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3 TITLE: Intraspecific variability in functional traits matters: Scots pine as a case of study¹

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15 The authors declare that the experiment comply with the current laws of the country in which the
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17 ABSTRACT

18 Introduction. Despite the fact that intraspecific trait variability is an important component of
19 species ecological plasticity and niche breadth its implications for community and functional
20 ecology have not been thoroughly explored.

21 Hypothesis/objective: We characterize the intraspecific functional trait variability of Scots pine
22 (*Pinus sylvestris*) in Catalonia (NE Spain), in order to: (1) compare it to the interspecific trait
23 variability of trees in the same region; (2) explore the relationships among functional traits and
24 between them and stand and climatic variables; and (3) study the role of functional trait variability
25 as a determinant of radial growth.

26 Methods. We considered five functional traits: wood density (WD), maximum tree height (H_{max}),
27 leaf nitrogen content (N_{mass}), specific leaf area (SLA) and leaf biomass-to-sapwood area ratio
28 ($B_L:A_S$). A unique dataset was obtained from the Ecological and Forest Inventory of Catalonia
29 (IEFC) including data from 406 plots.

30 Results. Intraspecific trait variation was substantial for all traits, with coefficients of variation
31 ranging between 8% for WD and 24% for $B_L:A_S$. In some cases, correlations among functional
32 traits differed from those reported across species (e.g., H_{max} and WD were positively related, SLA
33 and N_{mass} were uncorrelated). Our results show a hierarchy of effects in which stand age and
34 climate affect stand structure, which is the main source of variation for functional traits, which, in
35 turn, have a large effect on Scots pine radial growth. Overall, our model accounted for 47% of the
36 spatial variability in Scots pine radial growth.

37 Conclusion. Our study emphasizes the hierarchy of factors determining intraspecific variation in
38 functional traits in Scots pine, and their strong association to spatial variability in radial growth.

39 We claim that intraspecific trait variation is an important factor determining plant responses to

40 changes in climate and other environmental factors, and should be included in predictive models
41 of vegetation dynamics.

42 Key words: Forest structure, Functional traits, Growth, Intraspecific variability and *Pinus*
43 *sylvestris*.

Accepted manuscript

44 INTRODUCTION

45 One of the main goals of functional ecology is to relate the key functional traits that influence the
46 organism's performance (e.g., survival or growth) to population, community and ecosystem
47 processes (McGill *et al.* 2006; Westoby & Wright 2006). To this day, much effort has been
48 devoted to explore the correlations between plant traits, climatic conditions and fitness across
49 species (see Kattge *et al.* 2011 and Poorter *et al.* 2011 for a review), from which considerable
50 insight has emerged into general functional relationships and convergent evolution among
51 different taxa across growth forms, biomes or climatic regions (Reich *et al.* 1997; Wright *et al.*
52 2004). Interspecific studies using global datasets have found a close coordination among traits,
53 best exemplified by the leaf- (Wright *et al.* 2004) and wood economics spectra (Chave *et al.*
54 2009). These two spectra, describing global plant investment strategies, are thought to reflect a
55 mosaic of direct and indirect causal relationships among traits and have been found to be
56 decoupled from each other, at least in tropical trees (Baroloto *et al.* 2010).

57
58 The leaf economics spectrum, interpreted as the close coordination among leaf functional traits,
59 illustrates a classic continuum between species with fast return on investments of nutrients and dry
60 mass (high leaf nutrient concentrations, high rates of photosynthesis and respiration, short leaf life
61 span and low dry-mass investment per leaf area), to species with slow potential return, showing
62 opposite characteristics (Reich *et al.* 1997; Wright *et al.* 2004, 2005). On the other hand, the wood
63 economics spectrum has been described as a trade-off "triangle" opposing three key attributes of
64 wood: conductive efficiency, resistance to hydraulic failure and mechanical strength (Chave *et al.*
65 2009). This spectrum has been defined around one single trait: wood density (*WD*), which
66 integrates a substantial part of the variation in wood properties (Wright *et al.* 2010).

67

68 The relevance of functional traits arises from their potential impact on fitness, as it is generally
69 implied in their definition (Violle *et al.* 2007). However, our understanding of the relationships
70 among species-specific functional traits and plant demographic processes, such as growth or
71 mortality, has been quite limited and most of the evidence has been gathered in tropical
72 ecosystems (Poorter *et al.* 2008a, 2008b, 2010; but see Janse-Ten Klooster *et al.* 2007 and
73 Martínez-Vilalta *et al.* 2010 for studies on temperate and Mediterranean species, respectively).
74 Recent studies suggest that maximum plant height (H_{max}) and wood density (WD) are the traits
75 that best explain the variation in demographic rates across species. Tree height, defining
76 individual's capacity to intercept radiation, tends to be positively related to growth rate (Poorter *et*
77 *al.* 2008b; Martínez-Vilalta *et al.* 2010), but also involves costs in terms of construction and
78 maintenance of support and transport structures (Westoby *et al.* 2002; Mencuccini 2003). Wood
79 density is positively related to resistance to hydraulic failure (Hacke *et al.* 2001; Maherali *et al.*
80 2004) and survival, but negatively to radial growth rate (King *et al.* 2006a, 2006b; Poorter *et al.*
81 2008b; Martínez-Vilalta *et al.* 2010; Wright *et al.* 2010).

82
83 The fact that functional traits also vary widely within species has been recognized for a long time
84 (e.g., Clausen *et al.* 1948; Keddy 1992; Kleinschmit 1993) and explored by evolutionary
85 ecologists (Fox *et al.* 2001) and physiological ecologists (Lambers & Poorter 1992; Cordell *et al.*
86 1998; Diaz *et al.* 1998), but began only recently to be considered in studies of trait coordination
87 and community ecology. The use of average trait values to describe a given species is known to
88 hide much functional variation at two different ecological scales: within populations (Bolnick *et*
89 *al.* 2011) and across populations, particularly along environmental gradients (Albert *et al.* 2010a;
90 de Bello *et al.* 2010; Fajardo & Piper 2010; Hulshof & Swenson 2010). Besides the effects of
91 climate and resource availability, stand structure and development are also likely to be major

92 determinants of functional trait variability in trees, as they generate, and respond to, local
93 variations in climate and resource availability (e.g., Campetella *et al.* 2011). This aspect, however,
94 has received comparatively little attention in this context.

95
96 The growing interest in the intraspecific variability of plant functional traits can be explained by at
97 least two reasons. Firstly, despite the multiple tradeoffs described by interspecific studies, some
98 doubt emerges upon their persistence when accounting for intraspecific variability (Cianciaruso *et*
99 *al.* 2009; Albert *et al.* 2010b; Hulshof & Swenson 2010). Factors shaping trait coordination may
100 be different within and between species, which could result in dissimilarities between trait
101 relationships at these two levels, asking for prudence in the interpretation of such correlations as
102 true functional tradeoffs. Wright and Sutton-Grier (2012), for instance, found little support for the
103 leaf economics spectrum within local species pools in a controlled greenhouse experiment
104 examining the response of leaf traits of wetland species to environmental variability. Secondly,
105 not only the mean value, but also the overall variability (or plasticity) in functional traits is likely
106 to vary across species, with important implications for their response to changes in climate or
107 other environmental factors. Intraspecific trait variability defines the species' capacity to
108 maximize fitness along biotic and abiotic gradients and, ultimately, the breadth of its ecological
109 niche (Ackerly & Cornwell 2007; Cornwell *et al.* 2007; Martínez-Vilalta *et al.* 2009; Albert *et al.*
110 2010a). Functional trait variability within populations influences their ability to respond or evolve
111 in response to environmental changes (Nicotra *et al.* 2010). In this context, trait variability across
112 populations can be seen as an upper limit to the variability that could be realized within a given
113 population, and therefore could be used to constrain models in studies of vegetation responses to
114 directional environmental change (Wang *et al.* 2010; Benito Garzon *et al.* 2011; O'Neill & Night
115 2011).

