

1 **Title: Species richness influences the spatial distribution of**  
2 **trees in European forests**

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4 Running title: Tree species richness and the spatial arrangement

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52 comments from all authors.

53

#### 54 **ABSTRACT**

55 The functioning of plant communities is strongly influenced by the number of species in  
56 the community and their spatial arrangement. This is because plants interact with their  
57 nearest neighbors and this interaction is expected to be stronger when the interacting  
58 individuals are ecologically similar in terms of resource use. Recent evidence shows  
59 that species richness alters the balance of intra- vs. interspecific competition, but the  
60 effect of species richness, and phylogenetic and functional diversity on the spatial  
61 pattern of the plant communities remain less studied. Even far, how forest stand  
62 structure derived from past management practices can influence the relationship  
63 between species richness and spatial pattern is still unknown. Here, we evaluate the  
64 spatial distribution of woody individuals (DBH >7.5 cm) in 209 forest stands (i.e. plots)  
65 with an increasing level of species richness (from 1 up to 10 species) in six forest types  
66 along a latitudinal gradient in Europe. We used completely mapped plots to investigate  
67 the spatial pattern in each forest stand with point pattern techniques. We fitted linear  
68 models to analyze the ~~relationship-effect of between~~ species richness (positively  
69 correlated with phylogenetic diversity) and functional diversity ~~and-on~~ tree spatial  
70 arrangements. ~~We also~~ ~~controlled~~ ~~this relationship~~ by forest type and stand structure ~~in~~  
71 ~~terms of size classes~~ as a proxy of the management legacy. Our results showed a  
72 generalized positive effect of species richness and functional diversity on the degree of  
73 spatial clustering of trees, and on the spatial independence of tree sizes regardless of the  
74 forest type. Moreover, current tree spatial arrangements were still conditioned by its  
75 history of management; however its effect was independent of the number of species in

76 the community. Our study showed that species richness and functional diversity are  
77 relevant attributes of forests influencing the spatial pattern of plant communities, and  
78 consequently forest functioning.

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80 **Keywords:** spatial point pattern, intraspecific competition, plant-plant interactions,  
81 stand structure, functional diversity, mixed forests, FunDivEurope.

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# 1 **Species richness influences the spatial distribution of trees in European forests**

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17 models to analyze the effect of species richness (positively correlated with phylogenetic  
18 diversity) and functional diversity on tree spatial arrangements. We also controlled this  
19 relationship by forest type and stand structure as a proxy of the management legacy.  
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21 diversity on the degree of spatial clustering of trees, and on the spatial independence of  
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26 plant communities, and consequently forest functioning.

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## 28 INTRODUCTION

29 Anthropogenic actions have resulted in multiple changes at the global scale that  
30 have often caused biodiversity loss. Substantial theoretical and experimental evidence  
31 has demonstrated that the functioning of many forest ecosystems closely depends on its  
32 species diversity (Loreau 2001, Gamfeldt et al. 2013, van der Plas et al. 2016). As  
33 species often differ in their functional strategies deployed to exploit environmental  
34 resources (Hutchinson 1957, Silvertown 2004), the addition or loss of any species may  
35 impact the functioning of the entire community (Tilman et al. 1997). Moreover, it is  
36 often argued that forest multifunctionality occurs as a result of complementarity in  
37 resource use among functionally diverse species (Hooper et al. 2005). Thus, it is  
38 expected that two species with similar resource use strategies cannot stably coexist  
39 (MacArthur and Levins 1967). Still, modern coexistence theory also considers that two  
40 species will coexist if their niche differences overcome their fitness differences  
41 (Chesson 2000, Adler et al. 2007). Under this perspective, niche differences are  
42 estimated as the relative ratio between intra- and interspecific competition (Chesson  
43 2012). Niche differences operate as a stabilizing factor promoting coexistence when  
44 species limit themselves more than they limit others (Chesson 2000), i.e., when  
45 intraspecific competition has stronger effects than interspecific competition. Although  
46 the source of such differences remains unknown in many cases (Godoy et al. 2018),  
47 efforts have been made to relate them to plant functional traits (Kraft et al. 2015),  
48 including differences in phenology or morphology, or even to relate them to spatial  
49 segregation (Chesson 2000, Adler et al. 2007).

50 In plant communities like forest systems, space availability is a key feature  
51 influencing community functioning and structure (Tirado and Pugnaire 2003, Maestre et

52 al. 2005, 2012). Sessile organisms, such as trees, are forced to interact with their nearest  
53 neighbors, which results in forest stands with spatial patterns and tree size structures  
54 reflecting these interactions (Watt 1947, Stoll and Weiner 2000). The effects of plant-  
55 plant interactions on the spatial pattern of trees are well-known, with intraspecific  
56 competition leading to regular, self-thinned patterns (e.g. Kenkel 1988) and interspecific  
57 competition generating spatial segregation at larger scales (Kenkel 1994). These  
58 patterns agree with long-standing theory predicting that the processes of self-thinning in  
59 mixed stands (often termed “alien thinning”) are subtly different from those occurring in  
60 pure stands (Harper and McNaughton 1962). For example, Pretzsch et al. (2017)  
61 showed shifts in the slope of the stand self-thinning line due to packing density, which  
62 might be higher under mixed than monospecific conditions. The modern coexistence  
63 theory would explain this outcome as a consequence of indirect competition effects that  
64 only emerge in diverse systems (Saavedra et al. 2017). A reflection of the tree-tree  
65 interactions can be also observed in the spatial correlation of the tree sizes (DBH or  
66 basal area) within a tree community. Tree sizes in forests stands usually show negative  
67 spatial dependence, i.e., the sizes of two close trees is usually smaller than the sizes of  
68 two randomly chosen trees in the stand (Stoyan and Penttinen 2000). Translating it to a  
69 species diversity context, less spatial dependence in tree sizes should be expected in  
70 mixed communities in comparison to monospecific ones by minimizing the intraspecific  
71 interactions and increasing the interactions between individuals with different resource  
72 use strategies. Despite an increasing number of studies assessing the relationships  
73 between species richness, forest functioning and coexistence processes in the last  
74 decades (Jucker et al. 2014a, b, Liang et al. 2016, Benavides et al. 2019) only few of  
75 them have studied it from an spatially explicit approach and addressed other aspects of  
76 biodiversity such as phylogenetic or functional diversity.

77 European forests are characterized by a low number of tree species in  
78 comparison with other forests at similar latitudes, which is mostly due to species  
79 extinctions during the glacial periods and high anthropogenic pressures for centuries  
80 (Walter 1985). Over the last decades, a change in forest management policies  
81 encouraging mixed and structurally more diverse forest stands, has often caused  
82 relevant large-scale changes in tree spatial pattern as well as in species composition and  
83 forest structure (Johann 2007). Uneven-sized forest stands are usually considered stable  
84 in terms of structure and composition at long term (Larsen 1995, Schütz 2001). For old-  
85 growth forest systems, which have reached relative stability in terms of structure and  
86 composition, some authors have suggested that stabilizing niche differences (e.g.  
87 resource partitioning) override fitness differences among species (Chesson 2000, Adler  
88 et al. 2007, Barabás et al. 2016). Nevertheless, the relationship between forest structure  
89 derived from past management practices, species richness and the spatial pattern of trees  
90 has received little attention despite having relevant implications for ecosystem  
91 dynamics and functioning (Petritan et al. 2015).

92 In this paper, we examine the effect of species richness and phylogenetic and  
93 functional diversity on the spatial distribution of trees in 209 forest stands differing in  
94 species richness (ranging from 1 to 10 species). Forest stands were distributed in six  
95 regions along a latitudinal gradient in Europe, from Mediterranean to boreal forests.  
96 Assuming that in stable communities, such as mature European forests, the effects of  
97 intraspecific competition override those of interspecific interactions, we hypothesize  
98 that the frequency of intraspecific interactions decreases as species richness increases,  
99 resulting in less self-thinning and, therefore, less regular spatial patterns of trees in the  
100 community, and also less spatial dependence of tree sizes, regardless forest type and  
101 species identity. Our reasoning is that higher species richness promotes higher



102 phylogenetic and also could raise the functional diversity, which would result in an  
103 increase of different resource use strategies. In other words, resource niches of adjacent  
104 individuals overlap less in mixed communities due to fewer intraspecific interactions  
105 and thus, the distance between neighboring individuals is reduced (i.e. tree clustering).  
106 We also expect that the relationship between species richness and spatial pattern of trees  
107 is mediated by the stand structure, which in turn is derived from past management  
108 practices. In this line, we hypothesize higher tree clustering in stands structurally more  
109 diverse (i.e. uneven-sized stands), with higher species richness due to a different spatial  
110 resource utilisation and competition releases among co-occurring trees.

