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TITLE: Intraspecific variability in functional traits matters: Scots pine as a case of study[1]

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RUNNING TITLE: Intraspecific functional trait variation

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The authors declare that the experiment comply with the current laws of the country in which the experiment was performed. The authors declare that they have no conflict of interest.

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ABSTRACT

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

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

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

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

Conclusion. Our study emphasizes the hierarchy of factors determining intraspecific variation in functional traits in Scots pine, and their strong association to spatial variability in radial growth. We claim that intraspecific trait variation is an important factor determining plant responses to changes in climate and other environmental factors, and should be included in predictive models of vegetation dynamics.

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

INTRODUCTION

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

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

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

The fact that functional traits also vary widely within species has been recognized for a long time (e.g., Clausen *et al.* 1948; Keddy 1992; Kleinschmit 1993) and explored by evolutionary ecologists (Fox *et al.* 2001) and physiological ecologists (Lambers & Poorter 1992; Cordell *et al.* 1998; Diaz *et al.* 1998), but began only recently to be considered in studies of trait coordination and community ecology. The use of average trait values to describe a given species is known to hide much functional variation at two different ecological scales: within populations (Bolnick *et al.* 2011) and across populations, particularly along environmental gradients (Albert *et al.* 2010a; de Bello *et al.* 2010; Fajardo & Piper 2010; Hulshof & Swenson 2010). Besides the effects of climate and resource availability, stand structure and development are also likely to be major determinants of functional trait variability in trees, as they generate, and respond to, local variations in climate and resource availability (e.g., Campetella *et al*. 2011). This aspect, however, has received comparatively little attention in this context.

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

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

Here, we use a unique dataset compiled within the Ecological and Forest Inventory of Catalonia (abbreviated IEFC; Burriel et al. 2000-2004; http://www.creaf.uab.es/iefc/) to study the variability of key functional traits in Scots pine along a relatively wide environmental gradient. Specifically, we hypothesized that (1) functional trait variability across Scots pine populations is not negligible, and it is comparable in magnitude to interspecific trait variability of tree species found in the same region; (2) intraspecific relationships among functional traits is not necessarily consistent with the tradeoffs commonly reported across tree species, due to differences in the factors shaping trait coordination within and between species; (3) spatial variability in functional traits is associated to climatic differences but, also, to forest structural differences across sites; and (4) variability in functional traits buffers tree response to climate or stand structure across sites, so that the direct effects of climate and stand structure on radial growth are relatively small compared to the indirect effects mediated by functional traits.

METHODS

Study area and species

The area covered by this study includes all the forested territory of Catalonia (1.2 x 10^6 ha), NE Spain. The relief rises from sea level to more than 3,000 m a.s.l. in the Pyrenees, the main mountain system, including both coastal and continental land areas (Fig.1). Catalonia's climate is diverse mainly due to its physiographic complexity, with typical Mediterranean climate in most of its coastal area, continental Mediterranean climate in the inner part and mountain to alpine climates in the Pyrenees (Koppen's classification; Worldwide Bioclimatic Classification System 1996-2000). Vegetation types include Aleppo pinewoods, alpine pastures, deciduous woodlands, Mediterranean maquis, non-Mediterranean coniferous woodlands and sclerophyllous woodlands (Bolòs & Vigo 1984). The Iberian Peninsula constitutes the southwestern limit of Scots pine distribution, with important populations in the Pyrenees and several smaller populations scattered in southern and more arid locations (Castroviejo *et al.* 1986). Scots pine is the second most abundant tree species in Catalonia (after *Pinus halepensis*), where it occurs naturally and currently covers a total estimated area of 219,754 ha, distributed preferably on north-facing slopes between 800-1600 m a.s.l. Catalan populations of Scots pine are distributed across a wide range of climatic conditions (mean annual temperature from 3.6 to 14.6°C and mean annual precipitation from 413-1268 mm; Table 1). Spanish populations of Scots pine are known to be genetically different from the populations of Northern Europe (Alia *et al.* 2001).