116
117 Scots pine (*Pinus sylvestris*), with its extremely wide distribution from boreal regions to the
118 Mediterranean basin (Barbéro *et al.* 1998), is an ideal model for studies of intraspecific variability
119 of functional traits. In Europe there is a clear gradient between northern populations, mostly
120 limited by low temperatures (Hurme *et al.* 1997), and southern ones, where water availability
121 appears to be the critical ecological factor and records of drought-induced mortality are common
122 (Martínez-Vilalta & Pinol 2002; Bigler *et al.* 2006; Galiano *et al.* 2010). Several studies show, for
123 instance, that warmer conditions enhance Scots pine growth in northern latitudes or colder
124 populations, whereas they are detrimental in southern, Mediterranean areas (Martínez-Vilalta *et al.*
125 2008; Reich *et al.* 2008). Two main axes of variation have been defined that characterize
126 functional trait variability of Scots pine along wide climatic gradients. Firstly, needle lifespan
127 increases markedly and nutrient concentration in needles decreases with increasing latitude, a
128 pattern that has been linked to nutrient conservation (Oleksyn *et al.*, 2003). Secondly, there is
129 structural acclimation through modification of the leaf-to-sapwood area ratio ($A_L:A_S$), with lower
130 values in drier, southern sites (Palmroth *et al.* 1999; Mencuccini & Bonosi 2001; Martínez-Vilalta
131 *et al.* 2009). This pattern is consistent with the near isohydric behaviour of Scots pine to maintain
132 the integrity of the transpiration pathway (Irvine *et al.* 1998; Magnani *et al.* 2002; Zweifel *et al.*
133 2007; Poyatos *et al.* 2008) and with the lack of a strong physiological acclimatization to save
134 water through increased stomatal control (cf. Poyatos *et al.* 2007).

135
136 Here, we use a unique dataset compiled within the Ecological and Forest Inventory of Catalonia
137 (abbreviated IEFEC; Burriel *et al.* 2000-2004; <http://www.creaf.uab.es/ieffc/>) to study the variability
138 of key functional traits in Scots pine along a relatively wide environmental gradient. Specifically,
139 we hypothesized that (1) functional trait variability across Scots pine populations is not negligible,

140 and it is comparable in magnitude to interspecific trait variability of tree species found in the same
141 region; (2) intraspecific relationships among functional traits is not necessarily consistent with the
142 tradeoffs commonly reported across tree species, due to differences in the factors shaping trait
143 coordination within and between species; (3) spatial variability in functional traits is associated to
144 climatic differences but, also, to forest structural differences across sites; and (4) variability in
145 functional traits buffers tree response to climate or stand structure across sites, so that the direct
146 effects of climate and stand structure on radial growth are relatively small compared to the indirect
147 effects mediated by functional traits.

148

149 METHODS

150

151 Study area and species

152 The area covered by this study includes all the forested territory of Catalonia (1.2×10^6 ha), NE
153 Spain. The relief rises from sea level to more than 3,000 m a.s.l. in the Pyrenees, the main
154 mountain system, including both coastal and continental land areas (Fig.1). Catalonia's climate is
155 diverse mainly due to its physiographic complexity, with typical Mediterranean climate in most of
156 its coastal area, continental Mediterranean climate in the inner part and mountain to alpine
157 climates in the Pyrenees (Koppen's classification; Worldwide Bioclimatic Classification System
158 1996-2000). Vegetation types include Aleppo pinewoods, alpine pastures, deciduous woodlands,
159 Mediterranean maquis, non-Mediterranean coniferous woodlands and sclerophyllous woodlands
160 (Bolòs & Vigo 1984). The Iberian Peninsula constitutes the southwestern limit of Scots pine
161 distribution, with important populations in the Pyrenees and several smaller populations scattered
162 in southern and more arid locations (Castroviejo *et al.* 1986). Scots pine is the second most
163 abundant tree species in Catalonia (after *Pinus halepensis*), where it occurs naturally and currently

164 covers a total estimated area of 219,754 ha, distributed preferably on north-facing slopes between
165 800-1600 m a.s.l. Catalan populations of Scots pine are distributed across a wide range of climatic
166 conditions (mean annual temperature from 3.6 to 14.6°C and mean annual precipitation from 413-
167 1268 mm; Table 1). Spanish populations of Scots pine are known to be genetically different from
168 the populations of Northern Europe (Alia *et al.* 2001).

169

170 Data sources

171 The database of functional traits and growth of Scots pine is part of the Ecological and Forest
172 Inventory of Catalonia (IEFC), carried out by the Center for Ecological Research and Forestry
173 Applications (CREAF) between 1988 and 1998 (Burriel *et al.* 2000-2004;
174 <http://www.creaf.uab.es/iefc/>). This inventory sampled the whole forested area of Catalonia, NE
175 Spain. Plots were randomly selected within a grid including all forest areas for each county in
176 Catalonia. Plots were circular, had a radius of 10 m and were distributed with a density of one plot
177 per km². The sampling consisted in identifying and measuring all trees with diameter at breast
178 height (*DBH*) > 5 cm in each plot. An extended supplementary sampling was conducted on a
179 random subsample of 20% of the plots, carried out on one or two representative individuals of
180 each 5 cm diameter class of the dominant tree species in the plot. From each of these individuals,
181 stem wood cores and fully exposed branches of different sizes and order were sampled (N=1-11
182 per plot) and taken to the laboratory to determine wood density (*WD*), needle nutrient composition
183 and specific leaf area (*SLA*) (see methods below). Additionally, allometric relationships were used
184 to estimate the ratio of leaf biomass to sapwood area (*B_L:A_S*) at the tree level. Because of the
185 limited number of branches sampled per plot these relationships were calculated by combining
186 data from neighbouring plots (N=30-79). Since only one or few trees were sampled per plot, trait
187 variability within populations could not be characterized. In addition, low replication within plots

188 reduces the precision of our trait estimates at this level, although this limitation is contrasted by
 189 the relatively large amount of sampling plots covering the whole distribution of Scots pine in the
 190 study region.

191

192 Scots pine was dominant in 1,962 plots (18.4% of all sampled plots) in which it had an average
 193 density of 903 trees ha⁻¹, an average basal area of 21.6 m²ha⁻¹, an average canopy height of 13.1
 194 m, and an average tree age of 49 years (Burriel *et al.* 2000–2004). Since species were sampled
 195 proportionally to their abundance in each plot, and to make sure that our study included only those
 196 plots that were representative of Scots pine populations in Catalonia, we included in the analysis
 197 only those plots where Scots pine accounted for > 15% of the total tree basal area. Moreover, and
 198 since the inclusion of young (immature) stands could affect the conclusions of the study, we
 199 excluded all plots where stand age information was missing or where maximum Scots pine age
 200 was lower than 20 years, as Scots pine sexual maturity (measured as the presence of cones) is at c.
 201 15-20 years of age (Vilà-Cabrera *et al.* 2011a; 2014). This very conservative approach reduced the
 202 total number of plots covered in this study to 406, although not all variables were measured in all
 203 plots (see Table 1). In all cases, the main model results remained similar if all the analyses were
 204 conducted using all the plots (not shown).