111

## 112 **MATERIALS AND METHODS**

### 113 *Study design*

114 We based our study on a network of permanent plots designed within the  
115 FunDivEUROPE project (<http://www.fundiveurope.eu>) to explore the effect of tree  
116 species richness on different ecosystem functions in European forests (Baeten et al.  
117 2013). The plot network consists of 209 square plots of 30 m × 30 m distributed in six  
118 forest types, which span a wide bioclimatic European range: a boreal forest in Finland, a  
119 hemiboreal forest in Poland, a temperate forest in Germany, a sub-continental temperate  
120 forest in Romania, a temperate Mediterranean forest in Italy and a continental  
121 Mediterranean forest in Spain. In each forest type, plots were set up along a species  
122 richness gradient of the regional dominant tree species (Table A1). All sites are  
123 considered ancient forests, i.e., they have been continuously forested at least since the  
124 oldest available land-use maps (Baeten et al. 2013). Key features of the experimental  
125 design was the strict avoidance of a dilution gradient, special attention to community  
126 evenness and minimal covariation with other environmental factors. Therefore, plots

127 were selected ensuring two criteria: (i) all species represented in all richness levels,  
128 maximize evenness of the dominant species, i.e. relative abundance of the dominant  
129 species was as balanced as possible in all mixed plots; and (ii) minimize the presence of  
130 non-dominant species within the plot (i.e. preferably the summed basal area of these  
131 species is below 5% of the total basal area, with a maximum of ca. 10%), which also  
132 have very low or low representation in the whole forest. This latter criterion was not  
133 exclusive to include non-dominant species in the spatial pattern analyzes as their  
134 presence may alter the spatial arrangement of the rest of individuals in the community.  
135 Thus, the richness gradient ranged from monospecific to mixed stands including up to  
136 10 different tree species considering all species within a community, including non-  
137 dominant species (Table A1). Although some stands had been subject to management  
138 practices in the past (e.g. group cutting, coppicing, etc) depending on their species  
139 composition and forest type (an intense management in Finland whereas a low  
140 frequency of management practices in Spain or Romania), they were selected based on  
141 their current condition showing minimal signs of recent management. See Baeten et al.  
142 (2013) for further details on the experimental design, selection criteria of the forest  
143 stands and forest location.

144

#### 145 *Data collection*

146 In each forest stand (i.e. plot), all tree individuals (DBH > 7.5cm) were identified by  
147 species recorded their height and calculated their basal area. We also calculated the  
148 spatial coordinates (x, y) for each tree individual as the distance taken from each tree to  
149 a reference point (bottom-left corner) in each plot using a measuring tape or a ultrasonic  
150 distance measurer (Haglöf, Långsele, Sweden). Multi-steemed trees were considered as

151 a single individual by summing the basal area of all stems within each tree. Information  
152 on the number of trees per plot and forest type can be found in Table A2.  
153 Additionally, we recorded trait data for each identified species in the six study forests in  
154 order to quantify the functional component of the tree diversity in each plot. We focused  
155 on five key traits, which are considered to capture the plant strategy schemes: specific  
156 leaf area, wood density, maximum height, seed mass and shade tolerance (Westoby  
157 1998). Maximum height for all species and mean SLA for dominant species were  
158 obtained from field measurements (Benavides et al. 2019). Mean trait values for wood  
159 density, seed mass, shade tolerance and SLA for non-dominant species were obtained  
160 from different databases such as TRY (Kattge et al. 2011), LEDA (Kleyer et al. 2008),  
161 KEW (“Royal Botanic Gardens Kew” 2019), BioFlor (Kühn et al. 2004) and the  
162 literature (e.g. shade tolerance trait values from (Niinemets and Valladares 2006)),  
163 prioritizing as much as possible those trait measures performed in similar latitudes where  
164 species were present. See Table A3 for mean trait values of each species.

165 We calculated two different multifunctional indexes at plot level taking into  
166 account the species relative abundance: (i) Rao’s quadratic entropy (RaoQ; (Botta-  
167 Dukát 2005), which measures the mean functional dissimilarity between two randomly  
168 chosen individuals and (ii), functional dispersion index (FDis; Laliberté and Legendre  
169 2010) that calculates the mean distance in multidimensional trait space of individual  
170 species to the centroid of all species. Furthermore, we carried out the construction of the  
171 phylogenetic tree for all species identified in the field using the mega-tree implemented  
172 in the R package ‘V.PhyloMaker’ (i.e. GBOTB.extended.tre) (Jin and Quian 2019).  
173 Then, we calculated a phylogenetic diversity index (PD) at plot level (i.e. the total  
174 branch length spanned by the tree including all species in a local community; Faith  
175 (1992)), which is a biodiversity index that quantifies the combined genetic diversity

176 across species. PD and FDis were strongly correlated with species richness and RaoQ,  
177 respectively (Figure A1). Thus, they were excluded from subsequent analyses to avoid  
178 collinearity problems (Dormann et al. 2013). Correlations among diversity indices were  
179 carried out using the R package ‘corrplot’ (Wei and Simko 2017), the phylogenetic and  
180 functional diversity indices were calculated using the R package ‘picante’ (Kembel et  
181 al. 2010) and R package ‘FD’ (Laliberté et al. 2014), respectively.

182 Finally, we classified each stand (plot) into three categories: even-sized, semi-sized and  
183 uneven-sized, according to the distribution of DBH size classes (Lähde et al. 1994).  
184 Forest stand structures have often been described by their diameter distributions (Goff  
185 and West 1975), which have also been used as a proxy of differences in the  
186 management history of each stand that underlie the current forest spatial distribution  
187 (Schütz 2001, Petritan et al. 2015). Even-sized stands generally have a nearly bell-  
188 shaped diameter distribution with most of the trees in the average diameter class. An  
189 even-sized stand is typically a result of a previous shelterwood cutting system for forest  
190 management (Powell 2013). In some cases, stands may be dominated by two well-  
191 defined size classes (i.e. semi-sized stands) differing in diameter. This is typically  
192 associated to group cutting systems and coppicing. On the contrary, uneven-sized stands  
193 are characterized by a high density of tiny individuals (i.e. small DBH), and this density  
194 declines as size classes increase to the point where the largest size classes can be quite  
195 scattered. These stands typically arise when stands are managed using selection or  
196 group selection cutting systems as regeneration quickly fills the frequent canopy gaps  
197 originated and then competition reduces the number of individuals (Powell 2013).

## 198 *Analyses*

### 199 *Intraspecific interactions, species richness and functional diversity.*

200 We calculated the mean number of intraspecific neighbors for each species in each plot  
201 from the average of the number of conspecific individuals around each tree within a  
202 circle of radius spanning from 3.5 to 15 m with increment of 0.5 m. Then, we fitted a  
203 generalized linear model (McCullagh and Nelder 1989) to test our initial assumption  
204 that the frequency of intraspecific interactions would decrease with increasing species  
205 richness and phylogenetic and functional diversity. We included forest type (and its  
206 interaction with species richness) to control other intrinsic factors affecting the  
207 relationship between species diversity and the frequency of intraspecific interactions in  
208 each forest type.

#### 209 *Spatial pattern of the communities*

210 We employed two widely used summary statistics to characterize the spatial pattern of  
211 trees in each plot: Ripley's  $K$ -function ( $K$ ) and the nearest-neighbors distance  
212 distribution  $G$  (Diggle 2003, Loosmore and Ford 2006).  $K(r)$  estimates the expected  
213 number of points within a circle of radius  $r$  around a typical point of the pattern,  
214 weighted by the intensity (i.e., the density) of the plot (Diggle 2003).  $G(r)$  estimates the  
215 proportion of points of the pattern which have their nearest-neighbor at a distance equal  
216 or inferior to  $r$ . Therefore, both statistics summarize different aspects of the spatial  
217 pattern, based on second-order properties and nearest-neighbour distances, respectively  
218 (Diggle 2003). In any case, for a given spatial scale  $r$ , both functions render smaller  
219 values as the stand is more regular, and larger values as the stand is more clustered.

220 To stabilize the variance of the estimated functions, we transformed  $K(r)$  into the  $L$ -  
221 function (Diggle 2003), i.e.,  $L(r) = \sqrt{K(r)/\pi} - r$ , and used Fisher's arcsin  
222 transformation on  $G(r)$ , i.e.,  $\Phi(G(r)) = \arcsin\sqrt{G(r)}$  (Baddeley et al. 2015).

223 As we were also interested in the spatial distribution of tree sizes (measured as basal  
224 area), we computed also the mark-correlation function. For a quantitative variable  $m$

225 (e.g., the DBH or basal area) which varies throughout the points of a spatial point  
 226 pattern, the mark-correlation function is defined as  $k_{mm}(r) = \frac{c_{mm}(r)}{\mu^2}$ , where  $c_{mm}(r)$  is  
 227 the conditional mean of the product of the marks of all point-pairs  $(i, j)$  separated by a  
 228 distance  $r$ , and  $\mu$  is the mean of  $m$  (Illian et al. 2008). This measures the spatial  
 229 dependence of the marks (Baddeley et al. 2015).

