradient of decreasing forest-use intensity, not only did the  
278 number of larger species increase, but also a turnover of smaller species occurred.

279

## 280 **Discussion**

281 Previous studies have revealed the importance of the amount of dead wood for the species  
282 richness of saproxylic beetles (Grove 2002; Lassauce et al. 2011; Müller & Bütler 2010). We  
283 demonstrated for the first time that irrespective of the geographic scale and the species  
284 richness, dead wood amount (particularly large diameters and late decay stages) is also one of  
285 the most important biological legacies (for a definition, see Franklin et al. 2007) influencing  
286 the functional composition of saproxylic beetles in beech forests. Therefore, the current  
287 strategy of wood production in beech forests, which avoids clear-cuttings and relies on natural  
288 regeneration processes but depresses dead wood to low amounts, is insufficient as a  
289 conservation-oriented management strategy.

290 Cross-species analyses are often characterized by large scatter (see  $R^2$  values in Table 2).

291 Therefore, we used an assembly-based approach for testing our predictions (Fig. 1).

292 Assembly-based approaches are much more sensitive because they average across minor  
293 signals of species (Olalla-Tárraga et al. 2010). Our assembly-based approach based on  
294 functional traits revealed that with an increasing amount of dead wood, large and small  
295 species specialized on dead wood of large diameter enter the assemblages. This translated into  
296 an increase in body size diversity. In contrast, the diversity of the diameter niche decreased,  
297 which indicates a dominance of species preferring dead wood of large diameter when there is  
298 a high amount of dead wood. Body size correlates well with life history traits (Sibly et al.

299 2012). Larger species in particular are characterized by a long developmental time as well as  
300 low growth rates (Haack & Slansky 1987), which make them dependent on large pieces of  
301 dead wood (Brin et al. 2011). Although the volume of branches seems to be sufficient even  
302 for large-bodied beetles, the microhabitat requirements of these species might restrict them to  
303 large pieces (Stokland et al. 2012). The sensitivity of large species to increasing forest-use  
304 intensity has been exemplified for a few selected species, e.g., the long-horned beetle  
305 *Cerambyx cerdo* a species discussed as important ecosystem engineer due to its large galleries  
306 (Buse et al. 2007, Buse et al. 2008). Our finding of an additional turnover of small-bodied  
307 species along the gradient of dead-wood amount showed that also some small species are  
308 specialized on dead wood of large diameter (e.g., *Ropalodontus perforatus*, *Stenichnus*  
309 *godarti*). This was also underlined by the cross-species analysis, where species occurring in  
310 habitats with high amounts of dead wood had high demands for diameters of dead wood and  
311 late succession stages (Fig. 3). One may argue that very high amounts of dead wood disregard  
312 requirements of species preferring dead wood of small diameter. However, these species are  
313 less susceptible to effects of forest-use intensity and benefit already from moderate increases  
314 in dead wood amount of  $>20 \text{ m}^3 \text{ ha}^{-1}$  (Fig. 3).

315 Although our chosen traits are currently the best information available for functional  
316 links between assemblages and the environment, our analyses were still constrained because  
317 these variables are at best surrogates. One major future challenge is to collect more  
318 information on the biology of these species. For example, in a recent study, gut analysis of  
319 well-known species presumed to be predators revealed that fungi are a major food (Prikryl et  
320 al. 2012). Such gut or stable-isotope analyses are promising tools for estimating the trophic  
321 niche of saproxylics more precisely (Blüthgen et al. 2003).

322 In our analysis, the phylogenetic diversity was not affected by the habitat variables and  
323 therefore also not by forest-use intensity. As species richness decreases with increasing forest-

324 use intensity, species losses along this gradient occur randomly across the phylogeny.  
325 Therefore, analysis of phylogenetic diversity does not seem to be a promising method for  
326 understanding the assemblages of saproxylic beetles. Similarly, we found no response of  
327 functional diversity to our forest stand variables, even though the analysis of single traits  
328 revealed clear patterns. This demonstrated that measures of functional diversity that combine  
329 several traits might mask important ecological effects just as a pure diversity index might  
330 neglect the identity of species (Fleishman et al. 2006).