205

206 To estimate radial tree growth, the absolute growth rate of the 5 years before sampling (ΔR_5) was
 207 measured by core extraction and tree ring analysis in 1-10 trees per plot. The basal area increment
 208 (BAI) was calculated from the individual tree DBH at the time of sampling and ΔR_5 as:

$$209 \quad BAI_{annual} = \pi(R^2 - (R - \Delta R_5)^2) / 5$$

210 where R corresponds to $DBH/2$.

211

212 On the basis of previous studies, we selected five traits (see Table 1 and Figure S1 in Supporting
213 Information) that cover the most relevant dimensions of leaf and the wood economics spectra as
214 well as the major axes of variation describing Scots pine acclimation along environmental
215 gradients (cf. Introduction section): maximum tree height (H_{max} , m), wood density (WD , g cm^{-3}),
216 specific leaf area (SLA , $\text{cm}^2 \text{mg}^{-1}$), nitrogen content of leaves (N_{mass} , % mass), and the ratio of leaf
217 biomass to sapwood area at the tree level ($B_L:A_S$, Mg m^{-2}). These traits are among the most widely
218 studied in functional ecology (e.g.; Westoby *et al.* 2002; Westoby & Wright 2006; Wright *et al.*
219 2007), thus facilitating comparisons between studies.

220 Individual values for all studied functional traits were obtained as follows (see the IEFEC webpage,
221 <http://www.creaf.uab.es/iefec/>, for additional technical details): (1) H_{max} , which was defined as the
222 height of the tallest tree in the plot. Tree height was measured with a clinometer for each tree
223 present in the plot. (2) WD , calculated as the ratio of dry weight to fresh wood volume, was
224 measured on one wood core per plot taken on the stem of a representative tree. Fresh volume was
225 established by measuring precisely the dimensions of the cores. Samples were then weighted to a
226 precision of 0.001 g after having been oven dried for 48 h at 75°C. Please note that we could not
227 use the more broadly used term basic specific gravity because wood was dried below 100°C. (3)
228 N_{mass} was measured on a dried and ground subsample of sunlit needles (Cyclotec Foss Tecator
229 1093-001 grinder, Foss Analytical, Hilleroed, Denmark) from one tree per plot, representing all
230 cohorts present in the stems proportionally to their abundance. Chemical analyses were carried out
231 at the Scientific-Technical Service of the University of Barcelona using an elemental analyzer
232 (C.E. Instruments, Wigan, UK). (4) SLA , calculated as the ratio of fresh leaf surface to dry weight,
233 was also obtained from the same needle samples as N_{mass} . One-sided, projected needle surface was
234 obtained measuring precisely the length and width of the needles. Needles were then weighted to a
235 precision of 0.001 g after having been oven dried for 48 h at 75°C. (5) Tree-level $B_L:A_S$ ratios were

236 obtained from independent estimates of leaf biomass and sapwood area. The ratio of leaf biomass
237 (or area) to sapwood area is considered as a key factor for characterizing the hydraulic architecture
238 of trees in general and Scots pine in particular (Zweifel *et al.* 2007; Martínez-Vilalta *et al.* 2009).
239 We had branch level values of $B_L:A_S$ for 1-2 trees per plot for some of the plots and had access to
240 the size distribution of the primary branches in all sampled trees (N=6-10 trees per plot). Thus, we
241 calculated mean tree-level $B_L:A_S$ ratios per plot. First, we estimated the leaf biomass (B_L) of each
242 sampled tree by summing the leaf biomass of its branches, obtained multiplying the basal area of
243 each primary branch by the corresponding branch-level $B_L:A_S$ ratio, which was obtained by
244 combining allometric data from neighboring plots. Then, the stem sapwood area (A_S) of each tree
245 was estimated from its sapwood depth at breast height (visually estimated from wood cores).
246 Finally, tree-level estimates of B_L were divided by their corresponding A_S and averaged per plot.

247
248 A set of six variables, also collected within the IEFEC framework, were selected to represent plot
249 characteristics, competition and forest structure: terrain slope (S , °), average diameter at breast
250 height of Scots pine (DBH , cm), total tree density ($Dens$, tree ha⁻¹), maximum age of Scots pine
251 trees in the plot (Age , year), total plot basal area (BA , m² ha⁻¹) and percentage basal area belonging
252 to Scots pine ($\%BA$, %). Soil characteristics were not included in the IEFEC database nor were they
253 available from other sources.

254
255 The climatic data for each studied plot were obtained from the Climatic Digital Atlas of Catalonia
256 (CDAC). We included 6 climate variables: mean annual precipitation (P , mm), mean annual
257 temperature (T , °C), thermal amplitude (Amp , °C), annual potential evapotranspiration (PET , mm),
258 the ratio of annual precipitation to potential evapotranspiration ($P:PET$), and the ratio of summer
259 (June–August) precipitation to potential evapotranspiration ($P:PET_{sum}$).

260

261 Data analysis

262 We compared the ranges and coefficients of variation of the distributions of the five studied traits
263 (H_{max} , WD , SLA , N_{mass} , $B_L:A_S$) for Scots pine with those of the same traits measured across species
264 for the 44 most abundant forest trees in Peninsular Spain. The data on interspecific variability was
265 also obtained from the IEF dataset, either specifically for this study ($B_L:A_S$) or taken from
266 Martínez-Vilalta *et al.* (2010). Pearson correlation coefficients were used to assess the
267 relationships among functional traits. Additional linear models were fitted for each pairwise
268 relationship between traits including the effect of stand age (maximum Scots pine age), to assess
269 the effect of this variable on trait relationships.

270

271 Since climate and stand descriptors were highly correlated, we used principal components analysis
272 (PCA) to aid the selection of variables to be included in our final models within each group of
273 potential explanatory variables (climatic and stand characteristics). On the basis of those PCAs
274 (see Figure S2 in Supporting Information), two climatic variables (P and T) and two stand
275 variables ($Dens$ and DBH) were retained as relatively independent descriptors of climate and
276 forest structure, respectively.

277

278 To explore the relationships between each functional trait and climatic and forest structural
279 variables (T , P , $Dens$ and DBH), we fitted linear models using each of the five functional traits as
280 dependent variables. We also included the squared mean annual temperature (T^2) in the models to
281 account for possible non-linear effects of temperature. Finally, we included maximum age of
282 Scots pine trees in the plot (Age), to control for the effect of stand age. Since not all plots were
283 sampled the same year, sampling year was included as an additional explanatory factor in each

284 attribute model to control for temporal changes in the value of functional traits. Spatial
285 autocorrelation of the residuals was accounted for by using generalized least squares (GLS) with
286 either linear or spherical spatial autocorrelation structures. These models were similar in terms of
287 the fitted coefficients to the equivalent general linear models (GLM). Therefore, we only present
288 the GLS results here. Additionally, since linear and spherical spatial autocorrelation structures
289 gave nearly identical results and the former tended to fit the data better in terms of AIC (Akaike
290 Information Criterion) we only present the models corresponding to the linear autocorrelation
291 structures.