230 In order to get a “global” estimation of the spatial structure of the pattern in a range of  
 231 scales (defined by  $r_0$  and  $r_{max}$ ); we reduced each transformed summary function to a  
 232 single numerical value (Loosmore and Ford 2006). For this, we employed a statistic  
 233 partially similar to the well-known goodness-of-fit (GoF) statistics  $u$ , which was defined  
 234 as follows (Diggle 2003, Loosmore and Ford 2006, Wiegand and Moloney 2014,  
 235 Baddeley et al. 2015):

236

$$237 \quad DR_F = \sum_{r_0}^{r_{max}} (\hat{F}(r) - F(r)),$$

238 where  $\hat{F}(r)$  is the observed value of either  $L(r)$ ,  $\Phi(G(r))$  or  $k_{mm}(r)$  and  $F(r)$  their  
 239 respective expected values under a null model of spatial randomness (complete spatial  
 240 randomness, i.e., CSR, for  $L$  an  $\Phi$  and random labelling, i.e., random permutation of  
 241 marks, for  $k_{mm}$ ). In other words, we computed for each plot an estimation of how much  
 242 its spatial pattern of trees or tree sizes deviated from an hypothetical completely random  
 243 pattern. Note that, in comparison with the GoF statistics  $u$ , we did not square the  
 244 difference of functions in the summation as we were not interested in the absolute  
 245 difference from the expected value under CSR but in the net deviation and in its sign.  
 246 On the other hand, we did not test the spatial patterns in the plots against CSR or  
 247 random labelling, but simply used these null models as baseline, intermediate reference  
 248 level between “aggregated” and “regular” patterns in the case of tree patterns or  
 249 between positive and negative spatial dependence in the case of tree sizes.

250 Summary functions were computed with the package ‘spatstat’ (Baddeley et al. 2015) in  
251 R (R Development Core Team 2018). Following the recommendations of Baddeley et al.  
252 (2015) for plot sizes similar to ours, we computed the summary functions between  $r_0 =$   
253  $0.00$  and  $r_{\max} = 7.50$  m, with the default intervals in spatstat (i.e., around 0.15 m for the  
254 size of our plots), applying Ripley’s isotropic correction (Ripley 1977) for  $K$  and  $k_{mm}$ ,  
255 and using the Kaplan-Meier estimator of  $G$  to avoid edge effects.

256

257 *Species richness, functional diversity and spatial pattern of forest stands.*

258 Using the  $DR_F$  statistics defined previously, we summarized the spatial pattern of the  
259 forest stands at two different scales: from  $r_0=0.0$  to  $r_{\max}=7.5$  m (hereafter “medium  
260 scale”) and from  $r=0.0$  to  $r_{\max}=3.5$  m (hereafter “fine scale”). Note that the words  
261 “medium” and “fine” are relative, and we employed them to distinguish both scales in  
262 the context of the present study, without any further assumption.

263 We fitted linear models (Rao and Toutenburg 1995) for each statistics ( $DR_K$  and  $DR_G$   
264 and  $DR_{k_{mm}}$ ) and spatial scale (medium and fine scales) to test the effect of species  
265 richness and functional diversity on the spatial pattern of trees and tree sizes (as  
266 measured by  $DR_F$ ). We used  $DR_F$  as the response variable and species richness and  
267 functional diversity (RaoQ) as predictors. We included the median value of the tree  
268 basal areas for each stand (plot) as a covariable to account for tree sizes among forest  
269 stands (only for  $DR_K$  and  $DR_G$  models) together with stand structure (three levels),  
270 forest type, and their interactions with species richness to control by different  
271 management histories at stand level and other potential intrinsic local processes at forest  
272 level. We compared the full models with all possible models including predictors and  
273 covariables for each statistics ( $DR_F$  for  $K(r)$  and  $G(r)$  and  $k_{mm}(r)$ ), and scale.  
274 Specifically, we searched for the model that provided the best fit to the data using the

275 Akaike Information Criteria corrected for finite sample sizes (AICc; Burnham and  
276 Anderson 2002, Johnson and Omland 2004). To evaluate the consistency of the best  
277 models, we selected the set of competing models with  $\Delta\text{AICc}$  values  $< 2$ . We then  
278 calculated the weight for each effect in the full model, by summing the Akaike weights  
279 of the competing models in which they appear (Burnham and Anderson 2002). The  
280 weight for each effect ranged from 1 (present in the best model and all the competing  
281 models) to 0 (not present in any model), and was used to compare the importance of the  
282 effects appearing in the best model to those not included. When both forest type and  
283 stand structure were present in the best model (without interaction with species  
284 richness), Tukey *post-hoc* tests were performed to compare the relationship between  
285 spatial distribution and species richness among forests and stand structures.

286 Statistical analyses were carried out in R 3.5.0 (R Development Core Team  
287 2013), using package ‘stats’, package ‘car’ (Fox and Weisberg 2011), package  
288 ‘multcomp’ (Hothorn et al. 2008) and package ‘MuMIn’ (Barton 2019).

289

## 290 **RESULTS**

291 We found an overall trend of decreasing mean number of intraspecific neighbors  
292 with increasing species richness (positively correlated with phylogenetic diversity) and  
293 functional diversity (Figure 1; Table A4). This trend with species richness became  
294 significant from ‘fine’ (3.5 m) to larger scales (15 m) (Table A5). Significant  
295 differences in the mean number of intraspecific neighbors were observed among forest  
296 types, but its interaction with species richness was not significant (Table A4).

297 From the model selection method, we found that species richness and functional  
298 diversity were included as predictors to explain the spatial aggregation of trees for both  
299 spatial functions ( $K$ ,  $G$ ) and at both fine (0.0 - 3.5 m) and medium spatial scale (0.0 - 7.5



300 m) (Table 1, Table A6), with the only exception of FD for  $K(r)$  at medium scale.  
301 Particularly, we observed an overall positive trend of the spatial aggregation of trees  
302 with higher species richness and functional diversity in all cases where were included as  
303 predictors (Figure 2A-D, Table 1, Table A6). In other words, the tree distribution was  
304 less regular in plots with higher number of species and phylogenetically and  
305 functionally more diverse. In the same line, we also found that tree sizes (basal area)  
306 were more spatially independent as species richness and functional diversity increased  
307 at both fine and medium scale, i.e less negative values of  $k_{mm}(r)$  function were observed  
308 in stands with higher number of species and more phylogenetically and functionally  
309 diverse (Figure 2E, Table 1, Table A6). We also obtained that plots with greater tree  
310 sizes (high median values of basal areas) showed much less tree clustering (Table A6).  
311 Furthermore, forest type and the stand structure were two important predictors to  
312 explain the spatial distribution of trees in all cases (Figure 3, Figure A2, Table 1, Table  
313 A6). Particularly, we found that uneven-sized stands presented more tree clustering than  
314 the even- and semi-sized stands, becoming significantly different at medium and fine  
315 scale with  $K$  function (Figure A2). However, there were no significant interactions  
316 between species richness and forest type and stand structure (Table 1, Table A6) for any  
317 function ( $K$ ,  $G$  or  $k_{mm}$ ) and for any of the study scales, with the only exception of  $G$   
318 function at fine scale. In other words, the effect of species richness (and therefore, its  
319 correlated phylogenetic diversity) on the spatial pattern was similar, irrespective of the  
320 forest type and management legacy (Table A6).

321

## 322 **DISCUSSION**

323 Our study showed a generalized effect of species richness of the community  
324 (positively correlated with phylogenetic diversity) on the spatial distribution of trees at

325 the spatial scales analysed, suggesting a less regular spatial distribution of tree  
326 individuals as species richness increased along the entire European bioclimatic gradient.  
327 Our results suggest that this pattern is partly due to a greater functional diversity which  
328 would allow individual trees to live closer together in space, independently of their size  
329 (basal area), as it promotes complementarity in the resource use. Moreover, our study  
330 pointed out that the current tree spatial arrangements are conditioned by stand  
331 management history, but its influence on tree spatial pattern was independent to the  
332 number of species of the community.

333 In forest systems, it is widely assumed that the spatial distribution of trees  
334 changes with the stand development. Thus, early recruits usually appear in clumped  
335 distributions as a consequence of limited dispersal when forest regenerates naturally  
336 (Wiegand et al. 2007, Lara-Romero et al. 2016). However, this clumped pattern  
337 becomes more regular with time as some individuals grow and others die due to  
338 negative density-dependent thinning (Getzin et al. 2008, Chacón-Labela et al. 2014)  
339 including competitive interaction effects (Kenkel 1988, Getzin et al. 2006). As we  
340 expected, our previous assumption on decreasing the probability of intraspecific  
341 encounters as species richness, phylogenetic and functional diversity increase was  
342 confirmed. This result suggests that an increasing number of species in the community  
343 alters the balance between intra- and interspecific competition, and impacts on the  
344 community spatial pattern. The underlying mechanism is that plant-plant interactions in  
345 space become stronger as the interacting individuals are ecologically more similar in  
346 terms of resource use. In contrast, competitive interactions should be weaker when  
347 resource niches of adjacent individuals overlap less. An effect of reduced interspecific  
348 competition is that mixed stands usually outperform monospecific ones, at least in terms  
349 of growth (Vilà et al. 2007, Morin et al. 2011, Ruiz-Benito et al. 2014) and growth

350 resistance in drought periods (Gazol and Camarero 2016). For example, analyzing  
351 combinations of pairs of European tree species, Pretzsch and Biber (2016) showed that  
352 mixed stands attained higher densities than monospecific ones. In this line, our study  
353 went further and included the spatial tree layout, suggesting that individuals in richer  
354 and more functionally diverse communities occur closer to each other (Figure 2).

