

1 **Congruent patterns of functional diversity in saproxylic**
2 **beetles and fungi across European beech forests**

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4 **Running title:** Functional diversity in beech forests

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50 **Abstract**

51 **Aim:** Beech forests comprise a globally unique temperate forest type in Europe. The
52 dominance of beech in these forests developed during the ongoing post-glacial
53 northward re-colonization, concurrently with intensified forest use by humans. We
54 investigated how these two processes together with climate shaped the patterns of
55 functional diversity of two major species groups involved in wood decomposition and
56 whether functional diversity is determined on the local or regional species pool level.

57 **Location:** European beech forest distribution range.

58 **Taxon:** Saproxylic beetles and fungi.

59 **Methods:** We analysed records of 532,496 saproxylic beetles of 788 species and 8,630
60 records of 234 saproxylic fungal species based on sets of traits similar to both groups.
61 We tested how space, climate and landscape composition affect trait-based functional
62 diversity on local and regional scales. Using structural equation modelling, we tested
63 whether functional diversity is shaped on the local or regional scale.

64 **Results:** The response of local functional diversity of both saproxylic beetles and fungi
65 followed a highly congruent pattern of decreasing functional diversity towards the
66 north, with higher elevation and accounted for overall geographic gradients with higher
67 temperature, while increasing with higher precipitation. Structural equation modelling
68 revealed that local functional diversity is determined by community changes operating
69 on the level of the regional species pool.

70 **Main conclusions:** Our findings suggest that the functional diversity patterns of
71 saproxylic organisms in European beech forests are mainly determined on the regional
72 scale and driven by anthropogenic and biogeographical processes. To conserve the
73 variation and hotspots of functional diversity in beech forests, activities have to focus
74 on a broad spatial and climatic range of sites throughout Europe, including the primeval
75 forests in the east, as started by the UNESCO World Heritage selection of “Ancient and
76 Primeval Beech Forests of the Carpathians and Other Regions of Europe”.

77 **Keywords:** biogeographic history, dead wood, decomposition, *Fagus sylvatica*,
78 functional diversity, land-use intensity, saproxylic beetles, saproxylic fungi

79 **Introduction**

80 European beech forests define temperate forests in Central Europe in a globally unique
81 way (Peters, 1997). They are by far the predominant forest association, restricted to
82 Europe and dramatically affected by land-use change and intensification (Brunet, Fritz,
83 & Richnau, 2010). European beech (*Fagus sylvatica* L.) separated from Oriental beech
84 (*Fagus orientalis* Lipsky) about 8 Ma (Renner, Grimm, Kapli, & Denk, 2016). The
85 distribution pattern of European beech is the result of a complex history affected by
86 glaciations and humans. During the last glacial maximum (about 20,000 years ago),
87 European beech survived in several distinct refugia in southern Europe, but these
88 refugia contributed very differently to the re-colonization process (Magri, 2008), which
89 continues to date, with an expansion of several hundred metres per year towards the
90 north in Sweden (Björkman, 1996) and towards the northeast in Poland (Latalowa,
91 1992). Early on, natural beech forests began to be replaced by farmland and urban areas,
92 with decreasing historical land-use intensity from west to east (Rose, 1992; Peterken,
93 1996; Kaplan, Krumhardt, & Zimmermann, 2009, Rey et al., 2018), but distribution was
94 partly also favoured by humans regionally (Björkman, 1997).

95 The diversity patterns that we observe today in European beech forests evolved
96 under varying paleoclimatic conditions; therefore, the historical climate has shaped the
97 current distribution of biodiversity and ecosystems (Svenning, Eiserhardt, Normand,
98 Ordonze, & Sandel, 2015). An important determinant of current large-scale biodiversity
99 patterns is the climate of the Quaternary period, with its series of glacial and interglacial
100 phases (Hewitt, 2000). The distance to refugia during cold periods has shaped present
101 species ranges and reduced species richness far from refuges (Hewitt, 1999; Svenning et
102 al., 2010), but might also affect the functional components of biodiversity. For example,
103 the functional diversity of European plants decreases with distance to major glacial
104 temperate refugia and with higher historical climatic instability (Ordonez & Svenning,
105 2015). For organisms that depend on the occurrence of long-living species, such as
106 trees, the Quaternary legacy on functional components of biodiversity is more complex.
107 Willner, Pietro, & Bergmeier (2009) showed that the distance of European beech to the
108 nearest refugium is the strongest predictor of current lower plant species richness in the
109 understorey of European beech forests. This finding supports the hypothesis that species
110 associated with beech forests are limited by post-glacial dispersal rather than by
111 contemporary environmental factors (Willner et al.).

112 Nevertheless, species richness at various scales is often strongly influenced by
113 temperature and precipitation (e.g. H-Acevedo & Currie, 2003). Climatic variables
114 affect distribution, abundance and interaction of species by filtering climate-relevant
115 physiological and behavioural traits (Bellard, Bertelsmeier, Leadley, Thuiller, &
116 Courchamp, 2012). Due to direct feedback, functional diversity rather than species
117 richness is affected by existing climatic conditions (Wright et al., 2005; Bässler et al.,
118 2016). Finally, land-use intensification is a main driver of biodiversity decline in all
119 ecosystems (Kleijn et al., 2009; Paillet et al., 2010; Mora et al., 2011) and is
120 accompanied by multi-trophic homogenization of communities (Gossner et al., 2016).
121 Human resource exploitation can filter species communities by selecting against species
122 with particular functional traits (Pauly, Christensen, Dalsgaard, Froese, & Torres Jr.,
123 1998; Simons, Weisser, & Gossner, 2016). Thus, functional diversity decline through
124 land-use intensification can be steeper than the decline in species richness (Flynn et al.,
125 2009). For example, European saproxylic (i.e. dependent on dead wood) beetles and
126 fungi with large body or fruit body size, respectively, are more affected by forest-use
127 intensification than smaller species (Bässler, Ernst, Cadotte, Heibl, & Müller, 2014;
128 Seibold et al., 2015).