292
293 GLS models were also used to explore the determinants of spatial variation in radial growth. In
294 these models, *BAI* was the dependent variable, and four functional traits (H_{max} , WD , N_{mass} and
295 $B_L:A_S$) plus stand age and climatic and forest structural variables (T , T^2 , P , $Dens$ and DBH) were
296 included as explanatory variables. We did not include *SLA* in this analysis because it reduced
297 considerably the number of complete data points (from 202 to 84). Again, we conducted
298 preliminary analyses including sampling year as a fixed factor in the model. As no significant
299 effect of the sampling year was found, the year effect was removed from the final *BAI* models. As
300 before, spatial autocorrelation of the residuals was accounted for by using linear autocorrelation
301 structures. All analyses were conducted with R (R 2.13.0; The R Foundation for Statistical
302 Computing).

303
304 In addition, we used structural equation modeling (SEM) to compare alternative conceptual
305 models of the way growth was affected by functional traits, climate and stand characteristics. The
306 statistical advantage of using both GLS and SEM modeling is that GLS permits to measure
307 residuals spatial autocorrelation, while the latter can include direct and indirect relationships

308 among the variables. We compared three nested models: one with only stand age and climate
309 variables (P and T), a second one with stand age, climate and stand structure variables (P , T , $Dens$
310 and DBH) and a final one adding also the functional traits that were significantly (or marginally)
311 related to BAI in the previous GLS analysis. The models included covariation between the two
312 climate variables, between stand structure variables and among functional traits. The latter and
313 most comprehensive model was simplified stepwise until the fit of the model did not increase
314 further in terms of the Bayesian Information Criterion (BIC). All variables were standardized prior
315 to fitting the path models using the AMOS package (SPSS Inc., Chicago, IL, USA).

316

317 RESULTS

318 Intraspecific versus interspecific variability in functional traits

319 All studied traits showed substantial intraspecific variability (see Figure 2), with coefficients of
320 variation (CV) ranging from 7.6 % for WD to 23.8 % for $B_L:A_S$ (Table 2). In particular, WD and
321 N_{mass} showed the lowest differences in CV s within- and among species. Although intraspecific
322 variability of Scots pine was clearly lower than the variability found across species (Kolmogorov
323 Smirnov tests showed significant differences within- and among species for all five traits,
324 $p < 0.001$), its CV was remarkably high for a single species.

325

326 Relationships among functional traits

327 As expected, the functional traits studied did not vary independently of each other. H_{max} emerged
328 as a key trait, showing significant correlations with all the functional traits considered in this study
329 except N_{mass} . H_{max} had positive relationships with SLA and WD , and correlated negatively to $B_L:A_S$
330 (Fig. 3). WD , related positively to H_{max} and negatively to N_{mass} , was not correlated to SLA or $B_L:A_S$
331 (Fig. 3). In addition to its correlation to WD , N_{mass} showed a negative relationship with $B_L:A_S$ (Fig.

332 3). Leaf traits (*SLA* and N_{mass}) were not correlated with each other (Fig. 3). All the previous
 333 relationships remained significant and with similar sign and magnitude if the effect of stand age
 334 was accounted for, with the exception of the relationship between H_{max} and wood density, which
 335 was no longer significant ($P=0.81$).

336

337 Determinants of functional traits

338 The GLS models allowed us to explore the effects of climate and stand variables on the spatial
 339 variability of the studied functional traits (Table 3). For H_{max} , tree density and *DBH* explained
 340 more than a half of the variation in the data (model $R^2=0.53$). H_{max} was related positively to both
 341 density and *DBH*, which implied that H_{max} always increased with competition intensity. *WD* was
 342 positively related to stand age and precipitation (model $R^2=0.26$) (Table 3). The explanatory
 343 variables included in the N_{mass} model explained poorly the variation in the data (model $R^2=0.11$),
 344 and this functional trait was only related to *DBH* (positively) and to stand age (negatively). $B_L:A_S$
 345 was negatively related to both stand age, *DBH* and density (model $R^2=0.33$). Finally, *SLA*
 346 variation was significantly explained by three variables (model $R^2=0.15$), being positively related
 347 to *DBH* and *Dens* and negatively related to *P* (Table 3). The sampling year factor affected $B_L:A_S$,
 348 *SLA* and H_{max} .

349

350 Determinants of radial growth

351 The GLS including climatic, stand development and functional traits variables explained 47% of
 352 the variation in growth (*BAI*). In this model, *BAI* was positively related to N_{mass} , $B_L:A_S$, H_{max} and
 353 *P*, and negatively related to *Age* and *Dens* (Table 4). Interestingly, *BAI* was unrelated to *WD*,
 354 *DBH*, *T* or T^2 . The results of the path analysis strengthened the interpretation of the previous
 355 relationships. The final path model including climate, stand structure, stand age and functional

356 traits provided a good fit to the data ($\chi^2=15.6$, $N=202$, $P=0.212$) and explained a similar
357 percentage (43%) of the variation in *BAI* as the GLS model. The path diagram of this model (Fig.
358 4) shows the significant direct effect of the four functional traits, precipitation, stand age, *DBH*
359 and tree density on *BAI*. It also indicates indirect effects of temperature, precipitation, stand age,
360 *DBH* and density mediated by their effects on functional traits. The overall fit and explained
361 variance in *BAI* declined if functional traits were removed from the previous path model: $R^2=22\%$
362 for the model including only climatic variables and stand age ($\chi^2=0.0$, $P=0.999$) and $R^2=34\%$ for
363 the model including climate, stand structure variables and stand age ($\chi^2=0.3$, $P=0.559$).

364 DISCUSSION

365 Confirming our first hypothesis, variability in Scots pine functional traits across populations was
366 high, with some traits showing a particularly large variation, resulting either from local adaptation
367 or from a high plasticity of form and function among populations associated to environmental
368 gradients (Albert *et al.* 2010a). For all five traits, intraspecific trait variability was lower than the
369 interspecific variability observed across the 44 most abundant tree species in Spain (Martínez-
370 Vilalta *et al.* 2010). However, the intraspecific variation is remarkable considering it represented
371 the variation of only one against 44 species and that it excluded variation within populations. This
372 is in agreement with the growing consensus that within species variation in functional traits is not
373 negligible (Albert *et al.* 2010b; de Bello *et al.* 2010; Fajardo & Piper 2010). In fact, trait
374 variability across species would have been even smaller had we used only species coexisting with
375 Scots pine, reinforcing our conclusion. The large intraspecific variation observed in this study
376 supports the recent claim that representing functional trait variation of woody species by a single
377 species-specific value could be hardly adequate for vegetation models and functional studies (cf.
378 Albert *et al.* 2010b; Kattge *et al.* 2011), at least for widely distributed tree species such as Scots
379 pine.