355         The strength of plant-plant interactions, determined by how spatially close the  
356 individuals are, as well as their niche and fitness differences (*sensu* modern coexistence  
357 theory perspective; Chesson 2000, Adler et al. 2007), may affect the expression of  
358 ecological processes involved in species dynamics such as growth, regeneration, and  
359 mortality (Mokany et al. 2008). For instance, Chamagne et al. (2017) found that  
360 increasing tree species diversity enhanced individual growth in central European forest  
361 stands. Ngo Bieng et al. (2013) showed that intraspecific competition had a greater  
362 negative effect on growth of oak and pine species than interspecific competition in a  
363 mature mixed European forest. Further, these authors also found that the productivity of  
364 both pine and oak was affected by its spatial pattern, being higher when they grew in  
365 well-mixed stands than when they formed patchy mixtures. These examples suggest that  
366 complementarity in resource use is one of the primary mechanisms underlying increased  
367 performance of mixed stands over monocultures (Paquette and Messier 2011, Morin et  
368 al. 2011, Ratcliffe et al. 2017). As suggested by the positive effect of functional  
369 diversity both on tree clustering and on the independence of adjacent tree sizes,  
370 complementarity is also likely to underlie our observed spatial pattern affected by  
371 species richness regardless of the past silvicultural practices. Niche differentiation and  
372 resource partitioning between individuals allows trees to grow closer to each other, and  
373 thus lead to clustering patterns. The presence of stabilising niche differences is a  
374 precondition of complementarity (Barry et al. 2019), which, in turn favors species

375 coexistence and enhanced ecosystem functioning (Chesson 2000, Saavedra et al. 2017).  
376 In a modelling study of European temperate forests across a large climatic gradient  
377 similar to ours, Morin et al. (2011) found that the increase of productivity with species  
378 richness was mediated through functional complementarity in exploiting resources such  
379 as light. Particularly, Morin et al. (2011) found that higher species richness generated  
380 higher variation of shade tolerance and growing strategies, which in turn resulted in  
381 faster responses (i.e., re-colonization) to small-scale mortality events. Moreover,  
382 complementarity related to an increase of species richness in forests does not only  
383 enhance yield, i.e increased biomass production, but it may also affect the spatial  
384 distribution of biomass. So, for instance, species in mixed communities have showed  
385 complementarity in crown shapes, leading to increased canopy space filling which did  
386 not occur in monospecific stands (Jucker et al. 2014a, Pretzsch 2014). However, the  
387 complementarity effect in crown shapes found by Jucker et al. (2014a) in the same  
388 continental Mediterranean forest studied here, is partly due to past management  
389 practices. Certain management practices such as thinning often facilitate the vertical  
390 layering of species, which also give trees more space to expand their crowns, thereby  
391 changing their allometry (e.g. Pretzsch 2014). In our study, we have been able to isolate  
392 the effect of management legacy from the effect of species interactions on tree spatial  
393 distribution, and our results still suggest complementarity as the mechanism partly  
394 explaining the positive relationship between the tree clustering and species richness in  
395 our European study forests.

396         Looking for the influence of species richness on the spatial distribution of trees  
397 in forests along a wide European bioclimatic gradient, special attention should be paid  
398 to past management of such forests. Our study showed that the current spatial  
399 distributions of the study forests are, at least in part, a reflection of their history in

400 silvicultural practices. This means that stands structurally more diverse in terms of DBH  
401 showed higher tree aggregation in the same space than even-sized stands. This can be  
402 explained because the silvicultural practices generating uneven-sized stands promote  
403 higher variety in tree sizes as well as higher levels of vertical structure (Wolf 2005).  
404 Thus, individuals in uneven-sized stands make a better use of the resources in  
405 comparison to those in even-sized forests. On the contrary, planting and thinning  
406 regimes promoting even-sized stands (Mäkinen and Isomäki 2004, Bergh et al. 2014)  
407 lead to more regular spatial patterns when trees with similar resource demands compete  
408 strongly. Therefore, the influence of forest management practices on the spatial pattern  
409 of trees is straightforward, although it is expected that management signal fades  
410 throughout time as anthropogenic influence ceases (Rozas et al. 2009). In line with  
411 other studies, our work showed evidence of the importance of its consideration in  
412 spatial studies of plant communities for predicting ecosystem functionality (Rozas and  
413 Prieto 2000, Wolf 2005). In a similar way, our analyses also confirmed the existence of  
414 region-specific differences in the spatial pattern of trees among the studied forests  
415 (Figure 3), but demonstrated that the effect of species richness was the same for all of  
416 them, independently of forest type, its species composition and management history  
417 (Table 1, Table A6).

418

## 419 **CONCLUSIONS**

420 Our study has demonstrated that species richness shapes the spatial pattern of  
421 plant communities, partly mediated through an increase in the number of resource use  
422 strategies. Our results showed an increase in tree aggregation with increasing species  
423 richness that prevailed along the entire European bioclimatic gradient. In other words,  
424 tree species richness had a similar effect on the spatial distribution of individual trees

425 from boreal to Mediterranean forests. This finding points out to a neglected  
426 macroecological pattern in ecological research. Overall, our study provides empirical  
427 evidence of species richness is a relevant forest attribute that affects community  
428 structure and functioning given that certain key ecosystem processes (e.g. recruitment or  
429 seed dispersal) are strongly affected by tree spatial distribution. The knowledge gained  
430 through this study can help to formulate forest management guidelines supporting the  
431 maintainance and promotion of mixed forests and their ensuing ecosystem services and  
432 functions in the future.

433

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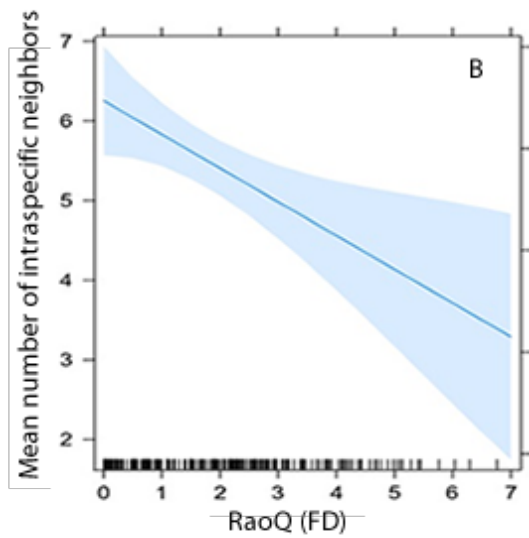
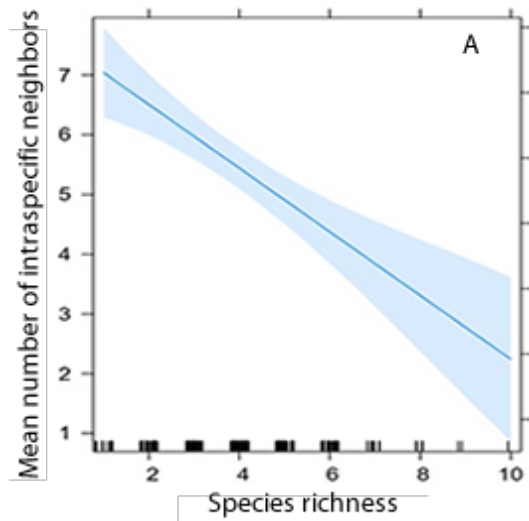
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**Table 1.** Summary table of the set of competing linear models ( $\Delta AICc < 2$ ) selecting by model selection method. Effect of species richness, functional diversity, the median value of tree sizes measured as basal area (BA\_median), stand structure (used as a proxy of the legacy of past management practices for each stand) and forest type on the spatial pattern of the forest stands ( $DR_F$ )  $DR_F$ : deviation from null model (complete spatial randomness or random labelling) estimated with Ripley’s  $K(r)$  function, nearest-

neighbour distance distribution  $G(r)$  function and mark correlation function  $k_{mm}(r)$ . Fine scale: differences estimated for the range between  $r_0 = 0.0$  and  $r_{max} = 3.5$  m. Medium scale: differences estimated for the range between  $r_0 = 0.0$  and  $r_{max} = 7.5$  m. In brackets is the relative weight of each predictor within the set of competing models, with its sign positive (+) or negative (-) for continuous variables. Df: degrees of freedom of the optimum model, AICc = average Akaike Information Criteria for limited sample sizes (AICc) of all competing models. Weight: mean Akaike weights can be interpreted as the mean probability that model is the best model for the observed data among all candidate set of models.  $R^2$ : coefficient of determination for the optimum model.