Data sources

The database of functional traits and growth of Scots pine is part of the Ecological and Forest Inventory of Catalonia (IEFC), carried out by the Center for Ecological Research and Forestry Applications (CREAF) between 1988 and 1998 (Burriel *et al.* 2000-2004; http://www.creaf.uab.es/iefc/). This inventory sampled the whole forested area of Catalonia, NE Spain. Plots were randomly selected within a grid including all forest areas for each county in Catalonia. Plots were circular, had a radius of 10 m and were distributed with a density of one plot per km^2. The sampling consisted in identifying and measuring all trees with diameter at breast height (*DBH*) > 5 cm in each plot. An extended supplementary sampling was conducted on a random subsample of 20% of the plots, carried out on one or two representative individuals of each 5 cm diameter class of the dominant tree species in the plot. From each of these individuals, stem wood cores and fully exposed branches of different sizes and order were sampled (N=1-11 per plot) and taken to the laboratory to determine wood density (*WD*), needle nutrient composition and specific leaf area (*SLA*) (see methods below). Additionally, allometric relationships were used to estimate the ratio of leaf biomass to sapwood area (B_L:A_S) at the tree level. Because of the limited number of branches sampled per plot these relationships were calculated by combining data from neighbouring plots (N=30-79). Since only one or few trees were sampled per plot, trait variability within populations could not be characterized. In addition, low replication within plots reduces the precision of our trait estimates at this level, although this limitation is contrasted by the relatively large amount of sampling plots covering the whole distribution of Scots pine in the study region.

Scots pine was dominant in 1,962 plots (18.4% of all sampled plots) in which it had an average density of 903 trees ha^{-1}, an average basal area of 21.6 m^{2}ha^{-1}, an average canopy height of 13.1 m, and an average tree age of 49 years (Burriel *et al.* 2000–2004). Since species were sampled proportionally to their abundance in each plot, and to make sure that our study included only those plots that where representative of Scots pine populations in Catalonia, we included in the analysis only those plots where Scots pine accounted for > 15% of the total tree basal area. Moreover, and since the inclusion of young (immature) stands could affect the conclusions of the study, we excluded all plots where stand age information was missing or where maximum Scots pine age was lower than 20 years, as Scots pine sexual maturity (measured as the presence of cones) is at c. 15-20 years of age (Vilà-Cabrera et al. 2011a; 2014). This very conservative approach reduced the total number of plots covered in this study to 406, although not all variables were measured in all plots (see Table 1). In all cases, the main model results remained similar if all the analyses were conducted using all the plots (not shown).

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

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

where *R* corresponds to *DBH*/2.

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

Individual values for all studied functional traits were obtained as follows (see the IEFC webpage, http://www.creaf.uab.es/iefc/, for additional technical details): (1) H_{max}, which was defined as the height of the tallest tree in the plot. Tree height was measured with a clinometer for each tree present in the plot. (2) *WD*, calculated as the ratio of dry weight to fresh wood volume, was measured on one wood core per plot taken on the stem of a representative tree. Fresh volume was established by measuring precisely the dimensions of the cores. Samples were then weighted to a precision of 0.001 g after having been oven dried for 48 h at 75ºC. Please note that we could not use the more broadly used term basic specific gravity because wood was dried below 100°C. (3) N_{mass} was measured on a dried and ground subsample of sunlit needles (Cyclotec Foss Tecator 1093-001 grinder, Foss Analytical, Hilleroed, Denmark) from one tree per plot, representing all cohorts present in the stems proportionally to their abundance. Chemical analyses were carried out at the Scientific-Technical Service of the University of Barcelona using an elemental analyzer (C.E. Instruments, Wigan, UK). (4) *SLA*, calculated as the ratio of fresh leaf surface to dry weight, was also obtained from the same needle samples as N_{mass}. One-sided, projected needle surface was obtained measuring precisely the length and width of the needles. Needles were then weighted to a precision of 0.001 g after having been oven dried for 48 h at 75ºC. (5) Tree-level B_L:A_S ratios were obtained from independent estimates of leaf biomass and sapwood area. The ratio of leaf biomass (or area) to sapwood area is considered as a key factor for characterizing the hydraulic architecture of trees in general and Scots pine in particular (Zweifel *et al.* 2007; Martínez-Vilalta *et al.* 2009). 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 the size distribution of the primary branches in all sampled trees (N=6-10 trees per plot). Thus, we calculated mean tree-level B_L:A_S ratios per plot. First, we estimated the leaf biomass (B_L) of each sampled tree by summing the leaf biomass of its branches, obtained multiplying the basal area of each primary branch by the corresponding branch-level B_L:A_S ratio, which was obtained by combining allometric data from neighboring plots. Then, the stem sapwood area (A_S) of each tree was estimated from its sapwood depth at breast height (visually estimated from wood cores). Finally, tree-level estimates of B_L were divided by their corresponding A_S and averaged per plot.