331 In our analysis, veteran trees provided a higher diversity of decay niches only on the  
332 European level. On the one hand, this underlines previous findings that such trees provide  
333 resources for species of a broad range of successional stages (Speight 1989). However, in our  
334 assembly approach, one has to keep in mind that only a few of the species within the  
335 hyperdiverse community of saproxylic beetles are restricted to hollow veteran trees. Most of  
336 the saproxylic beetles living in veteran trees develop also in logs or snags (Speight 1989). In  
337 addition, the resolution of our measurement of veteran trees was low.

338 Although we did not find a strong effect of time since protection, in contrast to the  
339 findings of a recent Europe-wide meta-analysis (Paillet et al. 2010), our data demonstrated  
340 that most biological legacies increased with time since protection (e.g., dead wood and  
341 protection,  $r = 0.47$ ; Fig. 1). This indicates two important points: 1) the availability of  
342 resources is more important than the general conservation status, and 2) high amounts of dead  
343 wood are found mostly in strict protected forests (Paillet et al. 2010). Furthermore, a  
344 fundamental assumption of our analysis is that the distribution of species across the sampled  
345 plots is in equilibrium with respect to the environmental variables. The low importance of  
346 time since protection indicates that equilibrium with respect to trait composition is reached  
347 within a very short time span.

348           To which extent are our results for saproxylic beetle species and beech forests  
349 transferable to other taxa or ecosystems? In European forests, species richness of saproxylic  
350 beetles is correlated with species richness of other taxonomic groups (Paillet et al. 2010), such  
351 as wood-inhabiting fungi, which exhibit a similar diversity in how they use dead wood as a  
352 habitat and nutrient source, and carabid beetles, bryophytes, and lichens, which use dead  
353 wood for colonization or shelter. Due to the increase in habitat diversity with the amount of  
354 dead wood (Müller & Bütler 2010), we expect that the functional trait composition of these  
355 groups will also change along gradients of dead-wood amount in temperate forests  
356 (Heilmann-Clausen & Christensen 2004; Stokland et al. 2012). The transferability to other  
357 biomes or ecosystems may be more complicated. Beech forests are shady and characterized  
358 by gap regeneration. In forests characterized by more open canopies, the patterns of traits and  
359 forest stand variables may change. Particularly boreal forests, which are dominated by  
360 conifers, regularly suffer stand-replacing disturbances such as fire. Thus, not only species  
361 richness (Lassauce et al. 2011) but also trait characteristics of saproxylic beetles may respond  
362 differently in boreal forests.

363           The most important conclusion from our analyses is that the composition of saproxylic  
364 beetle assemblages along a gradient of increasing amount of dead wood affects not only  
365 species richness but also the functional composition of assemblages. But what does this  
366 finding tell us other than “more dead wood should be left in the forest”? Analysis of the  
367 functional traits illuminated the qualitative weakness of the current practice — not only is a  
368 higher amount of dead wood needed, but also dead wood of large diameter and advanced  
369 stages of decay. This underlines the value of functional traits as indicators of structures or  
370 processes of ecosystems that are difficult to measure. Furthermore, our functional approach  
371 leads to some important recommendations for a cost-effective improvement of current  
372 silvicultural practices for a more conservation-oriented management of European beech



373 forests: 1) the amount of dead wood should be increased in managed stands from the current  
374  $5\text{--}10\text{ m}^3\text{ ha}^{-1}$  to  $> 20\text{ m}^3\text{ ha}^{-1}$ ; 2) because economic pressures often preclude the accumulation  
375 of higher amounts of dead wood, managers should conserve particularly dead wood of large  
376 diameter ( $\approx 50\text{ cm}$ ) and allow more dead wood in advanced stages of decomposition to  
377 develop; and 3) strict forest reserves — the only area in which high amounts of dead wood ( $>$   
378  $60\text{ m}^3\text{ ha}^{-1}$ ) can be allocated regularly — have to be conserved as an insurance, refuge, and  
379 source pool for habitat specialists. One future necessary step will be to expand our rules of  
380 thumb to more quantitative recommendations for dead-wood management in economic forests  
381 that optimize the trade-off between economy and ecology.