380
381 With regards to the second hypothesis, similar to interspecific studies using global datasets, our
382 intraspecific study found a close coordination among functional traits (Messier *et al.* 2010).
383 However, some relationships differed from those commonly reported across species, particularly
384 regarding the leaf- (Wright *et al.* 2004) and wood economics spectra (Chave *et al.* 2009).
385 Interestingly, pairwise trait correlations reported in this study were robust to differences in stand
386 age (the only exception being the relationship between H_{max} and WD). The differences in
387 correlations between traits at the intra- and interspecific levels could arise from the discrepancies
388 in the forces shaping the relationships among traits within- and among species. Although there is
389 no strong reason to expect intra-specific relationships to be a better indication of true functional
390 tradeoffs than inter-specific relationships, the fact that some functional relationships are not
391 consistent across ecological scales implies that they are likely to be mediated by indirect effects
392 involving third variables, and should thus be interpreted with caution. For example, we found a
393 positive relationship between H_{max} and WD , contrary to the negative relationship usually found
394 across species (Chave *et al.* 2009). This negative relationship was suggested to be mediated by the
395 opposition of WD and hydraulic efficiency (Wright *et al.* 2007). Our results show that this trade-
396 off is not necessarily apparent when comparing different populations of the same species.
397 Similarly, we did not find the usual relationship between SLA and N_{mass} described at the
398 interspecific level, which is one of the central tenets of the leaf economics spectrum (Wright *et al.*
399 2004, 2005). This lack of direct relationship between SLA and N_{mass} could be in principle related
400 to limited variation in leaf lifespan across the studied populations (cf., Janse-Ten Klooster *et al.*
401 2007; Lusk *et al.* 2008).

402

403 The main explanation behind the different relationships among traits within- and among species is
404 likely to be the combined effect of stand development, including age heterogeneity (e.g., *WD* and
405 *stand age* association) and variable availability to resources along environmental gradients (cf.
406 van Noordwijk & de Jong 1986). In our study, forest structure, climate and resource availability
407 were not constant across sites. A similar situation occurs in many interspecific studies, where
408 different species are sampled from different locations. Since functional traits are affected by
409 resource availability and may respond differently to climate and biotic interactions within- (e.g,
410 Fajardo & Pippert 2010; this study) and among species (e.g., Niinemets & Kull 2003; Wright *et al.*
411 2005), these effects have the potential to confound some of the relationships commonly reported
412 among traits. Our own results clearly show that functional traits vary across populations along
413 environmental gradients, even after accounting for differences in stand age. Climate and,
414 particularly, stand attributes explained a substantial proportion of the spatial variation in the
415 studied traits, ranging from 11% for N_{mass} to 53% for H_{max} . The effect of microhabitat-level
416 variation and variable availability of resources is difficult to control in field studies (but see e.g.
417 Cornwell & Ackerly 2009), as it would affect even trait relationships found within populations
418 (Bolnick *et al.* 2003; Messier *et al.* 2010), and this is clearly a line of research that requires further
419 attention.

420
421 Our results showed that $B_L:A_S$ has a key role in coordination among traits (Fig. 3) and as a
422 determinant of radial growth (Fig. 4) (cf. Sterck *et al.* 2012), which is consistent with previous
423 studies highlighting the importance of this trait (or $A_L:A_S$) in tree acclimation along climatic
424 gradients, being one of the most plastic hydraulic properties in pines in general (DeLucia *et al.*
425 2000) and Scots pine in particular (Martínez-Vilalta *et al.* 2009). We did not find, however, the
426 expected negative relationship with evaporative water demand (best represented by annual

427 temperature in our analysis) (Mencuccini & Bonosi 2001; Martínez-Vilalta et al. 2009). This
428 discrepancy is likely due to the fact that, unlike previous studies, we sampled a wide range of
429 stand structures, which explained most of the spatial variation in $B_L:A_S$ in our case. This, together
430 with the narrower range of environmental conditions covered in our study may explain also the
431 lack of relationship between temperature (or latitude) and N concentration in needles, as reported
432 in previous studies (Oleksyn *et al.* 2003).

433
434 Concerning our last hypothesis, one of the main findings of our study is that intraspecific variation
435 in functional traits explained a larger part of the spatial variation in radial growth rate than climate
436 or stand attributes per se. This is consistent with previous studies; for instance, Wright *et al.*
437 (2010) found that functional traits explain a considerable part of the interspecific variation in the
438 growth-mortality trade-off. It should be noted, however, that the factors considered in our study
439 explained only 47% of the variation in growth. This figure is comparable to those reported in a
440 previous study of Scots pine growth variability at larger regional scales (Vilà-Cabrera et al.
441 2011b), and it suggests that key variables were not included in our model or that measurement
442 errors were large, which can not be completely ruled out due to the extensive nature of the
443 sampling scheme. Plot-level functional trait variation emerged as a key aspect allowing Scots pine
444 individuals to buffer the effects of variability in biotic and abiotic conditions (King *et al.* 2005,
445 2006b; Poorter *et al.* 2006, 2008b; Martínez-Vilalta *et al.* 2010). The patterns we observed are
446 better described by a hierarchy of effects in which stand age and climate affect stand structure,
447 which is the main source of variation for functional traits, which, in turn, have a large effect on
448 Scots pine radial growth. This study adds a new dimension, intraspecific functional trait variation,
449 to previous work showing that the spatial variation in demographic rates of Scots pine is mostly
450 associated to stand structure (Vilà-Cabrera *et al.* 2011b). It remains to be explored whether the

451 central importance of functional traits observed for Scots pine growth would also emerge for
452 mortality rates or recruitment, and whether it applies to other tree species.

453

454 The implications of our results are substantial in the context of recently observed episodes of
455 widespread forest decline (Allen *et al.* 2010; Martínez-Vilalta *et al.* 2012; see also Martínez-
456 Vilalta & Piñol 2002 and Galiano *et al.* 2010 for episodes affecting Scots pine within the region
457 covered in this study) and for the prediction of species and community changes as a result of
458 climate change. The association among functional traits and climate enables species to buffer the
459 effects of climate on performance (Martínez-Vilalta *et al.* 2009). However, we show evidence here
460 supporting that this effect is likely to be more complex than previously regarded, at least for radial
461 growth, as it is mediated by stand structure. In any case, variation in functional attributes within a
462 species (including plasticity and other sources of variation within and across populations) is key to
463 understand niche segregation (cf. Sterck *et al.* 2013) and species' capacity to respond to biotic and
464 abiotic changes in the environment (Nicotra *et al.* 2010). Further studies are needed to disentangle
465 the effects of genetic variability, plasticity and local adaptation in these processes. Including a
466 proper characterization of this variability in vegetation models is essential to represent the true
467 acclimation and adaptation potential of species and should allow for improved predictions of
468 compositional and functional changes in plant communities in response to environmental changes,
469 compared to models using constant species-specific traits (Albert *et al.* 2010; Hulshof & Swenson
470 2010; Kattge *et al.* 2011).

471

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704

Accepted manuscript

705 ELECTRONIC SUPPLEMENTARY MATERIAL

706 The additional electronic supplementary material may be found in the online version of this article:

707

708 **Figure S1.** Geographic distribution of the five studied functional traits in Catalonia: (a) H_{max} , (b)
709 WD , (c) N_{mass} , as Leaf Nitrogen Concentration, (d) $B_L:A_S$ and (e) SLA .

710

711 **Figure S2.** Principal component analysis (PCAs) of (a) functional traits, (b) climatic variables and
712 (c) forest structural attributes.