A set of six variables, also collected within the IEFC framework, were selected to represent plot characteristics, competition and forest structure: terrain slope (*S*, °), average diameter at breast height of Scots pine (*DBH*, cm), total tree density (*Dens*, tree ha^{-1}), maximum age of Scots pine trees in the plot (*Age*, year), total plot basal area (*BA*, m^2 ha^{-1}) and percentage basal area belonging to Scots pine (%*BA*, %). Soil characteristics were not included in the IEFC database nor were they available from other sources.

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

Data analysis

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

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

To explore the relationships between each functional trait and climatic and forest structural variables (T, P, *Dens* and DBH), we fitted linear models using each of the five functional traits as dependent variables. We also included the squared mean annual temperature (T^2) in the models to account for possible non-linear effects of temperature. Finally, we included maximum age of Scots pine trees in the plot (*Age*), to control for the effect of stand age. Since not all plots were sampled the same year, sampling year was included as an additional explanatory factor in each attribute model to control for temporal changes in the value of functional traits. Spatial autocorrelation of the residuals was accounted for by using generalized least squares (GLS) with either linear or spherical spatial autocorrelation structures. These models were similar in terms of the fitted coefficients to the equivalent general linear models (GLM). Therefore, we only present the GLS results here. Additionally, since linear and spherical spatial autocorrelation structures gave nearly identical results and the former tended to fit the data better in terms of AIC (Akaike Information Criterion) we only present the models corresponding to the linear autocorrelation structures.

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

In addition, we used structural equation modeling (SEM) to compare alternative conceptual models of the way growth was affected by functional traits, climate and stand characteristics. The statistical advantage of using both GLS and SEM modeling is that GLS permits to measure residuals spatial autocorrelation, while the latter can include direct and indirect relationships among the variables. We compared three nested models: one with only stand age and climate variables (*P* and *T*), a second one with stand age, climate and stand structure variables (*P*, *T*, *Dens* and *DBH*) and a final one adding also the functional traits that were significantly (or marginally) related to *BAI* in the previous GLS analysis. The models included covariation between the two climate variables, between stand structure variables and among functional traits. The latter and most comprehensive model was simplified stepwise until the fit of the model did not increase further in terms of the Bayesian Information Criterion (BIC). All variables were standardized prior to fitting the path models using the AMOS package (SPSS Inc., Chicago, IL, USA).