382

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392

### 393 **Supporting Information**

394 Test for spatial independence (Appendix S1), Climate and landscape variables (Appendix S2),  
395 Species list and traits (Appendix S3), Phylogeny (Appendix S4), Relationship of body size  
396 and niche positions of species to forest-use intensity (Appendix S5), Results of linear  
397 regression analysis (Appendix S6), Correlation of individuals and mean body size (Appendix

398 S7), Correlation of effect sizes of single traits (Appendix S8), Correlation of dead-wood  
399 amount and mean body size and niche positions (Appendix S9), Correlation of dead-wood  
400 amount and maximum diameter (Appendix S10), and Supporting information references  
401 (Appendix S11) are available online. The authors are solely responsible for the content and  
402 functionality of these materials. Queries (other than absence of the material) should be  
403 directed to the corresponding author.

404

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- 531

For review only

532 **Table 1:** Predictor variables and information on the measurement unit used in the models of  
 533 the Europe-wide and regional data sets (for more details, see S2).

Variable type	Variable	Europe	Regional (Steigerwald)
<b>Geography</b>	<b>Latitude</b>	Northing (ETRS.1989 LAEA Projection)	-
	<b>Longitude</b>	Easting (ETRS.1989 LAEA Projection)	-
<b>Landscape</b> (3 km radius)	<b>Forest area</b>	CORINE types 311, 312, 313 [%]	-
	<b>Broad-leaf trees</b>	CORINE types 311 + 50% of 313, relative to total forest area [%]	-
	<b>Urban area</b>	Proportion of traffic and settlements (CORINE types: 111,112, 141,142) [%]	-
<b>Local climate</b> (1 km radius)	<b>Temperature</b>	WorldClim Bio10, mean temperature [°C]	-
	<b>Precipitation</b>	WorldClim Bio18; precipitation of the warmest month [mm]	-
<b>Forest stand</b> (1 ha surrounding)	<b>Protection</b>	Time since protection [years]	[yes/no]
	<b>Veteran trees</b>	Occurrence of trees > 250 years [yes/no]	Age of oldest tree
	<b>Dead wood</b>	Amount in three categories: low (0–29 m <sup>3</sup> ha <sup>-1</sup> ), medium (30–70 m <sup>3</sup> ha <sup>-1</sup> ), high (> 70 m <sup>3</sup> ha <sup>-1</sup> )	Amount [log(m <sup>3</sup> ha <sup>-1</sup> )]
	<b>Tree diversity</b>	Number of tree genera	Number of tree genera
	<b>Conifers</b>	Occurrence [yes/no]	[%]

534 **Table 2:** Results of a linear model on the relationship of the CCA axis positions to body size, and the niche positions dead-wood diameter, dead-  
 535 wood decay stage, and canopy cover using generalized least squares (GLS) with a correlation structure derived from the phylogenetic tree of all  
 536 sampled beetle species (752 species, see S3), using Pagel's  $\lambda$  (Pagel 1999) to correct for phylogenetic relatedness. Pagel's  $\lambda$  was optimized by  
 537 selecting the model maximizing the likelihood (Freckleton et al. 2002). Pagel's  $\lambda$  indicates the degree of phylogenetic constraints from 0 (not  
 538 constrained) to 1 (fully constrained).

Trait	Europe-wide scale				Regional scale				Trait mean (range)
	'conifer axis'		'dead wood/veteran tree axis'		'dead wood/veteran tree axis'		'conifer axis'		
	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	
	$R^2 = 0.023, \lambda = 0.182$		$R^2 = 0.067, \lambda = 0.099$		$R^2 = 0.118, \lambda = -0.030$		$R^2 = 0.002, \lambda = 0.011$		
Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value		
Intercept	-0.302	0.303	-0.034	0.898	0.089	<0.001	0.149	0.275	
Body size	-0.100	0.273	0.133	0.191	-0.117	0.172	-0.043	0.706	4.97 (0.5–50 mm)
Diameter	<b>0.262</b>	<b>0.004</b>	<b>0.541</b>	<b>&lt;0.001</b>	0.127	0.222	-0.059	0.652	2.35 (1–4)
Decay	0.116	0.263	0.131	0.265	<b>0.462</b>	<b>&lt;0.001</b>	0.011	0.938	2.99 (1–5)
Canopy cover	-0.014	0.846	0.012	0.892	<-0.001	0.998	-0.004	0.976	1.71 (1–3)