129 The environmental filtering effects on assembly processes can operate on
130 different geographical and temporal scales (Kraft et al., 2015). Geographical scales can
131 range from the biome to landscape level to the local habitat down to the microhabitat
132 niche of a species. Jiménez-Alfaro et al. (2018) showed that large-scale environmental
133 and historical factors affected the regional plant species diversity in European beech
134 forests, which in turn, in combination with local habitat conditions, determined species
135 richness of the local plant community. In beech forests, the megadiverse guilds of
136 saproxylic beetles and fungi are the two main agents involved in the important
137 ecosystem process of wood decomposition, which in turn can influence soil
138 biochemistry and therefore forest productivity (Kappes, Catalano, & Topp, 2007;
139 Carlyle, 1995). Beetles and fungi differ greatly in their biology and life history
140 (Stokland, Siitonen, & Jonsson, 2012). Fungi directly chemically decompose
141 lignocellulose with secreted enzymes, whereas beetles promote decomposition by
142 mechanical comminution and act as vectors of microorganisms, including fungi
143 (Stokland et al.; Seibold et al. 2018). The community compositions of beetles and fungi
144 and the occurrence of particular decomposer species depend mainly on resource
145 availability, but also on resource heterogeneity, resource connectivity and habitat

146 continuity on different scales, which in turn are influenced by both land-use intensity
147 and biogeographic legacies (Kouki, Hyvärinen, Lappalainen, Martikainen, & Similä,
148 2012; Bouget & Parmain, 2016; Seibold et al., 2016).

149 To enlarge our current understanding of the main drivers and scales of
150 biodiversity in European beech forests, including space, climate and land-use intensity,
151 we assessed the functional diversities of saproxylic beetles and fungi on a regional
152 (forest area) and local (beetle trap catch or fungi log sampling) scale based on the most
153 comprehensive standardized datasets across Europe. To calculate functional diversity,
154 we selected comparable species traits from trait categories that were similar in the two
155 taxa. Owing to the history of European beech after the last glaciation, we expected
156 combined effects of re-colonization history, climatic filters and anthropogenic land-use
157 intensity on the functional diversity of saproxylic communities. In particular, we
158 hypothesized a decreasing functional diversity of these communities (1) with distance to
159 the glacial refugia in south-western, southern, and south-eastern Europe, (2) towards dry
160 or cold climates unfavourable for the growth of European beech, and (3) with increasing
161 human land-use pressure on regional and European scales. Finally, we tested to which
162 extent these patterns are determined already on the regional species pool level.

163 **Material and Methods**

164 *Study area and saproxylic-assembly data*

165 We conducted our study on the continental scale across large parts of the distribution
166 range of beech-dominated forests, including different beech forest types ranging from
167 colline to montane zones. We focused on saproxylic species of beetles and fungi. We
168 use the term saproxylic according to the definition of Stokland et al. (2012): “any
169 species that depends, during some part of its life cycle, upon wounded or decaying
170 woody material from living, weakened or dead trees”. For our analyses, we compiled
171 1,404 flight-interception trap catches of saproxylic beetles covering one full vegetation
172 period nested in 105 beech-dominated managed and protected forest areas from 10
173 countries, and we sampled saproxylic fungi in fruiting body surveys of 1,814 fallen
174 beech logs nested in 53 different beech-dominated forest areas from 12 countries (Fig.
175 1). We defined a region as the forest area sampled by the sum of the traps or logs within
176 a district forest site, and the regional species pool as the total species present within the
177 traps or logs of one forest area. Local communities represented all species sampled per
178 trap or log. For further information on the sampling of saproxylic beetles and fungi, see

179 Appendix S1 in Supporting Information. The sampling procedures for beetles (mobile
180 taxon) with passive continuously collecting traps, and for fungi (sessile taxon) with
181 active object-oriented sampling differed. Also the sampling localities of the two taxa
182 differed broadly (Fig. 1). Two taxonomical and geographical independent datasets
183 represent two replications to understand assembly processes in European beech forests.

184 *Environmental data*

185 We described the three dimensions of space using latitudinal and longitudinal
186 coordinates (based on the ETRS 1989 projection) and elevation (metres above sea
187 level). We used latitude as a measure of distance of beech forest areas to glacial refugia
188 in southern Europe (Magri, 2008). We are aware that other proxies for distance of post-
189 glacial dispersal routes, e.g. proximity to refugia, can be used (e.g. Jiménez-Alfaro et
190 al., 2018). However, proximity to refugia based on a climatic suitability model of
191 European beech in the last glacial maximum can be applied with different potential
192 paleoclimatic scenarios and still neglects effects of landscape topography during re-
193 colonization. Thus, these proxies based on further assumptions also result in high
194 uncertainty (cf. Lehsten et al., 2014). Elevation of beech forest areas is related to the
195 biogeographical history because European beech started re-colonization of Europe after
196 glaciation at higher elevations before extending to lower elevations (Magri, 2008). We
197 used longitude as a proxy for the decreasing historical land-use intensity in European
198 beech forests from west to east (Rose, 1992; Peterken, 1996).