713

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714 **TABLE 1.** Descriptive statistics of the variables analyzed in this study. Transformations applied
 715 to achieve normality are specified in the last column.
 716

Variable	Acronym	Units	Range	N	Transformation
Growth					
Annual basal area increment	<i>BAI</i>	cm ²	1.05-34.13	406	Log _e
Traits					
Maximum tree height	<i>H_{max}</i>	m	8.51-24.98	403	Log _e
Wood density	<i>WD</i>	g cm ⁻³	0.35-0.79	369	
Nitrogen content of leaves	<i>N_{mass}</i>	%	0.54-2.27	364	
Leaf-biomass-to-sapwood area ratio	<i>B_L:A_S</i>	t m ⁻²	0.002-0.09	251	Log _e
Specific leaf area	<i>SLA</i>	cm ² mg ⁻¹	0.03-0.07	214	
Climatic variables					
Mean annual precipitation	<i>P</i>	mm	486.8-1231.0	406	
Mean annual temperature	<i>T</i>	°C	4.90-14.0	406	
Thermal amplitude	<i>Amp</i>	°C	7.93-14.28	406	
Potential evapotranspiration	<i>PET</i>	mm	708.41-1117.57	406	
Annual precipitation to potential evapotranspiration ratio	<i>P:PET</i>		0.48-1.63	406	
Summer precipitation to potential evapotranspiration ratio	<i>P:PET_{sum}</i>		0.23-1.21	406	

 Forest structure variables

Average diameter at breast height of Scots pine	<i>DBH</i>	cm	8.41-50.04	406	Log _e
Tree density (total)	<i>Dens</i>	tree ha ⁻¹	128-4244	406	Log _e
Slope	<i>S</i>	°	2-45.00	406	
Max age of Scots pine (stand age)	<i>Age</i>	year	20-244	406	Log _e
Plot Basal area (total)	<i>BA</i>	m ² ha ⁻¹	1.02-88.35	406	Log _e
Percent of basal area of Scots pine	<i>%BA</i>	%	17.28-100.00	406	Arcsinus√

718
719 **TABLE 2.** Variability of the five studied functional traits at the intra- and interspecific levels.

720 Interspecific variability in traits for the 44 dominant tree species in peninsular Spain was obtained
721 from Martínez-Vilalta et al. (2010).

722

	Intraspecific		Interspecific	
	Range	CV	Range	CV
<i>H_{max}</i>	8.51-24.98	7.6	6.00-38.80	34.4
<i>WD</i>	0.35-0.79	13.9	0.44-0.90	18.4
<i>N_{mass}</i>	0.54-2.27	18.5	0.81-4.04	37.3
<i>B_L:A_S</i>	0.002-0.09	23.8	0.002-0.14	67.8
<i>SLA</i>	0.03-0.07	17.3	0.02-0.25	49.9

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724 **TABLE 3.** GLS models of the effects of stand structure, climate and sampling year on the five
 725 studied functional traits. See Table 1 for abbreviations. Some variables were transformed to
 726 achieve normality (cf. Table 1). Regression coefficients (B Coefficients) and significance levels
 727 for each explanatory variable are given: ⁺ P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001; NS, P >
 728 0.1; NA, no data.

Variable	B coefficients				
	H_{max}	WD	N_{mass}	$B_L:A_S$	SLA
Intercept	NS	NS	NS	3.803***	NS
Age	NS	0.054***	-0.076**	-0.102**	NS
Stand structure					
DBH	1.737***	NS	0.445**	-0.964***	0.020***
$Dens$	0.339***	NS	NS	-0.312***	0.006*
Climate					
P	NS	0.0001**	NS	NS	-0.00001*
T	NS	NS	NS	NS	NS
T^2	NS	NS	NS	NS	NS
Sampling Year					
1989	NS	NS	NS	0.389**	NA
1990	NS	NS	NS	0.424*	NA
1991	-0.295*	NS	NS	0.355*	NA
1992	NS	NS	NS	NS	NA
1993	NS	NS	NS	NS	NS
1994	NS	NS	NS	0.308*	NS

B coefficients

Variable	H_{max}	WD	N_{mass}	$B_L:A_S$	SLA
1995	NS	NS	NS	NS	-0.009**
1996	NS	NS	NS	NS	-0.006*
1998	NS	NS	NS	NS	NA
R^2	53 %	26 %	11 %	33 %	15 %
N	403	369	364	251	214

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The Sampling Year 1988 was used as reference class for the Sampling Year factor.

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731 **TABLE 4.** GLS model of the effects of functional traits, stand structure and climatic variables on
 732 annual basal area increment (*BAI*) of Scots pine. See Table 1 for abbreviations. Some variables
 733 were transformed to achieve normality (cf. Table 1).

734

735

Variable	B coefficients	t	P
Intercept	1.478	2.668	<0.01
<i>Age</i>	-0.203	-6.326	<0.0001
Functional traits			
<i>H_{max}</i>	0.176	0.066	<0.01
<i>WD</i>	NS	NS	NS
<i>N_{mass}</i>	0.125	2.299	<0.05
<i>B_L:A_S</i>	0.241	4.656	<0.0001
Stand structure			
<i>DBH</i>	NS	NS	NS
<i>Dens</i>	-0.240	-2.997	<0.01
Climate			
<i>P</i>	0.001	3.840	<0.001
<i>T</i>	NS	NS	NS
<i>T²</i>	NS	NS	NS

$R^2=0.47$ and $N=202$

736 FIGURE LEGENDS

737 **Fig. 1.** Location of the Scots pine sampling plots of the Ecological and Forest Inventory of
 738 Catalonia (IEFC) considered in this study (black dots), represented on maps of mean annual
 739 temperature (°C) and annual precipitation (mm) in Catalonia (NE Spain).

740 **Fig.2.** Histograms of the five studied functional traits at the intra- and interspecific levels: (a) H_{max}
 741 ($N_{inter}=44$ and $N_{intra}=403$), (b) WD ($N_{inter}=44$ and $N_{intra}=369$), (c) N_{mass} ($N_{inter}=44$ and $N_{intra}=364$),
 742 (d) $B_L:A_S$ ($N_{inter}=27$ and $N_{intra}=251$) and (E) SLA ($N_{inter}=43$ and $N_{intra}=214$). Intraspecific data is
 743 from this study (Scots pine), whereas interspecific variability was obtained from Martínez-Vilalta
 744 *et al.* (2010) and corresponds to the 44 dominant tree species in peninsular Spain. See Table 1 for
 745 abbreviations.

746 **Fig.3.** Pairwise correlations among functional traits. Dashed and solid lines indicate negative and
 747 positive relationships, respectively. See Table 1 for abbreviations. Some variables were
 748 transformed to achieve normality (cf. Table 1). Pearson correlation coefficients are given for each
 749 relationship. Significance levels: $^+ P < 0.10$; $* P < 0.05$; $** P < 0.01$; $*** P < 0.001$.

750 **Fig.4.** SEM model relating growth, functional traits, stand structure and climate. Arrows indicate
 751 significant links between variables (single headed: directional path, double headed: covariance).
 752 Dashed and solid lines indicate negative and positive relationships, respectively. Only directional
 753 relationships are shown for clarity. Line width is proportional to the magnitude of the effect,
 754 identifying three categories from narrow to wide line: $P < 0.05$, $P < 0.01$ and $P < 0.001$. The
 755 number in brackets under BAI (endogenous variable) in the path diagram corresponds to the R^2
 756 value indicating the percentage of variance in that variable that is accounted for by the model. See
 757 Table 1 for abbreviations. Some variables were transformed to achieve normality (cf. Table 1).