539 **Figure Legends**

540 **Figure 1:** Conceptual framework showing the assumption of how forest-use intensity in near-  
541 to-nature silvicultural concepts in European beech forests may affect forest stand structures,  
542 and the predicted shifts (P1–P6) in functional trait composition of saproxylic beetle  
543 assemblages.

544 **Figure 2:** Ordination plot based on a canonical correspondence analysis of 1,156 samples of  
545 flight-interception traps on a Europe-wide scale (main plot) and of 69 samples on a regional  
546 scale (inset). The plots show the position of saproxylic beetle species (Europe: 709 species,  
547 regional: 284) along gradients composed of four forest stand variables (VT, occurrence of  
548 veteran trees; DW, amount of dead wood; CO, occurrence of conifers; TD, tree diversity).  
549 The figure indicates two gradients: a conifer axis (Europe-wide scale: CCA1, eigenvalue  
550 0.128; regional scale: CCA2, eigenvalue 0.156) and a dead wood/veteran tree axis (Europe-  
551 wide scale: CCA2, eigenvalue 0.084; regional scale: CCA1, eigenvalue 0.209).

552 **Figure 3:** Correlation between species traits and the position of a single species on a dead-  
553 wood amount axis on the regional scale. This axis was calculated as the mean value of log-  
554 transformed values of dead-wood amount across the plots on which a species occurred. The  
555 gray bars at the top of the figure show the frequency distribution of dead-wood amount. All  
556 species that were sampled on at least three plots were included (N = 149 species). For  
557 illustration, the scales of the original classification of dead-wood diameter niche, and dead-  
558 wood decay stage niche are given on the right y-axis.

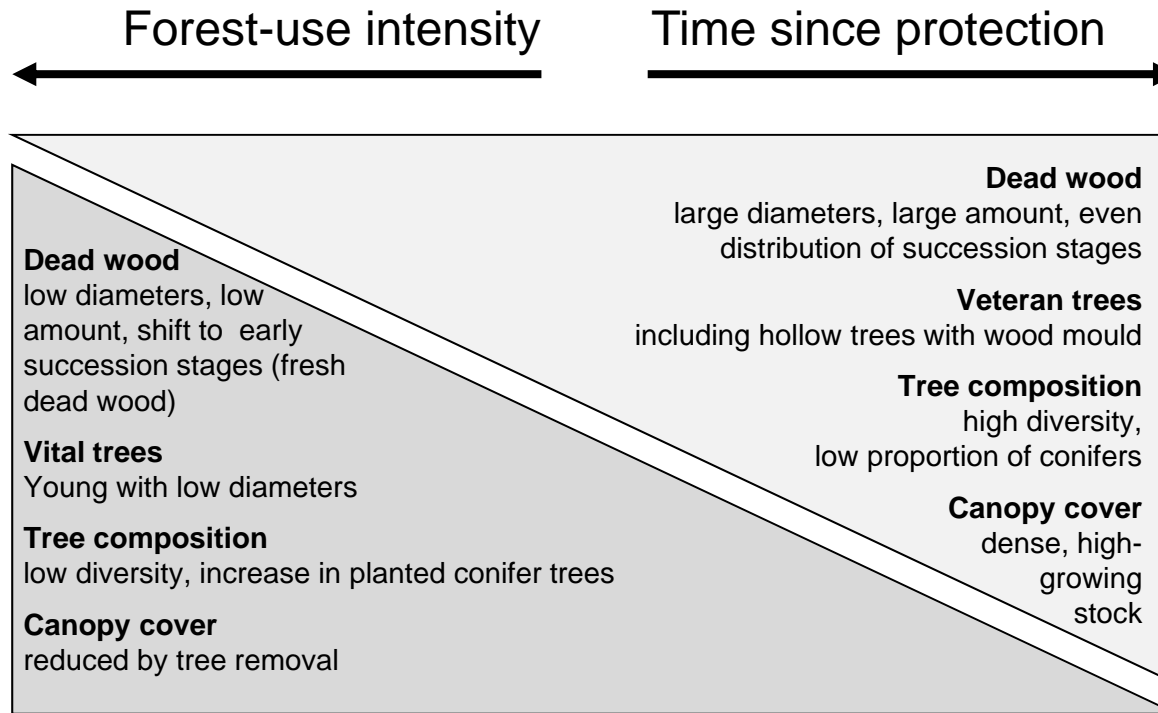
559 **Figure 4:** Results of linear regression analyses fitted by the linear model function (lm)  
560 (regional scale, white symbols) and a linear mixed effect model (lmer) using the forest stand  
561 as random factor (Europe-wide scale, grey symbols). Effects of predictor variables on effect  
562 sizes of phylogenetic diversity (PhylDiv), effect sizes of functional diversity (FuncDiv), and