199 In addition to space, we used landscape characteristics and climate as
200 environmental predictors. We used information from the pan-European project
201 CORINE Land Cover (www.corine.dfd.dlr.de) to calculate the following landscape
202 characteristics: proportion of human settlement as a measure of small-scale land-use
203 intensity, proportion of forest, and proportion of broad-leaved forest compared to the
204 forest area within a 3-km radius (for details, see Gossner et al., 2013 and Müller et al.,
205 2015). We extracted and used the local climatic variables mean temperature of the
206 warmest quarter (BIO10) and precipitation of the warmest quarter (BIO18) from
207 WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) grid data in 30 s
208 resolution and calculated mean values for a 1-km radius around sampled localities,
209 following the methodology of Gossner et al. (2013) and Müller et al. (2015). We
210 calculated all environmental variables for each local community (i.e. position of trap or
211 log) and for each regional community (i.e. forest area) as the mean of all traps or logs in
212 the forest area. To test for collinearity of climate and landscape predictor variables, we

213 calculated the variance inflation factor using the 'vif' function in the add-on package
214 'usdm' (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2013); the results indicated that
215 none of the local climate and landscape predictor variables had collinearity problems
216 (all values of $vif < 1.9$). A problem in many large-scale studies is that latitude correlates
217 with declining temperature (e.g. Deutsch et al., 2008; Zeuss et al., 2014), which may
218 complicate the interpretation of a biogeographic history effect (latitude as a gradient of
219 biogeographic history) and the effects of current climate (latitude as a proxy for
220 temperature). However, this correlation does not impact the distribution range of
221 European beech forests and was not a factor in our environmental datasets of beetles
222 and fungi (Appendix S3) because the distribution and thus the climatic niche of
223 European beech is at a higher elevation in the southern range of these trees (e.g.
224 Pyrenees, Apennines, Balkans) and at a lower elevation in their northern range (e.g.
225 Northern Germany, Denmark, Southern Sweden; Peters, 1997) of European beech
226 forests.

227 ***Functional traits***

228 Despite the generally different lifestyles of saproxylic beetles and fungi, we gathered a
229 set of functional traits of both taxa that reflect comparable trait categories. In relation to
230 the traits selected in Seibold et al. (2015), we selected biological and resource-related
231 traits available for both saproxylic groups (Table 2). Body size, decay niche, wood
232 diameter niche and host tree preference were traits we could collect for both groups.
233 Organismal body size is a highly integrative trait representing, for example, metabolic
234 rate, dispersal ability and demographic properties (LaBarbera, 1989). Resource-related
235 traits define the dimensions of the species niche within dead wood as a complex habitat
236 varying in space and time in its physical and chemical properties (Stokland et al., 2012).
237 For the calculation of resource-related traits, we followed the procedure of Gossner et
238 al. (2013) and determined the occurrence of species in ordered classes: decay niche,
239 alive, freshly dead, initiated, advanced decomposition, extremely decomposed; wood
240 diameter niche, <15, 15–35, 35–70, >70 cm; canopy niche, open, semi-open, closed.
241 The frequency of occurrence of each species in each category was then described by
242 weighting scores based on the calculated mean niche position (for details, see Appendix
243 S2 and Gossner et al. 2013). Note that the host tree association of a species reflects the
244 preference of that species and is not an exclusive category. We tested for collinearity of
245 traits separately for saproxylic beetles and fungi using the 'vif' function in the add-on
246 package 'usdm' (Naimi et al., 2013); the results indicated that none of the traits chosen

247 had collinearity problems (all values of $vif < 1.7$; for a correlation matrix plot, see
248 Appendix S2). Trait data were gathered from primary literature and other publications
249 and were also determined by authors with expertise and by external experts. Data on the
250 traits of saproxylic beetles and fungi, detailed references, and methods of trait sampling
251 are presented in Appendix S2.

252 *Statistical analyses*

253 All analyses were performed in R version 3.3.3 (R Core Team, 2015). We used a
254 measure of functional diversity describing divergence, i.e. how similar are the species
255 within an assemblage (Cadotte & Davis, 2016). Functional diversity was calculated as
256 the mean pairwise distance (MPD) between functional traits in the functional space of
257 co-occurring species (Webb, Ackerly, Mcpeck, & Donoghue, 2002; Mouillot, Graham,
258 Villéger, Mason, & Bellwood, 2012). To control for variations in the number of species
259 in the different assemblages and to obtain a metric for the assembly patterns, we applied
260 a null-model approach to our final functional diversity, using the tip-shuffling method
261 (Cadotte & Davis, 2016). This provided standardised effects sizes of the mean pairwise
262 distances (SES MPD), which we calculated with 999 randomisations using the function
263 'ses.mpd' in the add-on package 'picante' (Kembel et al., 2010). Functional diversity
264 based on species-by-species distance matrices was calculated using the Gower distance
265 (Gower, 1971) of the presence–absence datasets of saproxylic beetles and fungi, using
266 the 'gowdis' function in the add-on package 'FD' (Laliberte & Legendre, 2010). The
267 dissimilarity coefficient of Gower (1971) can simultaneously combine continuous and
268 categorical traits. Functional diversity was calculated for each local and regional
269 community of beetles and fungi.