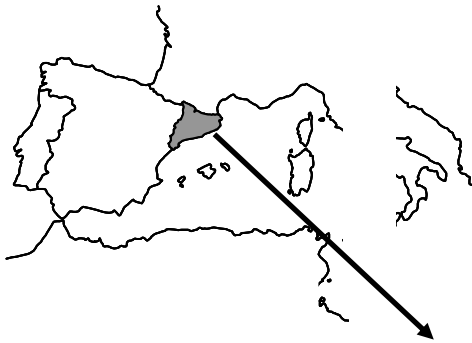
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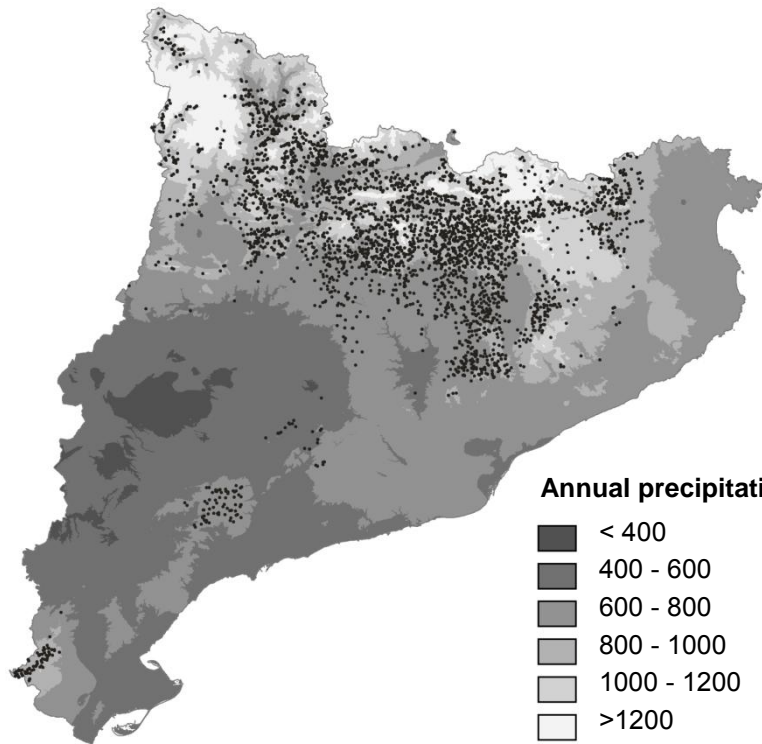
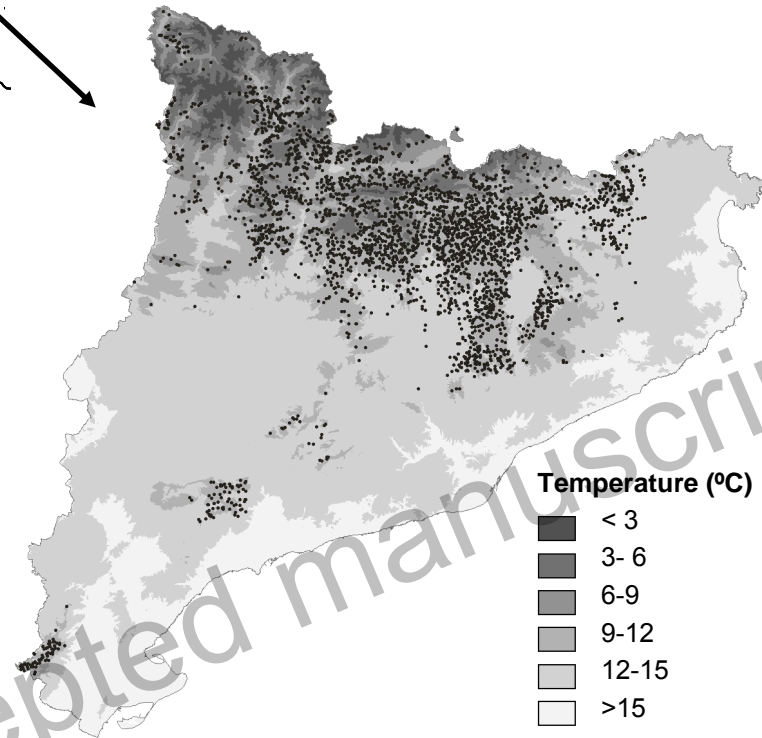
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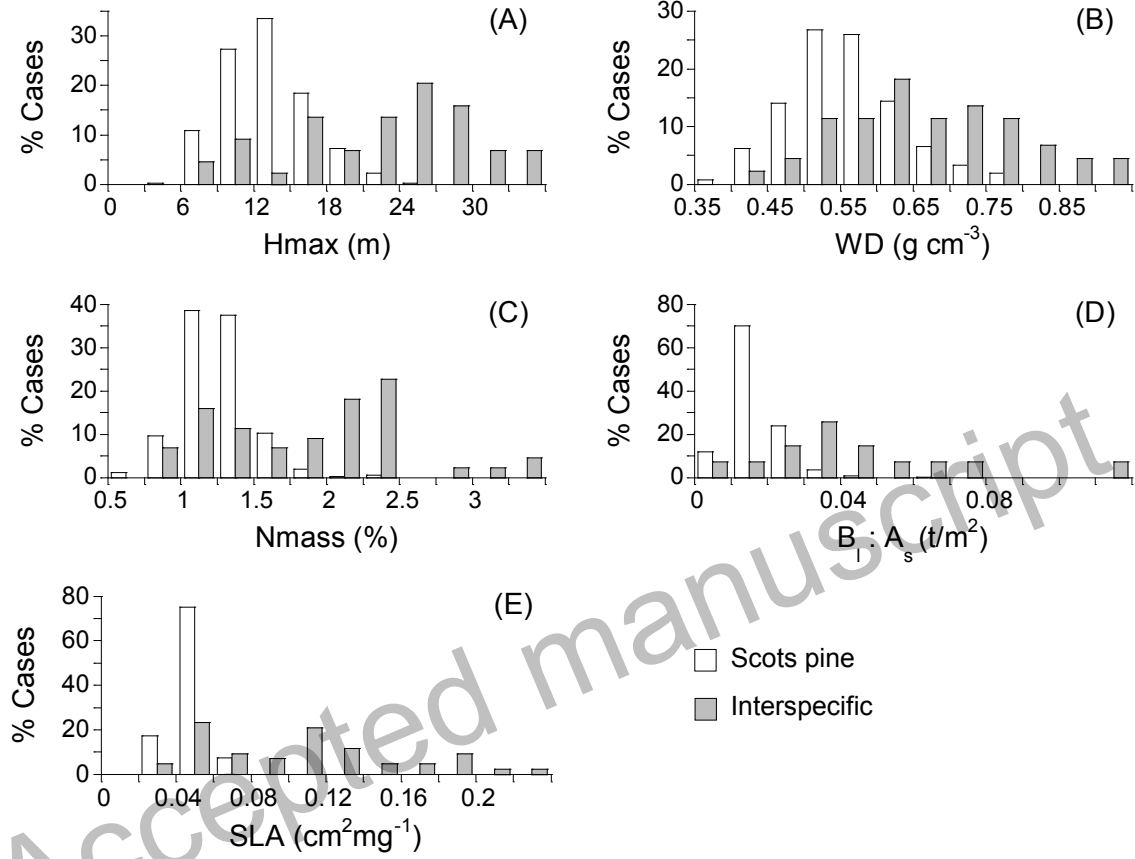