| Predictors                       | $DR_K$   |          | $DR_G$   |          | $DR_{K_{mm}}$ |          |
|----------------------------------|----------|----------|----------|----------|---------------|----------|
|                                  | Medium   | Fine     | Medium   | Fine     | Medium        | Fine     |
| Species Richness                 | + (0.19) | + (0.5)  | + (0.46) | + (0.51) | + (0.27)      | + (0.14) |
| Functional Diversity             |          | + (0.17) | + (0.46) | + (0.15) | + (0.23)      | + (0.38) |
| BA_median                        | - (1)    | - (1)    | - (1)    | - (1)    | n.i           | n.i      |
| Stand structure                  | (0.71)   | (0.86)   |          | (0.84)   | (0.84)        | (0.69)   |
| Forest type                      | (1)      | (1)      | (1)      | (1)      | (1)           | (1)      |
| Species richness*Forest type     |          |          |          | + (0.12) |               |          |
| Species richness*Stand structure |          |          |          |          |               |          |
| <i>No. models (AICc &lt; 2)</i>  | 4        | 3        | 4        | 5        | 4             | 5        |
| <i>Df</i>                        | 10       | 11       | 9        | 10       | 9             | 9        |
| <i>AICc</i>                      | 2665.3   | 2350.2   | 1981.1   | 1855.5   | 1194.2        | 2289.3   |
| <i>Weight</i>                    | 0.333    | 0.25     | 0.25     | 0.20     | 0.25          | 0.20     |
| $R^2$                            | 0.53     | 0.45     | 0.37     | 0.5      | 0.12          | 0.10     |

622 **Figure 1.** Results from the linear model testing the effect of species richness and  
623 functional diversity of the community on the mean number of intraspecific neighbors,  
624 calculated for each species within 7.5 m of radius around each individual in the spatial  
625 pattern.



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633 **Figure 2.** A-D) Changes in the statistics  $DR_K$  (K-Ripley) and  $DR_G$  (nearest-neighbor)  
 634 quantifying the net deviation of the observed spatial pattern from a random spatial  
 635 pattern at medium (0-7.5m) and fine scale (0-3.5m) with increasing species richness and  
 636 functional diversity of the community. E) Changes in the statistic  $DR_{k_{mm}}$  quantifying the

637 net deviation of the observed pattern of basal area distribution from a random labelling  
638 null model with increasing functional diversity.

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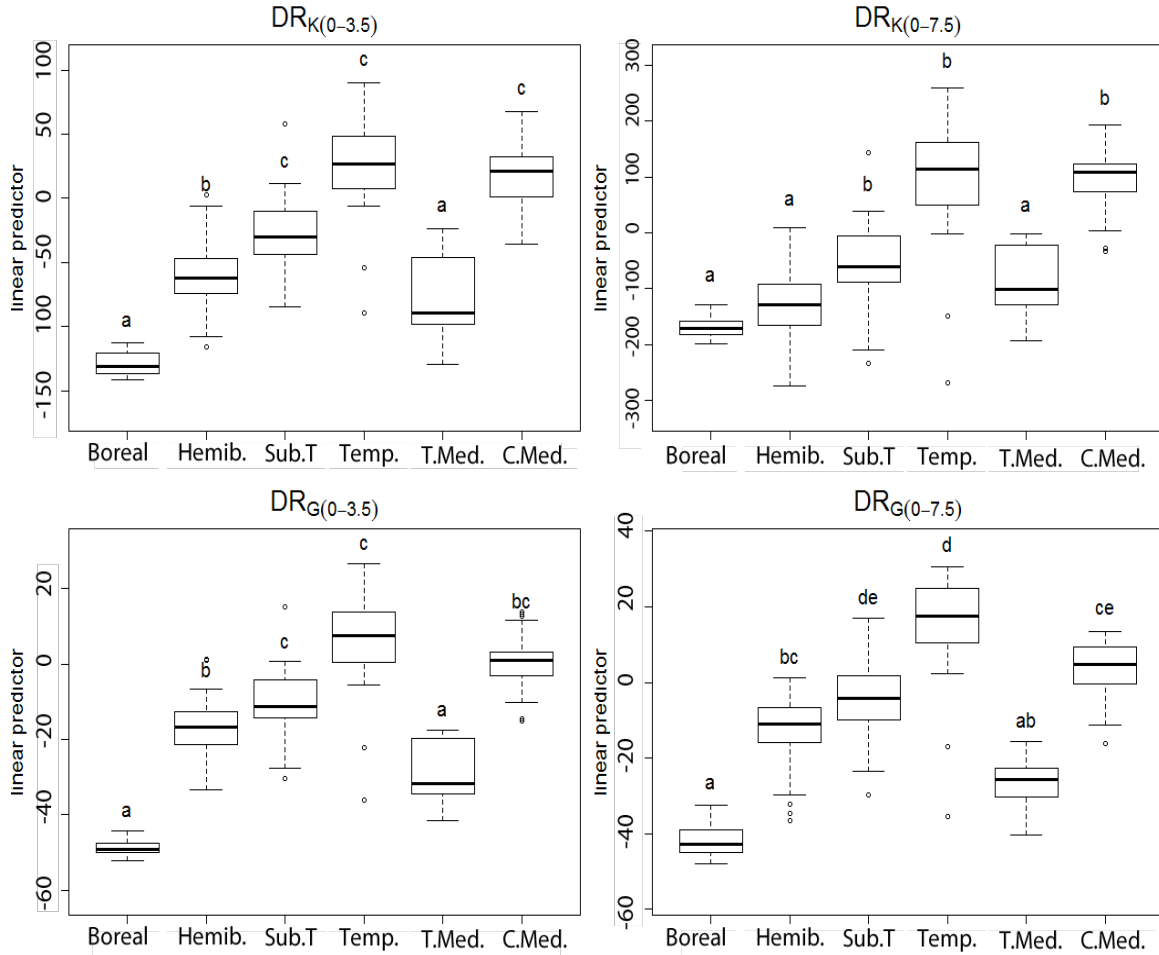
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658 **Figure 3.** Statistics  $DR_K$  (K-Ripley) and  $DR_G$  (nearest-neighbor) quantifying the net  
659 deviation of the observed spatial pattern from a random spatial pattern at two different  
660 scales [Fine:0-3.5m and medium: 0-7.5m] for each forest type. Letters indicate groups  
661 of forest types without significant differences in spatial pattern (Results of Tukey's

662 posthoc-tests). Abbreviations of forest types are Hemib-. (hemiboreal), Sub-. T. (sub-  
 663 continental temperate), Temp. (temperate), T. Medit. (temperate Mediteranean) and C.  
 664 Medit. (continental Mediterranean).



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671 **Supporting information**

672 Appendix A: Supplementary description of the study forests and additional analyses.

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## Appendix A.

**Table A1.** Description of the six different forest types of the study, including their location, the whole range of canopy species with a diameter at height breast > 7.5 cm, species richness range and the number of plots selected in each forest type.