563 single traits are shown. The predictor variables include geographic, landscape, regional  
564 climate (Europe-wide scale only), and local habitat variables. Single traits are the mean values  
565 and effect sizes of diversity (measured as dispersion using null models with 999  
566 randomizations) of body size, and dead-wood niche characteristics (diameter, decay, canopy  
567 cover). Analysis on the regional scale is based on the complete data set (flight-interception  
568 traps, hand collection methods). The shaded areas indicate the range of non-significant values  
569 with a slight difference in the border of significance (t-value Europe-wide 1.998; regional  
570 1.960). For detailed values see Appendix S6.

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**Ecological predictions for saproxylic beetle communities:**

P1: Increase in phylogenetic diversity

P2: Increase in functional diversity

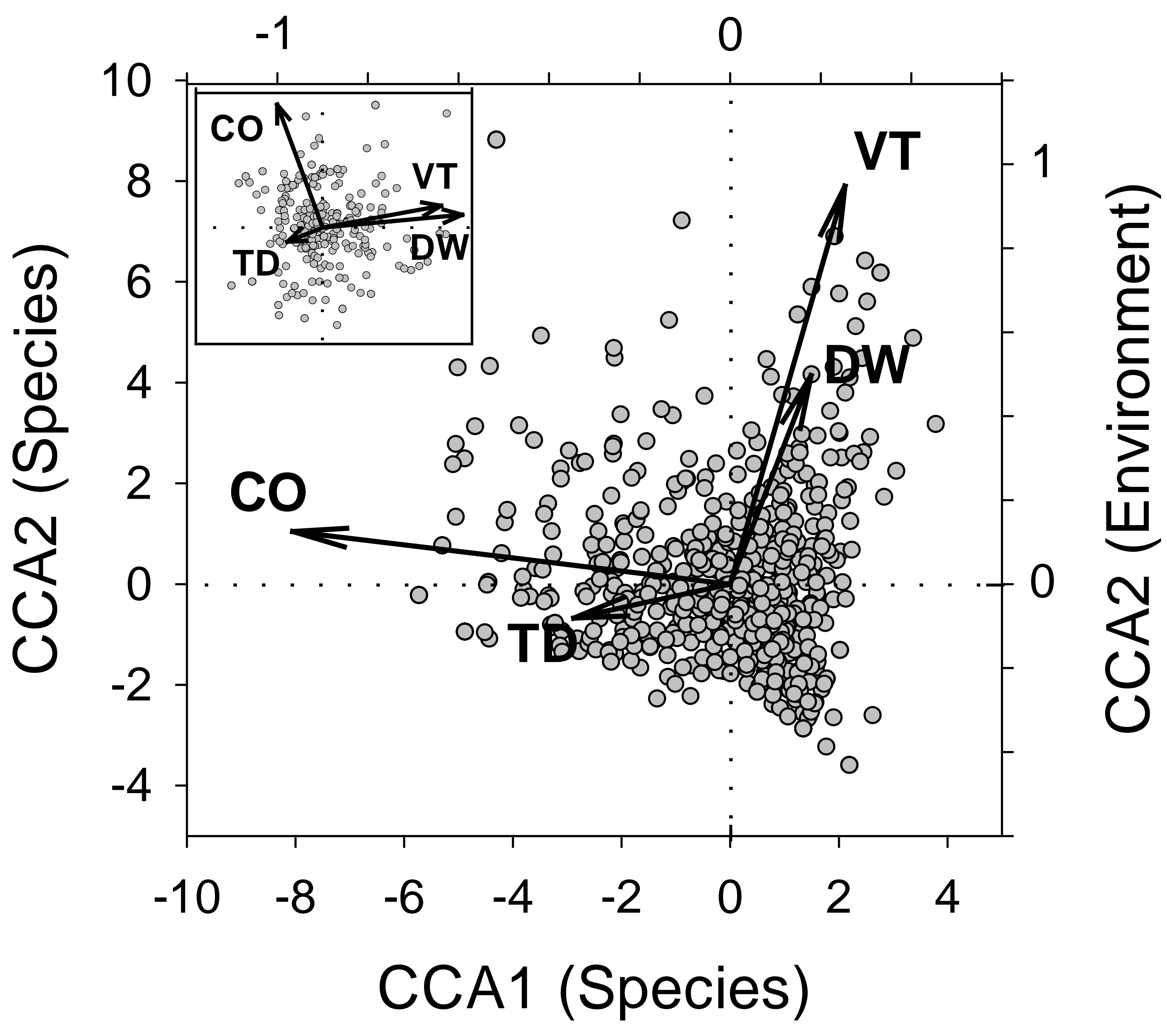
P3: Increase in mean body size and body size diversity