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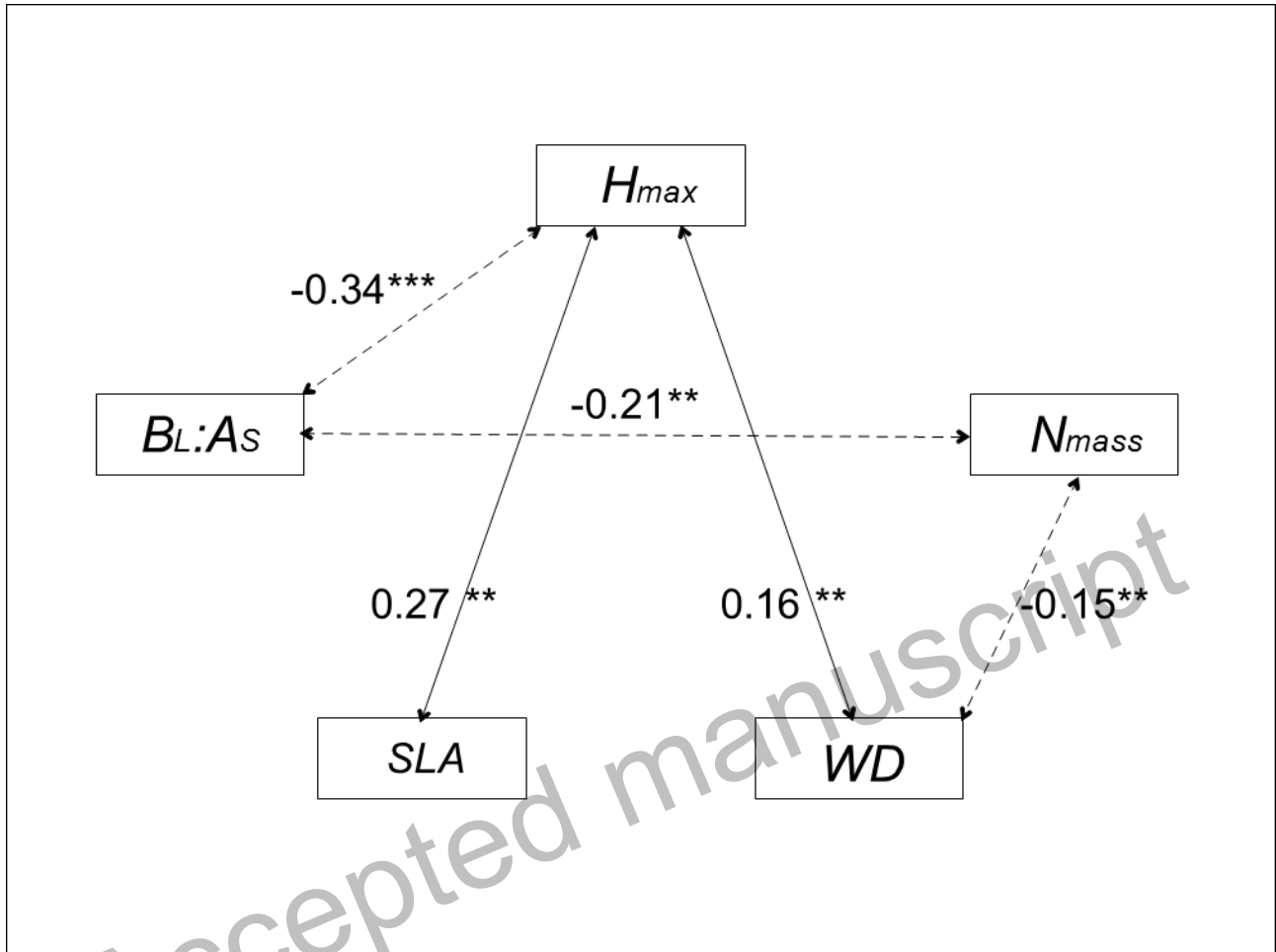
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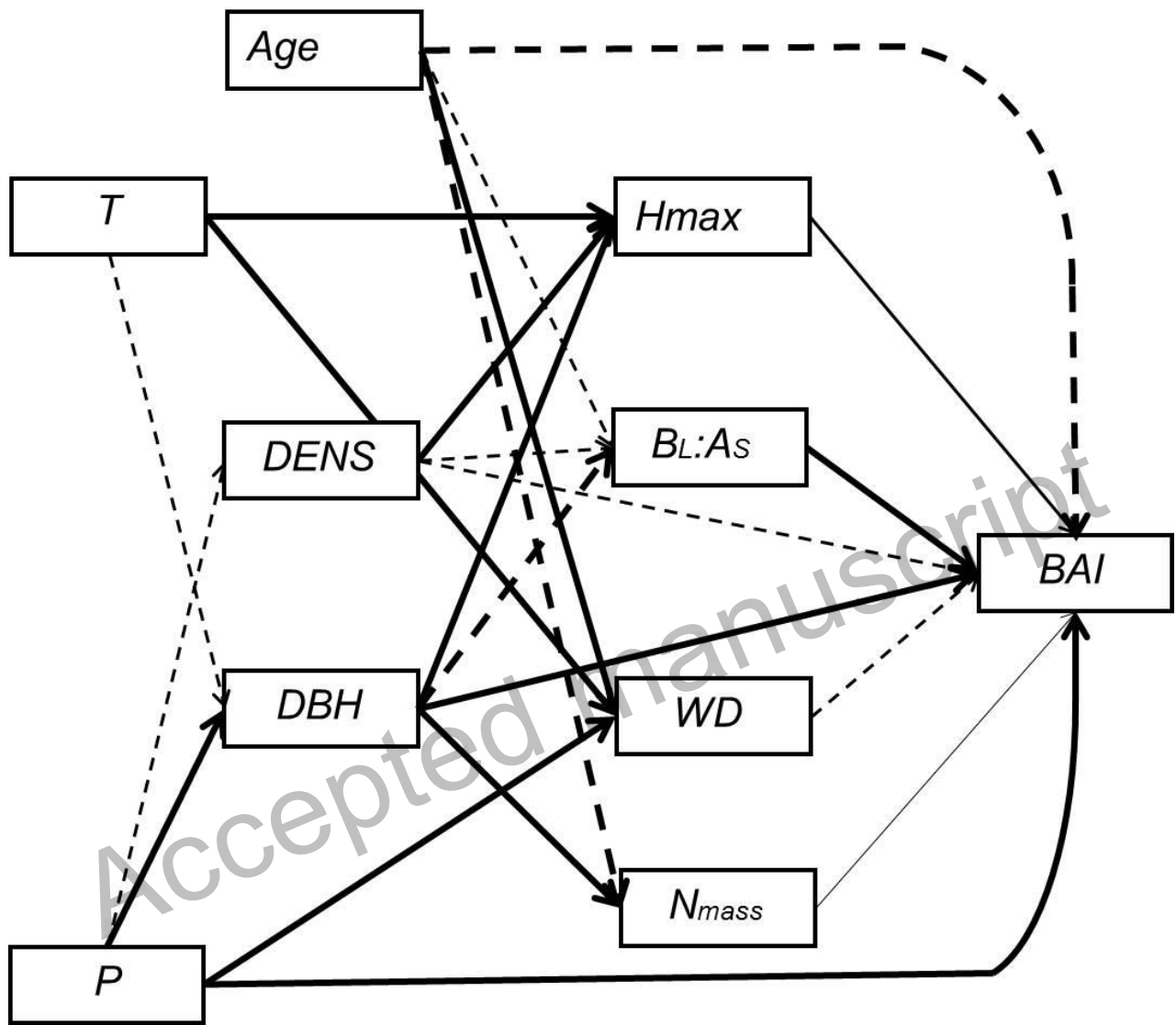
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