270 We first tested our predictions separately for local and regional functional
271 diversity. For local functional diversity, we applied linear mixed-effects models with
272 our set of environment predictor variables representing space, climate and landscape
273 (Table 1), separately for beetles and fungi. To control for replicated measurements
274 within the same forest area, forest area was treated as a random term. For regional
275 functional diversity, we applied linear models with our set of environment predictor
276 variables representing space, climate and landscape (Table 1), separately for beetles and
277 fungi. Secondly, to test direct and indirect effects of the predictors at the regional and
278 local community levels, we used structural equation modelling (Shipley, 2016) and
279 added regional functional diversity as a predictor to the model of local functional
280 diversity. We used the function 'sem.coefs' in the add-on package 'piecewiseSEM'

281 (Lefcheck, 2016), which allows the creation of lists of models with random effects to
282 control for nested measurements and accounts for data distribution (Shipley, 2016).
283 Single-path coefficients were scaled by mean and variance to make single-variable
284 importance comparable.

285 **Results**

286 Our final dataset for beetles included 105 forest areas for regional functional diversity
287 and 1,401 traps for local functional diversity. The final dataset for fungi included 53
288 forest areas for regional functional diversity and 1,618 logs for local functional
289 diversity. These datasets comprised 532,496 records of 788 saproxylic beetle species
290 and 8,630 records of 234 saproxylic fungus species. The functional diversity of
291 saproxylic beetles and fungi indicated the clumping of traits at both local (beetles: -1.52
292 ± 1.26 (mean SES \pm SD), Appendix Fig. S4.6; fungi: -1.39 ± 1.04 , Appendix Fig. S4.8)
293 and regional (beetles: -2.40 ± 1.81 , Appendix Fig. S4.7; fungi: -2.90 ± 1.17 , Appendix
294 Fig. S4.9) scales. Thus, both the species within local assemblages and the regional
295 species pools were more similar in their trait characteristics than would occur by chance
296 (considering the random composition of European fungus and beetle communities).

297 The response of functional diversity of saproxylic beetles to environmental
298 variables on the local and regional scales followed the same patterns as that of
299 saproxylic fungi (Fig. 2; Appendix Table S4.3). However, the structural equation model
300 indicated that environmental filtering of functional diversity by space, climate and
301 landscape composition operated mainly on the regional scale, which was congruent for
302 saproxylic beetles and fungi (Fig. 3; Appendix Table S4.4). Functional diversity of
303 saproxylic beetles and fungi congruently decreased towards northern Europe (Fig. 2;
304 Fig. 3; Appendix S4). Moreover, the functional diversity of both groups decreased with
305 increasing elevation and temperature (Fig. 2; Fig. 3; Appendix S4). With higher
306 precipitation, functional diversity of saproxylic beetles and fungi congruently increased
307 (Fig. 2; Fig. 3; Appendix S4). The regional functional diversity of beetles was higher in
308 eastern Europe than in the west, and the proportion of urban areas in the landscape had a
309 negative effect on local functional diversity (Fig. 2; Fig. 3; Appendix S4). The
310 proportion of urban areas in the landscape also negatively affected fungal functional
311 diversity but operated on the regional scale (Fig. 2; Fig. 3; Appendix S4). The results
312 regarding the functional diversity of saproxylic beetles were robust when conifer-
313 associated beetle species were excluded from the analyses (Fig. S4.10). Results of

314 models with raw values of functional diversity (observed mean pairwise distances of
315 species traits within communities) of beetles and fungi were similar (Appendix S5).

316 **Discussion**

317 Our independent datasets of saproxylic beetles and saproxylic fungi yielded congruent
318 response patterns of functional diversity to space and climatic and landscape variables
319 across the biogeographical range of European beech forests. Most of these patterns were
320 already determined on the scale of the regional species pool. In line with our
321 expectation, functional diversity of saproxylic organisms decreased along a historical
322 re-colonization gradient of European biota from south to north. A suitable climate
323 regime for European beech consistently promoted the functional diversity of associated
324 saproxylic taxa of beetles and fungi. Furthermore, we found a negative effect of the
325 proportion of urban areas in the landscape on functional diversity and also a negative
326 effect of land-use intensity along the east-west continental gradient; the latter was
327 significant only for beetles.

328 ***Functional clumping of decomposers across Europe***

329 Over the biogeographical range of European beech, functional diversities of the
330 associated saproxylic taxa showed clumping, which could be explained mainly on the
331 regional species pool level. This suggests that local and regional saproxylic
332 communities were functionally less diverse than could be expected based on a random
333 sample of the species in our study. We consider this trend to be general, as about 90%
334 of the species of saproxylic taxa that can be expected based on our sampling protocols
335 (i.e. gamma diversity; sample coverage of 99.7%, see Appendix S6) were covered by
336 our study throughout the entire biogeographical range of European beech forests.
337 Therefore, saproxylic communities comprised species with more similar morphological
338 traits, in particular ecological niche requirements, than could have been expected from a
339 random community composition across European beech forests. The consistent filtering
340 effects on the functional diversities of saproxylic beetles and fungi across Europe in the
341 present study might thus be driven by biogeographic history, climate and gradients of
342 land-use intensity, which we discuss in the following paragraphs.