RESULTS

Intraspecific versus interspecific variability in functional traits

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

Relationships among functional traits

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

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

Determinants of functional traits

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

Determinants of radial growth

The GLS including climatic, stand development and functional traits variables explained 47% of the variation in growth (*BAI*). In this model, *BAI* was positively related to N_{mass}, $B_L{:}A_{S,}$ *Hmax* and *P*, and negatively related to *Age* and *Dens* (Table 4). Interestingly, *BAI* was unrelated to *WD*, *DBH*, *T* or T^2. The results of the path analysis strengthened the interpretation of the previous relationships. The final path model including climate, stand structure, stand age and functional traits provided a good fit to the data (χ^2=15.6, N=202, P=0.212) and explained a similar percentage (43%) of the variation in *BAI* as the GLS model. The path diagram of this model (Fig. 4) shows the significant direct effect of the four functional traits, precipitation, stand age, *DBH* and tree density on *BAI*. It also indicates indirect effects of temperature, precipitation, stand age, *DBH* and density mediated by their effects on functional traits. The overall fit and explained variance in *BAI* declined if functional traits were removed from the previous path model: R^2=22% for the model including only climatic variables and stand age (χ^2=0.0, P=0.999) and R^2=34% for the model including climate, stand structure variables and stand age (χ^2=0.3, P=0.559).

DISCUSSION

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

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

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

Our results showed that $B_L{:}A_S$ has a key role in coordination among traits (Fig. 3) and as a determinant of radial growth (Fig. 4) (cf. Sterck et al. 2012), which is consistent with previous studies highlighting the importance of this trait (or $A_L{:}A_S$) in tree acclimation along climatic gradients, being one of the most plastic hydraulic properties in pines in general (DeLucia *et al.* 2000) and Scots pine in particular (Martínez-Vilalta *et al.* 2009). We did not find, however, the expected negative relationship with evaporative water demand (best represented by annual temperature in our analysis) (Mencuccini & Bonosi 2001; Martínez-Vilalta et al. 2009). This discrepancy is likely due to the fact that, unlike previous studies, we sampled a wide range of stand structures, which explained most of the spatial variation in B_L:A_S in our case. This, together with the narrower range of environmental conditions covered in our study may explain also the lack of relationship between temperature (or latitude) and N concentration in needles, as reported in previous studies (Oleksyn *et al*. 2003).

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

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

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ELECTRONIC SUPPLEMENTARY MATERIAL

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

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

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

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

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

Forest structure variables					
Average diameter at breast height of Scots pine	*DBH*	cm	8.41-50.04	406	Log_e
Tree density (total)	*Dens*	tree ha^{-1}	128-4244	406	Log_e
Slope	*S*	º	2-45.00	406	
Max age of Scots pine (stand age)	*Age*	year	20-244	406	Log_e
Plot Basal area (total)	*BA*	m^2 ha^{-1}	1.02-88.35	406	Log_e
Percent of basal area of Scots pine	%*BA*	%	17.28-100.00	406	Arcsinus√

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TABLE 2. Variability of the five studied functional traits at the intra- and interspecific levels. Interspecific variability in traits for the 44 dominant tree species in peninsular Spain was obtained from Martínez-Vilalta et al. (2010).

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

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

	B coefficients				
Variable	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

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

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

Variable	B coefficients	t	P
Intercept	1.478	2.668	<0.01
Age	-0.203	-6.326	<0.0001
Functional traits			
H_{max}	0.176	0.066	<0.01
WD	NS	NS	NS
N_{mass}	0.125	2.299	<0.05
$B_L{:}A_S$	0.241	4.656	<0.0001
Stand structure			
DBH	NS	NS	NS
Dens	-0.240	-2.997	<0.01
Climate			
P	0.001	3.840	<0.001
T	NS	NS	NS
T^2	NS	NS	NS