| Forest type               | Location                         | Coordinate         | Canopy species (DBH ≥ 7.5 cm)  | Dominant canopy trees (>90% plot basal area)  | Species richness range | No. of plots |
|---------------------------|----------------------------------|--------------------|--|---|------------------------|--------------|
| Boreal                    | North Karelia region (Finland)   | (62.6° N, 29.9° E) | <i>Alnus</i> sp., <i>Betula pendula</i> , <i>Betula pubescens</i> , <i>Picea abies</i> , <i>Pinus sylvestris</i> , <i>Populus tremula</i> , <i>Salix caprea</i> , <i>Sorbus aucuparia</i>  | <i>Betula</i> sp., <i>Picea abies</i> , <i>Pinus sylvestris</i> ,   | 1-7                    | 28           |
| Hemiboreal                | Bialowieza Forest (Poland)       | (52.7° N, 23.9° E) | <i>Acer pseudoplatanus</i> , <i>Acer platanoides</i> , <i>B. pendula</i> , <i>Carpinus betulus</i> , <i>Corylus avellana</i> , <i>Fagus sylvatica</i> , <i>Fraxinus excelsior</i> , <i>P. abies</i> , <i>P. sylvestris</i> , <i>P. tremula</i> , <i>Quercus robur</i> , <i>Sorbus aucuparia</i> , <i>Tilia cordata</i> .   | <i>B. pendula</i> , <i>Carpinus betulus</i> , <i>P. abies</i> , <i>P. sylvestris</i> , <i>Quercus robur</i>           | 2-6                    | 43           |
| Sub-continental temperate | Carpathian Mountains (Romania)   | (47.6° N, 25.3° E) | <i>Abies alba</i> , <i>A. pseudoplatanus</i> , <i>Alnus</i> sp., <i>Betula</i> sp., <i>C. betulus</i> , <i>F. sylvatica</i> , <i>F. excelsior</i> , <i>P. abies</i> , <i>P. tremula</i> , <i>Ulmus minor</i>   | <i>Abies alba</i> , <i>A. pseudoplatanus</i> , <i>F. sylvatica</i> , <i>P. abies</i>                                  | 1-6                    | 28           |
| Temperate                 | Hainich National Park (Germany)  | (51.5° N, 10.2° E) | <i>Acer campestre</i> , <i>Acer platanoides</i> , <i>A. pseudoplatanus</i> , <i>Alnus glutinosa</i> , <i>Alnus incana</i> , <i>B. pendula</i> , <i>C. betulus</i> , <i>Crataegus</i> sp., <i>F. sylvatica</i> , <i>F. excelsior</i> , <i>P. abies</i> , <i>P. sylvestris</i> , <i>Prunus avium</i> , <i>Q. petraea</i> , <i>Q. robur</i> , <i>Quercus rubra</i> , <i>S. caprea</i> , <i>Sorbus torminalis</i> , <i>Tilia cordata</i> , <i>Tilia platyphyllos</i> , <i>Ulmus glabra</i>   | <i>A. pseudoplatanus</i> , <i>F. sylvatica</i> , <i>F. excelsior</i> , <i>P. abies</i> , <i>Q. petraea</i>            | 1-7                    | 38           |
| Temperate Mediterranean   | Southern Central Tuscany (Italy) | (43° N, 11° E)     | <i>A. campestre</i> , <i>Acer monspessulanum</i> , <i>Arbutus unedo</i> , <i>C. betulus</i> , <i>Castanea sativa</i> , <i>Chamaecyparis lawsoniana</i> , <i>Corylus avellana</i> , <i>F. sylvatica</i> , <i>Fraxinus ornus</i> , <i>Ilex aquifolium</i> , <i>Ostrya carpinifolia</i> , <i>P. tremula</i> , <i>P. avium</i> , <i>Pseudotsuga menziesii</i> , <i>Quercus cerris</i> , <i>Quercus crenata</i> , <i>Quercus ilex</i> , <i>Q. petraea</i> , <i>Quercus pubescens</i> , <i>Sorbus domestica</i> , <i>S. torminalis</i> , <i>T. cordata</i> | <i>Castanea sativa</i> , <i>Ostrya carpinifolia</i> , <i>Quercus cerris</i> , <i>Quercus ilex</i> , <i>Q. petraea</i> | 1-10                   | 36           |
| Continental Mediterranean | Alto Tajo Natural Park (Spain)   | (40.7° N, -1.9° E) | <i>Buxus sempervirens</i> , <i>Crataegus</i> sp., <i>Juniperus communis</i> , <i>Juniperus oxycedrus</i> , <i>Juniperus phoenicia</i> , <i>Juniperus</i> sp., <i>Juniperus thurifera</i> , <i>Pinus nigra</i> , <i>P. sylvestris</i> , <i>Quercus faginea</i> , <i>Q. ilex</i> , <i>Viburnum</i> sp.   | <i>Pinus nigra</i> , <i>P. sylvestris</i> , <i>Quercus faginea</i> , <i>Q. ilex</i>                                   | 1-7                    | 36           |



**Table A3.** Mean trait values used for calculating functional diversity indexes. Mean values obtained from global databases: TRY (Kattge et al. 2011), LEDA (Kleyer et al. 2008), KEW (“Royal Botanic Gardens Kew.” 2019), BioFlor (Kühn et al. 2004) and literature (e.g. shade tolerance trait values from Niinemets and Valladares (2006)). MH: maximum height (m). Sm: seed mass (g). SLA: specific leaf area (mm<sup>2</sup>/mg). WD: wood density (g/cm<sup>3</sup>). ST: shade tolerance ranging from 0 (no tolerance) to 5 (maximal tolerance).

| Species             | MH    | SM   | SLA   | WD   | ST   | Forest type |
|---------------------|-------|------|-------|------|------|-------------|
| Alnus_incana        | 11.80 | 0.00 | 17.34 | 0.55 | 2.30 | Boreal      |
| Betula_pendula      | 26.20 | 0.00 | 14.28 | 0.56 | 2.03 | Boreal      |
| Betula_pubescens    | 21.90 | 0.00 | 14.39 | 0.65 | 1.85 | Boreal      |
| Picea_abies         | 26.00 | 0.01 | 3.01  | 0.46 | 4.45 | Boreal      |
| Pinus_sylvestris    | 25.60 | 0.01 | 2.86  | 0.47 | 1.67 | Boreal      |
| Populus_tremula     | 18.80 | 0.00 | 15.33 | 0.45 | 2.22 | Boreal      |
| Salix_caprea        | 14.50 | 0.00 | 14.40 | 0.45 | 2.16 | Boreal      |
| Sorbus_aucuparia    | 8.90  | 0.00 | 13.90 | 0.70 | 2.73 | Boreal      |
| Acer_campestre      | 23.20 | 0.11 | 13.80 | 0.65 | 3.18 | Temperate   |
| Acer_platanoides    | 31.30 | 0.13 | 18.30 | 0.65 | 4.20 | Temperate   |
| Acer_pseudoplatanus | 35.20 | 0.10 | 22.18 | 0.55 | 3.73 | Temperate   |
| Alnus_glutinosa     | 22.80 | 0.00 | 14.58 | 0.55 | 2.71 | Temperate   |
| Alnus_incana        | 10.50 | 0.00 | 20.11 | 0.55 | 2.30 | Temperate   |
| Betula_pendula      | 26.60 | 0.00 | 13.66 | 0.54 | 2.03 | Temperate   |
| Carpinus_betulus    | 33.00 | 0.05 | 25.90 | 0.75 | 3.97 | Temperate   |
| Crataegus_monogyna  | 6.90  | 0.10 | 11.70 | 0.57 | 1.93 | Temperate   |
| Fagus_sylvatica     | 39.10 | 0.25 | 26.68 | 0.60 | 4.56 | Temperate   |
| Fraxinus_excelsior  | 42.40 | 0.07 | 13.92 | 0.65 | 2.66 | Temperate   |
| Picea_abies         | 36.40 | 0.01 | 4.25  | 0.32 | 4.45 | Temperate   |
| Pinus_sylvestris    | 27.10 | 0.01 | 3.78  | 0.48 | 1.67 | Temperate   |
| Prunus_avium        | 16.10 | 0.19 | 10.10 | 0.55 | 3.33 | Temperate   |
| Quercus_petraea     | 37.80 | 0.99 | 13.63 | 0.59 | 2.73 | Temperate   |
| Quercus_robur       | 35.10 | 3.36 | 14.67 | 0.65 | 2.45 | Temperate   |
| Quercus_rubra       | 34.30 | 3.69 | 16.00 | 0.42 | 2.75 | Temperate   |
| Salix_caprea        | 17.70 | 0.00 | 14.40 | 0.45 | 2.16 | Temperate   |
| Sorbus_torminalis   | 21.30 | 0.03 | 35.73 | 0.75 | 3.38 | Temperate   |
| Tilia_cordata       | 27.40 | 0.04 | 27.17 | 0.45 | 4.18 | Temperate   |
| Tilia_platyphyllos  | 26.20 | 0.15 | 26.99 | 0.45 | 4.00 | Temperate   |
| Ulmus_glabra        | 27.40 | 0.01 | 28.13 | 0.65 | 3.53 | Temperate   |
| Acer_platanoides    | 27.90 | 0.13 | 18.30 | 0.65 | 4.20 | Hemiboreal  |
| Acer_pseudoplatanus | 11.60 | 0.10 | 16.17 | 0.55 | 3.73 | Hemiboreal  |
| Betula_pendula      | 43.30 | 0.00 | 15.18 | 0.54 | 2.03 | Hemiboreal  |
| Carpinus_betulus    | 33.80 | 0.05 | 25.90 | 0.75 | 3.97 | Hemiboreal  |
| Corylus_avellana    | 17.30 | 0.81 | 22.66 | 0.49 | 3.53 | Hemiboreal  |
| Fagus_sylvatica     | 22.50 | 0.25 | 22.19 | 0.60 | 4.56 | Hemiboreal  |
| Fraxinus_excelsior  | 34.10 | 0.07 | 13.92 | 0.65 | 2.66 | Hemiboreal  |
| Picea_abies         | 40.20 | 0.01 | 4.25  | 0.32 | 4.45 | Hemiboreal  |
| Pinus_sylvestris    | 41.70 | 0.01 | 3.53  | 0.48 | 1.67 | Hemiboreal  |