343 ***Gradient of biogeographic history***

344 Many studies investigating latitude consider the south–north gradient as a gradient of
345 declining temperature (e.g. Deutsch et al., 2008; Zeuss et al., 2014). However, this is

346 not the case in European beech forests, where in the north the temperature decline is
347 counteracted by an elevation decline covering the distribution range of European beech
348 forests (Appendix S3). Thus, in European beech forest latitude represents a gradient of
349 biogeographic history made pronounced by palaeoclimatic oscillations between cold
350 and warm periods (Hewitt, 2000; see the Methods section for different proxies of
351 biogeographic history). We measured within the latitudinal range of European beech
352 forests a decrease in functional diversity toward the north. More specifically, functional
353 traits were more clustered in the north than in the south. This indicates that the
354 dominant assembly pattern of decomposers shifts from a more random ecological drift
355 in the south to habitat filtering in the north. The underlying process might be explained
356 by the ongoing post-glacial northward expansion of beech forest (Magri, 2008). In other
357 words, community composition and structure in the northern range of European beech
358 forests might not yet have reached equilibrium with the environment. For obligate
359 forest-associated taxa, such as saproxylic organisms, dispersal and adaptation to new
360 suitable regions could even be concomitant with longer temporal lags (Yang et al.,
361 2010). Conversely, lower functional diversity in the north could be caused not only by
362 local habitat filtering, but also by facilitation of re-colonization of saproxylic species,
363 with specific functional traits leading to functional clustering in correlation with
364 distance to refugia during cold periods. This has been found to be the case for plant
365 species across Europe, where the ratio of realized-to-potential functional richness and
366 dispersion are highest in areas with low climatic instability and close to the major
367 glacial refugia (Ordonez & Svenning, 2015).

368 *Climatic filter on functional diversity*

369 European beech forests have their ecological optimum under Atlantic climatic
370 conditions, which are more pronounced in the west and less pronounced in the east,
371 where climatic conditions become increasingly continental until European beech
372 reaches its eastern distribution limit (Peters, 1997). In contrast to the positive effect of
373 increasing temperature for taxonomic diversity of saproxylic beetles (Müller et al.,
374 2015) and saproxylic fungi (Abrego, Bässler, Christensen, & Heilmann-Clausen, 2015)
375 in European beech forests, we found a negative effect of increasing temperature for
376 functional diversity of both species groups when we accounted for overall geographic
377 gradients (latitude and elevation). Saproxylic communities in European beech forests
378 with higher temperatures are functionally less diverse than those in forests with lower
379 temperatures. This is a functional filter that already operates on the regional scale of

380 different forests, with the local scale simply being a blueprint thereof. In this case, we
381 assumed a stronger environmental filtering of functional traits under higher temperature
382 regimes, often related to desiccation stress. In global and regional diversity analyses, it
383 has also been shown that different facets of diversity do not obligatorily match and that
384 taxonomic and functional diversities can differ in response to climatic filters (Stuart-
385 Smith et al., 2013; Bässler et al., 2016; Bae et al., 2018). Thus, for diversity
386 conservation, multiple facets of biodiversity should be considered and approaches that
387 integrate diversity facts for prioritization and incorporate the complementarity of site
388 selection should be promoted [see Cadotte and Tucker (2018) for a recent new concept
389 involving a holistic approach]. Precipitation, another regional climatic filter of the
390 functional diversity of saproxylic beetles and fungi in European beech forests, also had
391 a significant effect, with generally higher functional diversity in moister climates. We
392 therefore hypothesised that higher precipitation in beech forests favours tree species,
393 such as Norway spruce (*Picea abies* (L.) H. Karst.) and silver fir (*Abies alba* Mill.), that
394 promote the functional diversity of saproxylic species. In general, we conclude that a
395 higher functional diversity of saproxylic communities can be found in regions with
396 climatic conditions favouring European beech growth, namely sufficient precipitation
397 and a moderate temperature regime (Peters, 1997).

398 ***Negative effect of land-use intensity on functional diversity***

399 Negative effects of land-use intensity can cause effects on the landscape scale or arise as
400 a result of extensive land-use intensity on the continental and global scales (Foley et al.,
401 2005; Brunet et al., 2010; Strona et al., 2016). We found a negative effect of land-use
402 intensity on functional diversity of saproxylic beetles and fungi in European beech
403 forests on the landscape scale (i.e. proportion of urban area within a 3-km radius).
404 Higher land-use intensity thus strengthened the effect of habitat filtering on species
405 assemblages, which results in lower functional diversity and ultimately in functional
406 homogenization, as shown for taxonomic diversity (Gossner et al., 2016). The
407 functional diversity decrement observed in our study lends support to the idea that
408 species loss is not a random process and affects some species more strongly than others
409 because of particular functional traits, as shown by a modelling approach of extinction
410 risk of saproxylic beetles (Seibold et al., 2015). Saproxylic beetles of lowlands, large
411 species and species that rely on wood of large diameter, broad-leaved trees, or open
412 canopy had a higher extinction risk, which well reflects forestry intensification in
413 European forests in the last centuries (Seibold et al.). On the continental scale, only

414 saproxylic beetles had functionally more diverse communities in eastern Europe than in
415 the west, which follows human land-use history in Europe (Rose, 1992; Peterken, 1996)
416 and the more ancient beech forests in the east (e.g. Carpathians).