R^2=0.47 and N=202

FIGURE LEGENDS

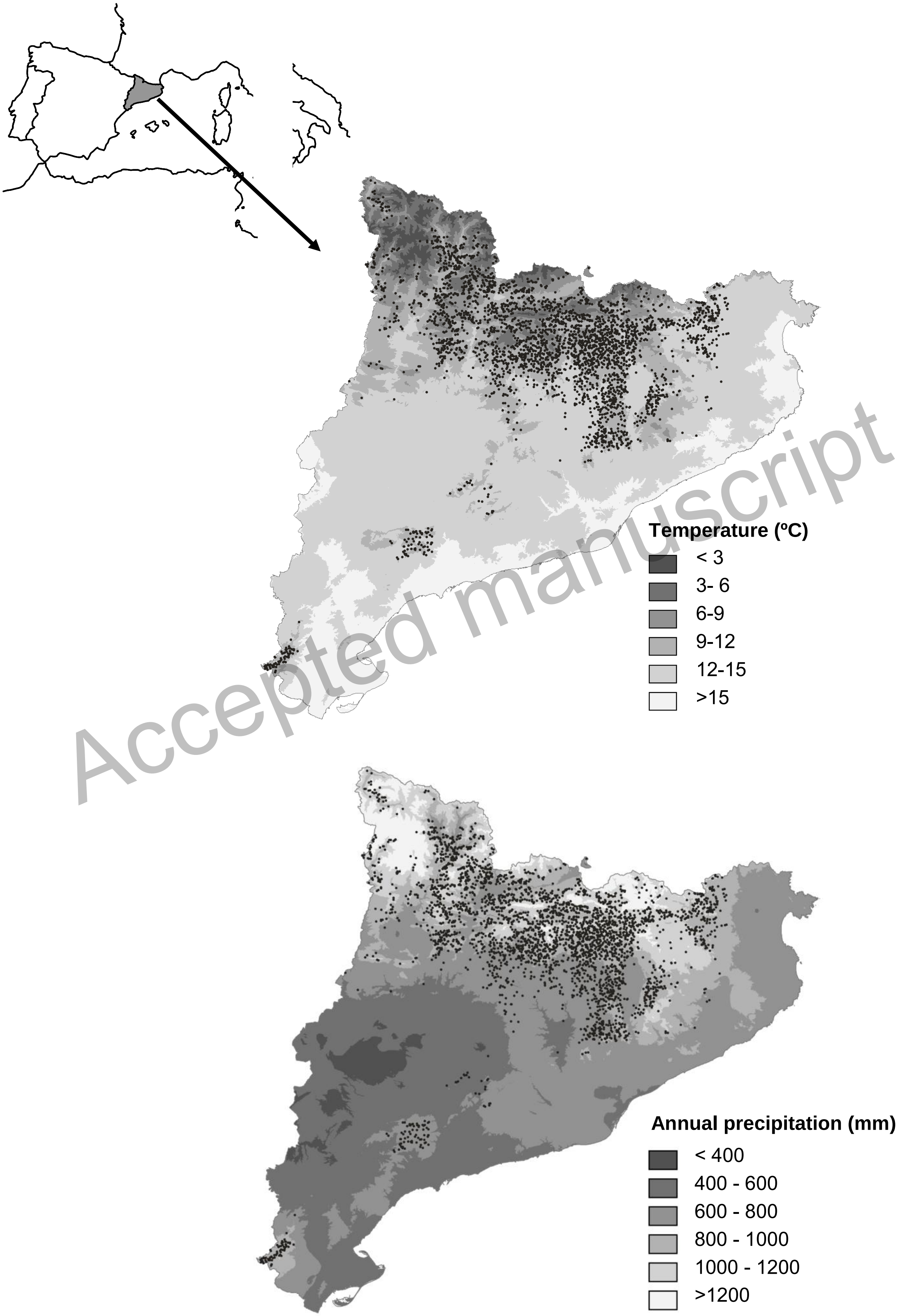
Fig. 1. Location of the Scots pine sampling plots of the Ecological and Forest Inventory of Catalonia (IEFC) considered in this study (black dots), represented on maps of mean annual temperature (ºC) and annual precipitation (mm) in Catalonia (NE Spain).

Fig.2. Histograms of the five studied functional traits at the intra- and interspecific levels: (a) H_{max} (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), (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 from this study (Scots pine), whereas interspecific variability was obtained from Martínez-Vilalta *et al.* (2010) and corresponds to the 44 dominant tree species in peninsular Spain. See Table 1 for abbreviations.