|                          |       |      |       |      |      |                           |
|--------------------------|-------|------|-------|------|------|---------------------------|
| Populus_tremula          | 35.60 | 0.00 | 15.33 | 0.45 | 2.22 | Hemiboreal                |
| Quercus_robur            | 42.50 | 3.36 | 14.67 | 0.65 | 2.45 | Hemiboreal                |
| Sorbus_aucuparia         | 11.20 | 0.00 | 13.90 | 0.70 | 2.73 | Hemiboreal                |
| Tilia_platyphyllos       | 26.80 | 0.09 | 27.08 | 0.45 | 4.00 | Hemiboreal                |
| Abies_alba               | 43.60 | 0.07 | 4.78  | 0.45 | 4.60 | Subcontinental temperate  |
| Acer_pseudoplatanus      | 39.70 | 0.10 | 12.67 | 0.55 | 3.73 | Subcontinental temperate  |
| Alnus_glutinosa          | 22.90 | 0.00 | 17.34 | 0.55 | 2.30 | Subcontinental temperate  |
| Betula_pendula           | 18.20 | 0.00 | 14.34 | 0.53 | 2.03 | Subcontinental temperate  |
| Carpinus_betulus         | 20.70 | 0.05 | 25.90 | 0.75 | 3.97 | Subcontinental temperate  |
| Fagus_sylvatica          | 42.80 | 0.25 | 19.35 | 0.58 | 4.56 | Subcontinental temperate  |
| Fraxinus_excelsior       | 32.00 | 0.07 | 13.92 | 0.65 | 2.66 | Subcontinental temperate  |
| Picea_abies              | 45.50 | 0.01 | 4.35  | 0.36 | 4.45 | Subcontinental temperate  |
| Populus_tremula          | 27.70 | 0.00 | 15.33 | 0.45 | 2.22 | Subcontinental temperate  |
| Ulmus_minor              | 31.30 | 0.01 | 26.07 | 0.65 | 1.20 | Subcontinental temperate  |
| Buxus_sempervirens       | 3.20  | 0.01 | 7.03  | 0.21 | 4.05 | Continental mediterranean |
| Crataegus_monogyna       | 3.90  | 0.10 | 11.70 | 0.46 | 1.93 | Continental mediterranean |
| Juniperus_communis       | 4.50  | 0.03 | 6.28  | 0.65 | 1.71 | Continental mediterranean |
| Juniperus_oxycedrus      | 5.50  | 0.29 | 5.84  | 0.55 | 1.67 | Continental mediterranean |
| Juniperus_phoenicia      | 4.50  | 0.02 | 6.06  | 0.55 | 1.84 | Continental mediterranean |
| Juniperus_thurifera      | 8.10  | 0.04 | 5.95  | 0.53 | 1.68 | Continental mediterranean |
| Pinus_nigra              | 20.70 | 0.02 | 3.62  | 0.42 | 2.10 | Continental mediterranean |
| Pinus_sylvestris         | 23.50 | 0.01 | 2.89  | 0.43 | 1.67 | Continental mediterranean |
| Quercus_faginea          | 16.80 | 1.87 | 11.87 | 0.59 | 3.13 | Continental mediterranean |
| Quercus_ilex             | 11.50 | 2.31 | 4.36  | 0.82 | 3.02 | Continental mediterranean |
| Viburnum_opulus          | 5.70  | 0.03 | 16.75 | 0.40 | 2.66 | Continental mediterranean |
| Acer_campestre           | 9.70  | 0.11 | 13.11 | 0.65 | 3.18 | Mediterranean temperate   |
| Acer_monspessulanum      | 11.90 | 0.12 | 12.24 | 0.61 | 2.66 | Mediterranean temperate   |
| Arbutus_unedo            | 14.90 | 0.00 | 8.19  | 0.29 | 2.66 | Mediterranean temperate   |
| Carpinus_betulus         | 20.10 | 0.05 | 27.42 | 0.75 | 3.97 | Mediterranean temperate   |
| Castanea_sativa          | 24.10 | 7.65 | 14.70 | 0.50 | 3.15 | Mediterranean temperate   |
| Chamaecyparis_lawsoniana | 13.40 | 0.00 | 7.17  | 0.45 | 3.67 | Mediterranean temperate   |
| Corylus_avellana         | 16.60 | 0.81 | 32.13 | 0.49 | 3.53 | Mediterranean temperate   |
| Fagus_sylvatica          | 12.20 | 0.25 | 22.10 | 0.66 | 4.56 | Mediterranean temperate   |
| Fraxinus_ornus           | 25.30 | 0.04 | 17.50 | 0.20 | 3.02 | Mediterranean temperate   |
| Ilex_aquifolium          | 15.00 | 0.03 | 6.85  | 0.41 | 3.86 | Mediterranean temperate   |
| Ostrya_carpinifolia      | 27.50 | 0.01 | 25.50 | 0.77 | 3.94 | Mediterranean temperate   |
| Populus_tremula          | 21.70 | 0.00 | 15.33 | 0.45 | 2.22 | Mediterranean temperate   |
| Prunus_aviium            | 10.60 | 0.19 | 10.10 | 0.55 | 3.33 | Mediterranean temperate   |
| Pseudotsuga_menziesii    | 17.80 | 0.02 | 7.16  | 0.43 | 2.78 | Mediterranean temperate   |
| Quercus_cerris           | 33.70 | 4.21 | 14.80 | 0.70 | 2.55 | Mediterranean temperate   |
| Quercus_crenata          | 15.20 | 4.21 | 10.00 | 0.70 | 2.55 | Mediterranean temperate   |
| Quercus_ilex             | 26.00 | 2.31 | 4.36  | 0.82 | 3.02 | Mediterranean temperate   |
| Quercus_petraea          | 29.30 | 0.99 | 13.42 | 0.66 | 2.73 | Mediterranean temperate   |
| Quercus_pubescens        | 10.90 | 0.63 | 14.48 | 0.64 | 2.31 | Mediterranean temperate   |
| Sorbus_domestica         | 17.10 | 0.03 | 9.90  | 0.84 | 3.53 | Mediterranean temperate   |
| Sorbus_torminalis        | 21.00 | 0.03 | 35.73 | 0.75 | 3.38 | Mediterranean temperate   |

|               |       |      |       |      |      |                         |
|---------------|-------|------|-------|------|------|-------------------------|
| Tilia_cordata | 10.10 | 0.04 | 27.17 | 0.45 | 4.18 | Mediterranean temperate |
|---------------|-------|------|-------|------|------|-------------------------|

**Table A4.** Summary table of the fitted generalized linear model assessing the effect of species richness, functional diversity and forest type on the mean number of intraspecific neighbors calculated for all species in all forests within a radius of 7.5 m. Data shown are the degrees of freedom (df), the LR test based on Chis-square statistic and the statistical significance level of model using Type II ANOVA, the estimated coefficients for species richness (Coef.) and the coefficient of determination of the model  $R^2$ .

|                        | <b>d.f.</b> | <b>Coef.</b> | <b>LR Chisq</b> | <b>p-value</b> |
|------------------------|-------------|--------------|-----------------|----------------|
| Intercept              | -           | 2.35         | -               | -              |
| Species richness       | 1           | -0.09        | 21.731          | ***            |
| Functional diversity   | 1           | -0.06        | 7.864           | **             |
| Forest type            | 5           | -            | 35.625          | ***            |
| Richness * Forest type | 5           | -            | 5.720           | n.s            |
| $R^2$                  |             | 0.39         |                 |                |

**Table A5.** Results from the generalized linear models testing the effect of the species richness (SR) on the mean number of intraspecific neighbors calculated for pooling all species from all forests at different radius (from 3 m to 15 m). Bold figures highlight the ‘fine’ (3.5 m) and ‘medium’ (7.5 m) scale used in our study.

| <b>r</b>   | <b>SR</b>        | <b>LR Chisq</b> | <b>Pr (&gt;Chisq)</b> |
|------------|------------------|-----------------|-----------------------|
| 3.0        | -0.010034        | 0.428           | 0.51300               |
| <b>3.5</b> | <b>-0.031876</b> | <b>3.826</b>    | <b>0.05047</b>        |
| 4.0        | -0.042448        | 6.267           | 0.01230               |
| 4.5        | -0.053953        | 9.329           | 0.00226               |
| 5.0        | -0.061973        | 11.423          | 0.00073               |
| 5.5        | -0.075316        | 15.989          | 0.00006               |
| 6.0        | -0.085646        | 20.573          | 0.00001               |
| 6.5        | -0.094433        | 23.852          | 0.00000               |
| 7.0        | -0.102780        | 27.791          | 0.00000               |
| <b>7.5</b> | <b>-0.108526</b> | <b>30.700</b>   | <b>0.00000</b>        |
| 8.0        | -0.114631        | 33.345          | 0.00000               |
| 8.5        | -0.121728        | 35.789          | 0.00000               |
| 9.0        | -0.128407        | 39.013          | 0.00000               |
| 9.5        | -0.131783        | 40.260          | 0.00000               |
| 10.0       | -0.136811        | 41.488          | 0.00000               |
| 10.5       | -0.139874        | 41.638          | 0.00000               |
| 11.0       | -0.143413        | 43.834          | 0.00000               |
| 11.5       | -0.146331        | 45.587          | 0.00000               |
| 12.0       | -0.149813        | 47.101          | 0.00000               |
| 12.5       | -0.153164        | 48.726          | 0.00000               |
| 13.0       | -0.154826        | 49.406          | 0.00000               |
| 13.5       | -0.156151        | 49.443          | 0.00000               |
| 14.0       | -0.160449        | 51.936          | 0.00000               |
| 14.5       | -0.162660        | 53.277          | 0.00000               |
| 15.0       | -0.163498        | 53.326          | 0.00000               |