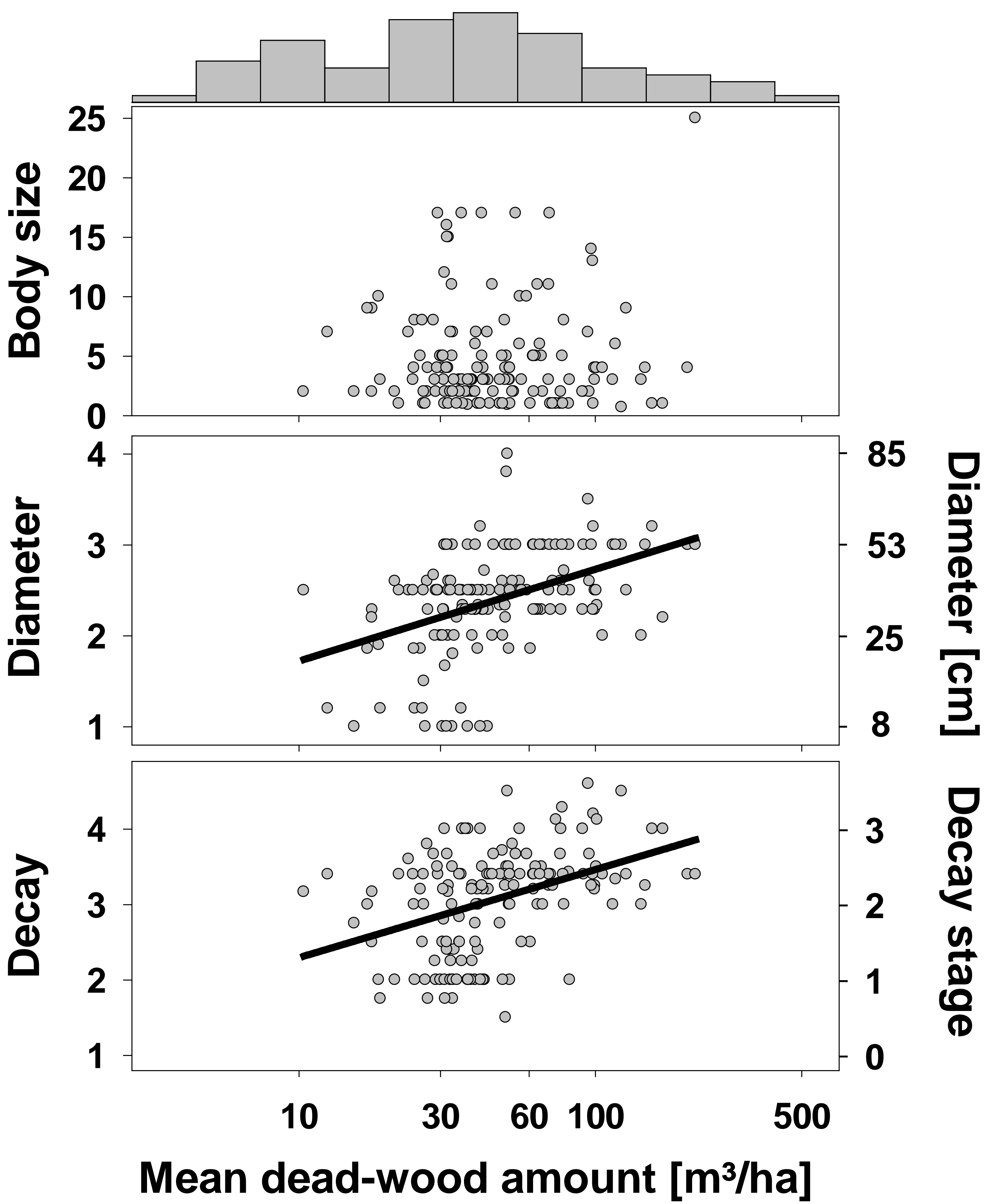
P4-6: Increase of mean niche position and diversity