417 ***Functional diversity and the regional species pool***

418 We found a clear pattern of biogeographic history, climate and landscape composition
419 operating as filters of functional diversity on the regional species pool level; local
420 functional diversity just represented a blueprint. This assembly process was the same for
421 saproxylic beetles and fungi. Therefore, the functional trait space of species in a local
422 habitat or even on a particular substrate in the case of fungi was determined by the
423 regional species pool of forest areas and not predominantly by local habitat
424 characteristics. These findings perfectly match the beta-diversity patterns of saproxylic
425 beetles in European beech forests, with highest species turnover between different forest
426 areas (Müller et al., 2012). They also support findings on the dispersal of saproxylic
427 fungi and beetles on larger scales (Komonen & Müller, 2018). Jiménez-Alfaro et al.
428 (2018) also showed that biogeographical and climatic factors filter plant species
429 richness in European beech forest on the regional species pool level and that only small
430 operative habitat conditions further alter local species diversity. Although the lifestyles
431 of saproxylic beetles and saproxylic fungi highly differ, a functional filter dominated on
432 the regional pool of both groups.

433 ***Implications for the conservation of biodiversity in European beech forests***

434 Due to the high variety of European beech forest habitats, these forests harbour about
435 70% of the saproxylic beetles in Central Europe (Müller et al., 2012). Local taxonomic
436 diversity and especially threatened species in European beech forests are promoted by
437 high amounts of dead wood, high numbers of veteran trees, high dead-wood diversity,
438 high diversity of tree-related microhabitats and long habitat continuity (Ódor et al.,
439 2006; Brunet et al., 2010; Paillet et al., 2010; Stokland et al., 2012; Bouget, Larrieu,
440 Nusillard, & Parmain, 2013; Seibold et al., 2016). Our results add new evidence that the
441 functional diversities of saproxylic beetles and fungi in European beech forests were
442 congruently filtered by biogeographic history, climate and human land-use intensity and
443 that beech forests mainly differ on a landscape scale in their functional space of
444 saproxylic organisms. These congruent results for saproxylic beetles and fungi provide
445 an opportunity to protect areas with high functional diversity simultaneously for these
446 two hyper-diverse taxa in the decomposition of wood. However, protecting a few beech
447 forest sites is not sufficient to protect the range of functional diversity in European

448 beech forests. Instead, a comprehensive network of protected areas representing the
449 geographical and climate range of European beech forests is necessary to protect the
450 entire functional range of biodiversity. Thus, conservationists and politicians have to
451 reinforce their efforts to promote and expand suitable European-wide conservation
452 strategies, such as the Natura 2000 network with 13 different European beech forest
453 habitat types, including four priority habitat types and the UNESCO World Heritage of
454 “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe”.
455 This is all the more urgent because, in the face of climate change, it has been predicted
456 that areas of high functional diversity in European beech forest in southern and eastern
457 Europe will be most affected by climate warming (Jones, Murphy, & Noguer, 1995;
458 Seneviratne, Lüthi, Litschi, & Schär, 2006). A double hit by climate change and the
459 reduction of buffering structures, such as dead wood, by management (Müller et al.,
460 2015) might push beech ecosystems out of their resilience range (Seidl, Spies, Peterson,
461 Stephens, & Hicke, 2016).

462

463 **Tables**

464 **Table 1:** Environmental predictor variables used for evaluation of functional diversity
 465 of saproxylic assemblages in European beech forests. Measurement units and the
 466 covered range of variables for the assemblage data of saproxylic beetles and fungi are
 467 given.

Variable type	Variable	Definition	Range beetles		Range fungi	
			min.	max.	min.	max.
Space	Latitude	Northing (ETRS. 1989 ^a LAEA projection ^b)	1734686	3675177	2079978	3780088
	Longitude	Easting (ETRS. 1989 ^a LAEA projection ^b)	3548213	5391177	3453436	5780088
	Elevation	Metres above sea level (m a.s.l.)	5 m	1843 m	-5 m	1667 m
Local climate (1-km radius)	Temperature	WorldClim Bio10, mean temperature of the warmest quarter (°C)	11.7 °C	18.5 °C	12.3 °C	22.0 °C
	Precipitation	WorldClim Bio18; precipitation of the warmest quarter (mm)	106 mm	434 mm	107 mm	409 mm
Landscape (3-km radius)	Forest area	CORINE ^c types 311, 312, 313 (%)	4%	100%	1%	100%
	Deciduous forest	CORINE ^c types 311 + 50% of 313, relative to total forest area CORINE ^c types 311, 312, 313 (%)	8%	100%	7%	100%
	Urban area	Proportion of traffic and settlements (CORINE ^c types: 111,112, 141,142) (%)	0%	31%	0%	41%

468 Abbreviations: ^aERTS, European Terrestrial Reference System; ^bLAEA, Lambert azimuthal equal-area
 469 projection; ^cCORINE, Pan-European project CORINE Land Cover (CLC) (CORINE 2006).

470

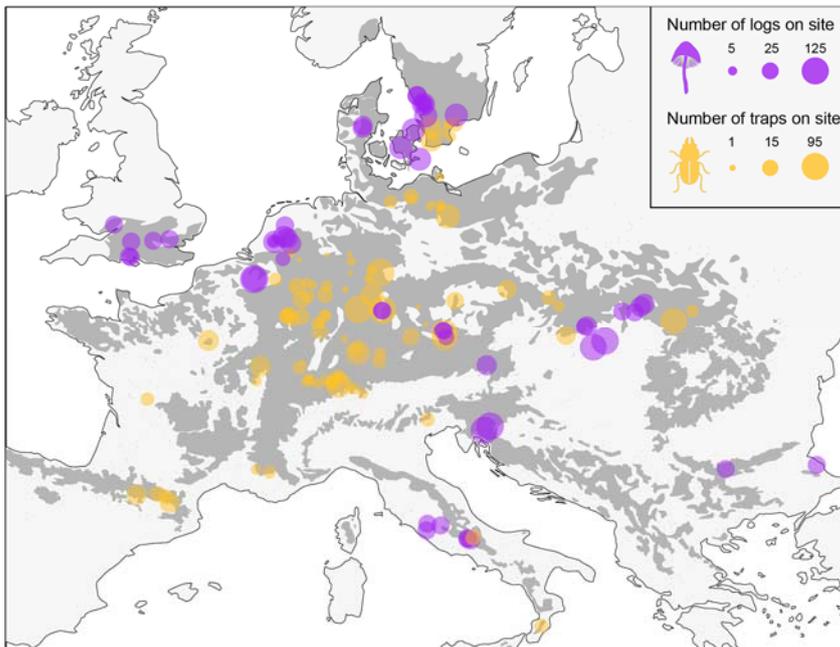
471 **Table 2:** Definition of traits of saproxylic beetles and fungi used for the calculation of
 472 functional diversity. Numbers in parentheses indicate the number of conforming
 473 species.