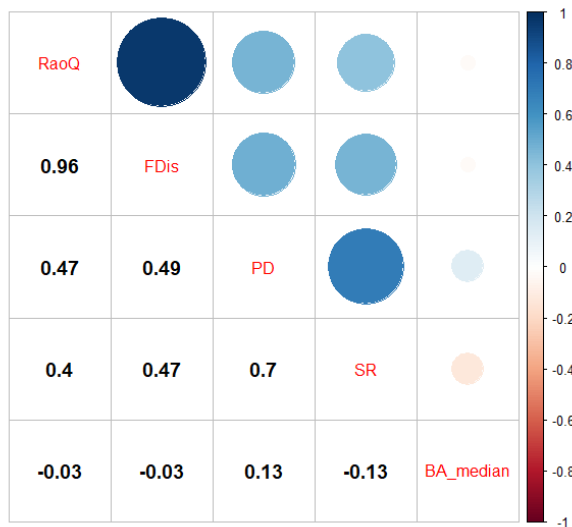
**Table A6.** Optimum model and set of competing models ( $\Delta AICc < 2$ ) testing the effect of species richness (SR), functional diversity (FD), the median value of the tree sizes measured as basal area (BAm<sub>ed</sub>), stand structure (SS: used as a proxy of the legacy of past management practices in each forest stand) and forest type (FT) on observed spatial pattern of trees (DR<sub>K</sub> and DR<sub>G</sub>) and statistic  $DR_{k_{mm}}$  quantifying the spatial correlation in tree sizes. Df: degree of freedom, AICc = Akaike Information Criteria for limited sample sizes (AICc),  $\Delta AICc$ : difference in AICc between models and the optimum. Weight: Akaike weights can be interpreted as the probability that model is the best model for the observed data, given the candidate set of models. R<sup>2</sup>: coefficient of determination for the optimum model. (+): predictor included in the model.

|                                    | Intercept | SR     | FD     | BAm <sub>ed</sub> | SS | FT | SR*SS | SR*FT | Df | AICc   | $\Delta AICc$ | Weight | R <sup>2</sup> |
|------------------------------------|-----------|--------|--------|-------------------|----|----|-------|-------|----|--------|---------------|--------|----------------|
| <i>Medium scale</i>                |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| <b>DR<sub>K</sub></b>              |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| Model 1                            | -33.13    |        |        | -2393             | +  | +  |       |       | 10 | 2664.3 | 0.00          | 0.516  | 0.53           |
| Model 2                            | -92.11    |        |        | -2685             |    | +  |       |       | 8  | 2665.5 | 1.15          | 0.289  |                |
| Model 3                            | -50.22    | +3.52  |        | -2377             | +  | +  |       |       | 11 | 2666.3 | 1.95          | 0.195  |                |
| <b>DR<sub>G</sub></b>              |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| Model 1                            | -34.49    |        | +2.30  | -334.6            |    | +  |       |       | 9  | 1980.7 | 0.00          | 0.298  | 0.37           |
| Model 2                            | -38.97    | +2.01  |        | -335.0            |    | +  |       |       | 9  | 1980.7 | 0.01          | 0.297  |                |
| Model 3                            | -31.77    |        |        | -350.3            |    | +  |       |       | 8  | 1981.1 | 0.41          | 0.243  |                |
| Model 4                            | -38.57    | +1.38  | +1.58  | -329.0            |    | +  |       |       | 10 | 1982.0 | 1.24          | 0.161  |                |
| <b>DR<sub>k<sub>mm</sub></sub></b> |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| Model 1                            | -109.80   |        |        | ni                | +  | +  |       |       | 9  | 2392.9 | 0.00          | 0.341  | 0.12           |
| Model 2                            | -131.70   | +4.56  |        | ni                | +  | +  |       |       | 10 | 2393.3 | 0.46          | 0.271  |                |
| Model 3                            | -118.30   |        | +4.56  | ni                | +  | +  |       |       | 10 | 2393.7 | 0.82          | 0.227  |                |
| Model 4                            | -69.94    |        |        | ni                |    | +  |       |       | 7  | 2394.4 | 1.50          | 0.161  |                |
| <i>Fine scale</i>                  |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| <b>DR<sub>K</sub></b>              |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| Model 1                            | -87.05    | +4.76  |        | -790.0            | +  | +  |       |       | 11 | 2349.3 | 0.00          | 0.354  | 0.45           |
| Model 2                            | -63.92    |        |        | -811.9            | +  | +  |       |       | 10 | 2349.4 | 0.12          | 0.333  |                |
| Model 3                            | -70.30    |        | +3.27  | -789.8            | +  | +  |       |       | 11 | 2350.8 | 1.48          | 0.169  |                |
| Model 4                            | -124.30   | +6.40  |        | -923.0            |    | +  |       |       | 9  | 2351.1 | 1.80          | 0.144  |                |
| <b>DR<sub>G</sub></b>              |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| Model 1                            | -29.42    |        |        | -274.08           | +  | +  |       |       | 10 | 1854.5 | 0.00          | 0.222  | 0.50           |
| Model 2                            | -34.89    | + 1.13 |        | -268.89           | +  | +  |       |       | 11 | 1855.3 | 0.82          | 0.147  |                |
| Model 3                            | -45.41    | + 1.59 |        | -305.09           |    | +  |       |       | 9  | 1855.9 | 1.46          | 0.107  |                |
| Model 4                            | -31.13    |        | + 0.87 | -268.18           | +  | +  |       |       | 11 | 1856.0 | 1.56          | 0.101  |                |
| Model 5                            | -42.79    | + 3.91 |        | -240.64           | +  | +  |       | +     | 16 | 1856.5 | 1.98          | 0.082  |                |
| <b>DR<sub>k<sub>mm</sub></sub></b> |           |        |        |                   |    |    |       |       |    |        |               |        |                |
| Model 1                            | -92.12    |        |        | ni                | +  | +  |       |       | 9  | 2288.5 | 0.00          | 0.277  | 0.10           |
| Model 2                            | -100.40   |        | +4.42  | ni                | +  | +  |       |       | 10 | 2288.5 | 0.04          | 0.271  |                |
| Model 3                            | -64.17    |        |        | ni                |    | +  |       |       | 7  | 2289.0 | 0.58          | 0.207  |                |
| Model 4                            | -103.80   | +2.42  |        | ni                | +  | +  |       |       | 10 | 2289.9 | 1.40          | 0.138  |                |
| Model 5                            | -66.89    |        | +2.748 | ni                |    | +  |       |       | 8  | 2290.3 | 1.89          | 0.108  |                |

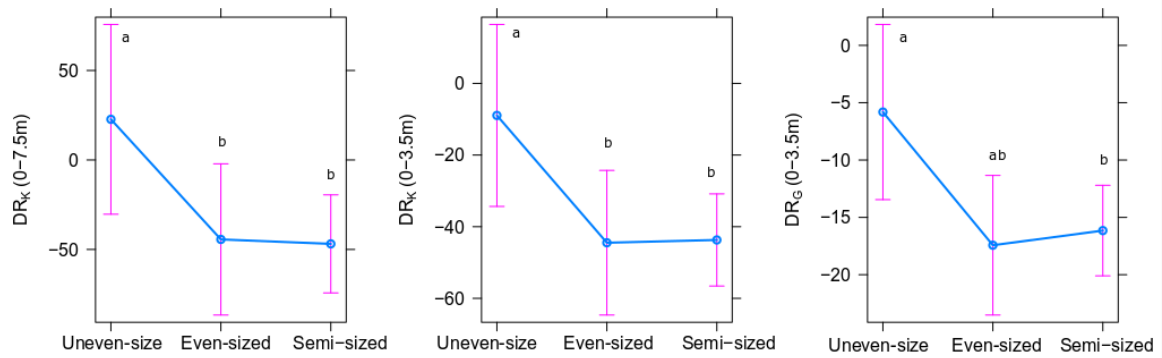


**Figure A1: Correlation structure of the predictors. Spearman's rank correlation of variables is shown. Positive and negative correlation is indicated in blue and red circles, respectively. RaoQ index: Rao's quadratic entropy as a measure of functional diversity. FDis: functional dispersion. PD: phylogenetic diversity. SR: species richness and BA\_median: median value of basal areas for each plot.**

**Con formato:** Fuente: (Predeterminado) Times New Roman, 12 pto, Negrita



**Figure A2.** Statistics of  $DR_K$  (K-Ripley) and  $DR_G$  (nearest-neighbor) quantifying the net deviation of the observed spatial pattern from a random spatial pattern at two different scales [Fine: 0-3.5 m and medium: 0-7.5 m] for each forest stand structure type (used as a proxy of the legacy of past management practices). Letters indicate forest structures without significant differences in spatial pattern (Results from Tukey's posthoc-tests). The graph  $DR_G$  at medium scale is not included as variable 'stand structure' was not selected in the best model (see Table A6).



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