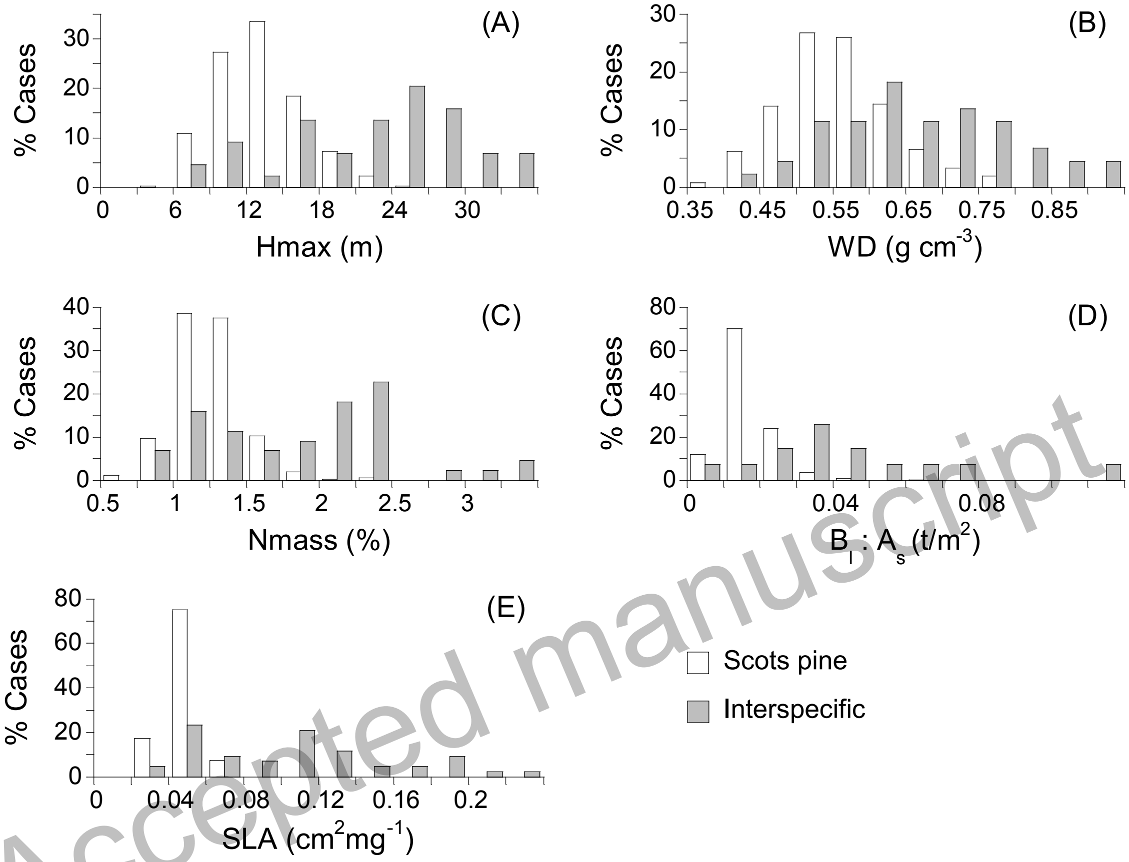
Fig.3. Pairwise correlations among functional traits. Dashed and solid lines indicate negative and positive relationships, respectively. See Table 1 for abbreviations. Some variables were transformed to achieve normality (cf. Table 1). Pearson correlation coefficients are given for each relationship.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