	Trait	Definition	Min	25 % Quartile	Median	75 % Quartile	Max	Species with missing data
Beetles (791)	Body size	Mean body length of the beetle in dorsal view (mm)	0.5	2.1	3.9	7.0	50.0	1
	Decay niche	Preferred decay stage (fresh = 1 to decomposed = 5)	1.0	2.0	3.2	3.4	5.0	16
	Wood diameter niche	Preferred dead-wood diameter (small = 1 to large = 4)	1.0	1.9	2.5	3.0	4.0	16
	Host tree preference	Broad-leaved (531), conifer (168), both (81)	-	-	-	-	-	11
	Feeding type	Xylophagous (412), mycetophagous (181), saprophagous (15), predatory (181)	-	-	-	-	-	2
	Canopy niche	Preferred canopy cover (sunny = 1 to shady = 3)	1.0	1.5	1.5	2	3	18
	Elevation	Preferred elevation zone (planar = 1 to alpine = 5)	1.0	2.0	2.0	2.0	4.5	50
Fungi (249)	Body size	Surface of fruiting body (mm ²)	0.9	6.3	16.8	20.4	125.7	0
	Decay niche	Preferred decay stage (fresh = 1 to decomposed = 5)	1.0	2.3	3.0	3.5	5.0	0
	Wood diameter niche	Preferred dead-wood diameter (small = 1 to large = 4)	1.3	2.5	2.5	2.9	3.8	0
	Host tree preference	Broad-leaved (190), conifer (20), both (24), beech specialist (15)	-	-	-	-	-	0
	Fruiting body type	Agaric (161), polypore (88)	-	-	-	-	-	0
	Range of decay classes	Plasticity of suitable decay stage	1.0	2.0	4.0	5.0	5.0	0