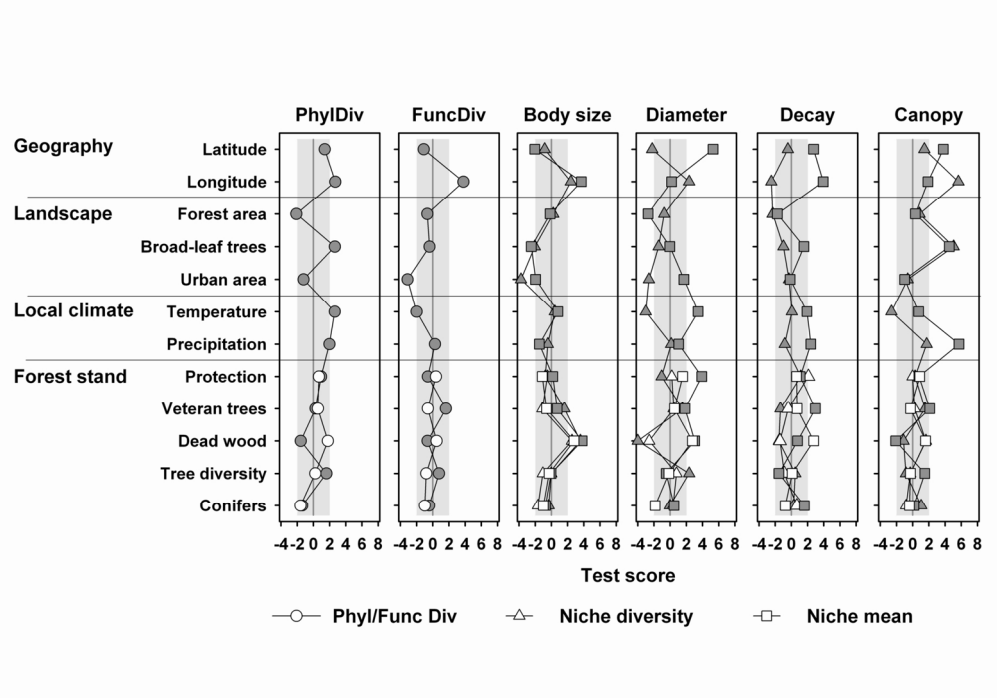
4) diameter 5) decay 6) canopy cover



# CCA1 (Environment)







155x109mm (300 x 300 DPI)

Preview only



192x144mm (300 x 300 DPI)

View only



232x146mm (200 x 200 DPI)

view only