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

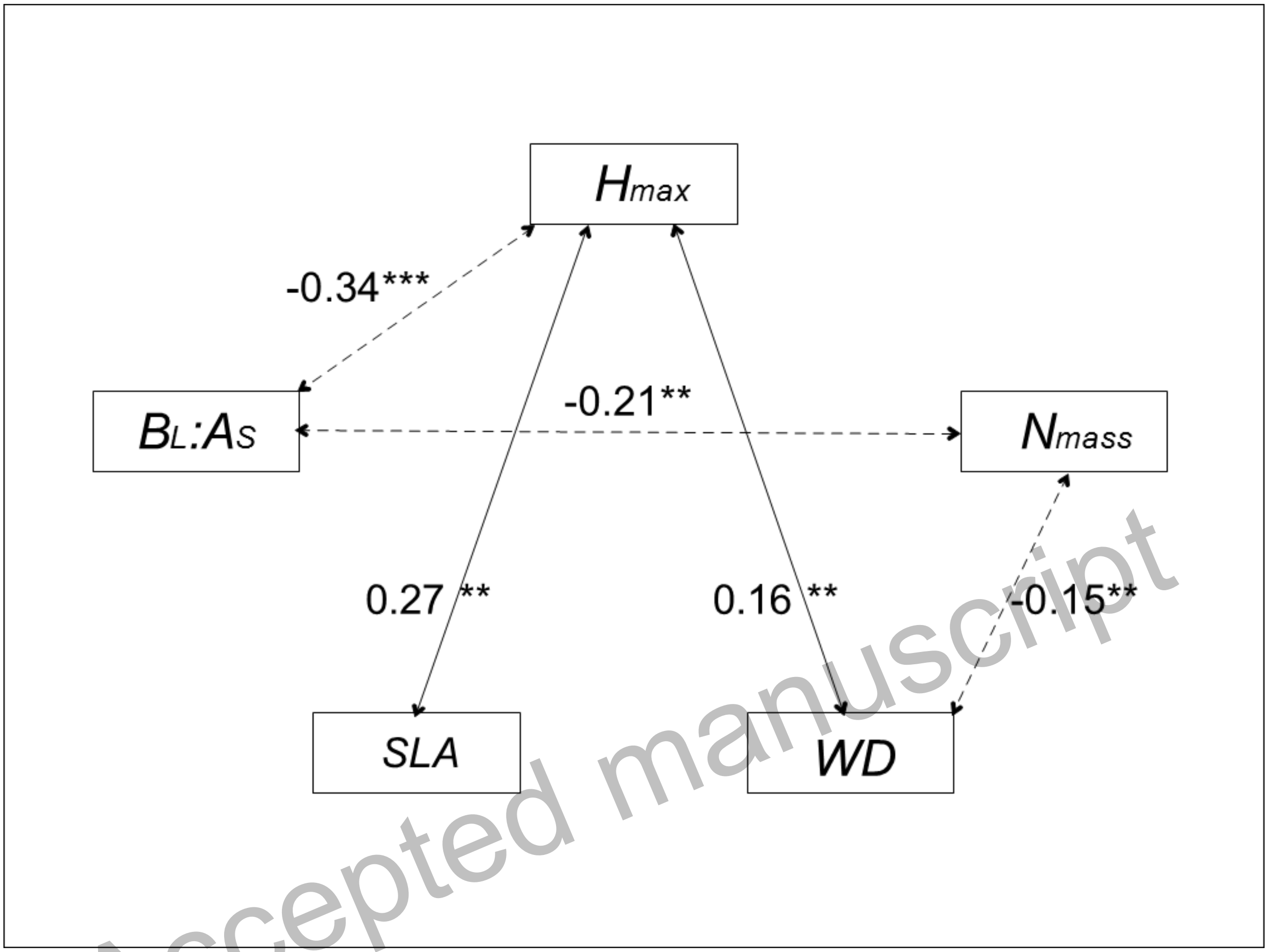
1.


Temperature (ºC)
< 3
3- 6
6-9
9-12
12-15
>15
Annual precipitation (mm)
< 400
400 - 600
600 - 800
800 - 1000
1000 - 1200
>1200

2.


(A)
% Cases
0
10
20
30
0
6
12
18
24
30
Hmax (m)
(B)
% Cases
0
10
20
30
0.35
0.45
0.55
0.65
0.75
0.85
WD (g cm^{-3})
(C)
% Cases
0
10
20
30
40
0.5
1
1.5
2
2.5
3
Nmass (%)
(D)
% Cases
0
20
40
60
80
0
0.04
0.08
$B_l : A_s$ (t/m^2)
(E)
% Cases
0
20
40
60
80
0
0.04
0.08
0.12
0.16
0.2
SLA (cm^{2}mg^{-1})
☐ Scots pine
▨ Interspecific

3.



4.