474

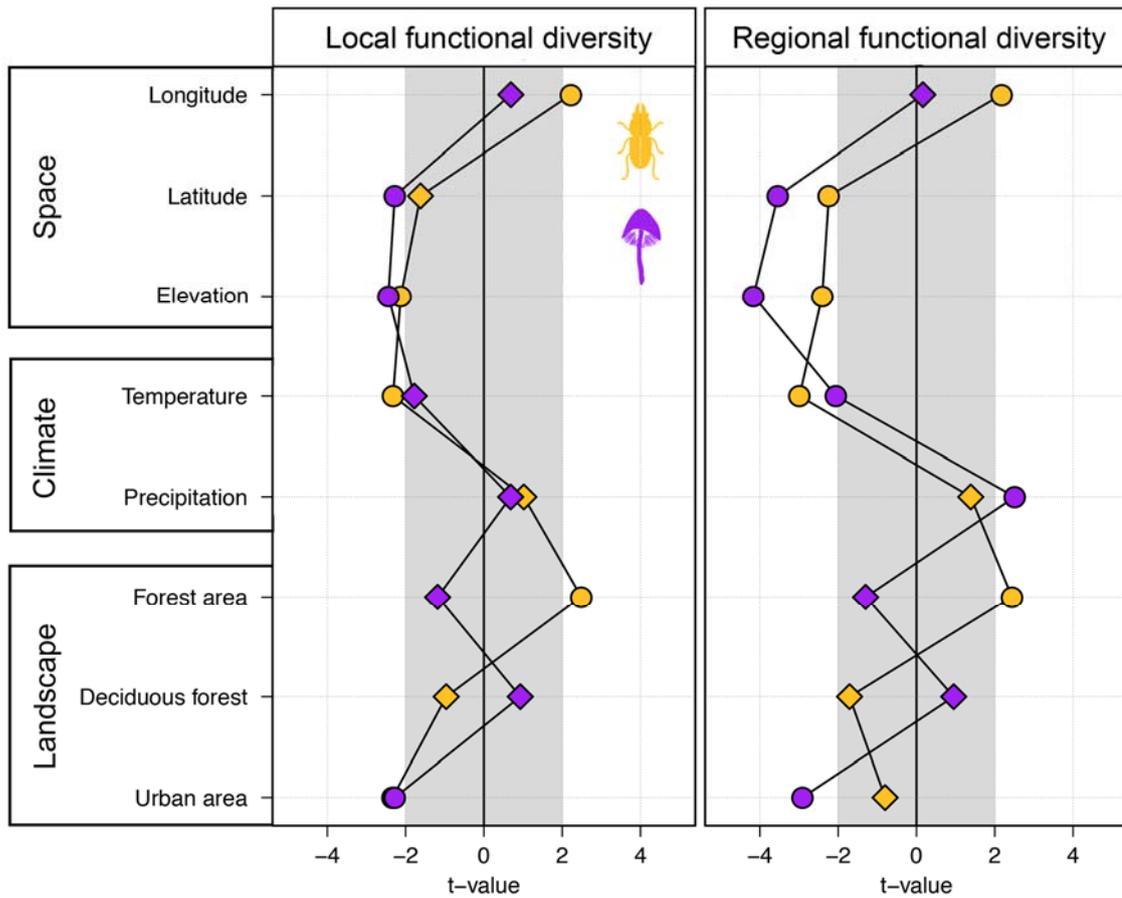
475

476 **Figures and legends**



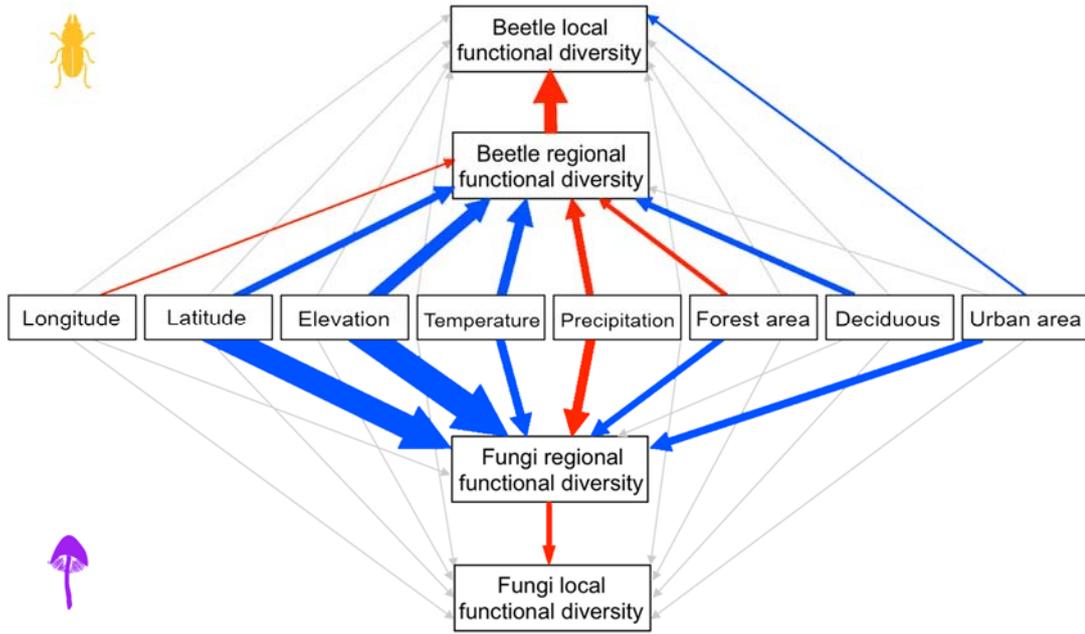
477

478 **Figure 1:** Map of Europe showing the study area and sampling locations of saproxylic
479 assemblage data (EPSG 3035; ETRS89 equal area projection). The occurrence of
480 European beech, including natural and naturalized stands, is shown in grey
481 (*EUFORGEN*), purple dots indicate the sampling locations for saproxylic fungi and
482 yellow dots indicate the sampling locations for saproxylic beetles. Point size refers to
483 the number of samples of local communities sampled within each regional forest area.



484

485 **Figure 2:** Response of local and regional functional diversity (standardized effect sizes
 486 of the mean pair-wise distances) of saproxylic beetles (yellow) and fungi (purple) to
 487 predictor variables representing space, climate and landscape in European beech forests.
 488 Circles indicate significant effects ($p < 0.05$) and diamonds indicate non-significant
 489 effects (lines between points are for visual purposes only); shaded areas indicate ranges
 490 of non-significant values (t-values: ± 2.0).



491

492 **Figure 3:** Structural equation models indicating relationships between predictor
 493 variables representing space, climate and landscape and regional and local functional
 494 diversity of saproxylic beetles (top) and fungi (bottom). The scale of path coefficients of
 495 positive (red) and negative (blue) relationships correspond to arrow width. All test paths
 496 are shown; non-significant ones are in grey.

497

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697

698 **Biosketch**

699 The '*Beech boys*' were initially a group of fungus specialists who sampled saproxylic
700 fungi in European beech forests. This group recently joined a group of saproxylic beetle
701 specialists to become a European-wide community of dead-wood ecologists. Dead-
702 wood ecology is a growing discipline with the potential of contributing to a broad field
703 of general biological questions.

704 **Supporting information**

705 Additional supporting information may be found in the online version of this article at
706 the publisher's website:

707 **Appendix S1** Sampling of saproxylic assemblages.

708 **Appendix S2** Trait data of saproxylic beetles und fungi.

709 **Appendix S3** Correlations of environmental variables.

710 **Appendix S4** Functional diversity of saproxylic beetles and fungi on local and regional
711 scale across European beech forests.

712 **Appendix S5** Results of observed values of functional diversity of saproxylic beetles
713 und fungi.

714 **Appendix S6** Sample coverage and species diversity estimation.

715 **Data accessibility statement**

716 Trait data of 791 saproxylic beetle species and 249 saproxylic fungus species (Appendix
717 S2) are provided with this article. Some of the data pertain to endangered species and
718 are therefore classified; to protect these species, data on their occurrence cannot be
719 made available to the general public.