Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient

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Summary

- Trait variability in space and time allows plants to adjust to changing environmental conditions. However, we know little about how this variability is distributed and coordinated at different levels of organization.
- For six dominant tree species in NE Spain (three Fagaceae, three Pinaceae) we quantified the inter- and intraspecific variability of a set of traits along a water availability gradient. We measured leaf mass per area (LMA), leaf nitrogen concentration (N), carbon isotope composition in leaves ($\delta^{13}C$), stem wood density (WD), the Huber value (Hv, the ratio of cross-sectional sapwood area to leaf area), sapwood-specific and leaf-specific stem hydraulic conductivity (K_S and K_L, respectively), vulnerability to xylem embolism (P_{50}) and the turgor loss point (P_{tlp}).
- Differences between families explained the largest amount of variability for most traits, although intraspecific variability was also relevant. Species occupying wetter sites showed higher N, P_{50} and P_{tlp}, and lower LMA, $\delta^{13}C$ and Hv. However, when trait relationships with water availability were assessed within species they held only for Hv and P_{tlp}.
- Overall, our results indicate that intraspecific adjustments along the water availability gradient relied primarily on changes in resource allocation between sapwood and leaf area and in leaf water relations.

Keywords: drought, Huber value, hydraulic traits, intraspecific variation, interspecific variation, leaf economics spectrum, turgor loss point, water availability.

Introduction

Understanding the patterns underlying the huge diversity in plant form and function across different organizational levels is a central goal for ecologists. This diversity arises from a combination of genetic variation and phenotypic plasticity and results in adaptations to a range of environmental conditions across space and time (Bradshaw, 1965, 2006). In the last decades, trait-based ecology has emerged as a renewed discipline with the potential to be applied to dynamic global vegetation models (Van

Bodegom *et al.*, 2012; Harper *et al.*, 2016) and improve predictions of vegetation responses to environmental changes (Lavorel & Garnier, 2002; McGill *et al.*, 2006). The use of traits emphasizes species phenotypic values over taxonomic characteristics, facilitating the comparison among species and environments (Westoby & Wright, 2006). Identifying trade-offs that appear repeatedly because of evolutionary constraints has become a major research topic because they have the potential to reflect ecological strategies (Westoby *et al.*, 2002; Laughlin, 2014; Adler *et al.*, 2014). One of the dimensions that has received more attention is the leaf economics spectrum (LES), which highlights the trade-off between the dry mass and nutrient investments in leaf construction and the time required for obtaining returns on those investments (Reich *et al.*, 1997; Wright *et al.*, 2004). However, how exactly to describe and integrate complex community dynamics and predict ecosystem-level responses to environmental changes from individual-level trait measurements remains a challenge (Shipley *et al.*, 2016; Funk *et al.*, 2017).

Functional variability of plants has been frequently collapsed at the species level by using mean values, thus ignoring intraspecific trait variability (ITV). However, much work has shown that ITV is relevant when making predictions about plant community assembly and ecosystem functioning (Violle et al., 2012). This is particularly the case when we move from global to more regional scales (Messier *et al.*, 2010; Albert *et al.*, 2012; Violle *et al.*, 2012; Siefert *et al.*, 2015) and from organ-level traits to integrative traits involving several organs, as the latter tend to be more sensitive to the environment and show higher ITV as a result of local genetic adaptation and phenotypic plasticity (Marks, 2007; Siefert *et al.*, 2015). Thus, incorporating the variability of traits along environmental gradients among different levels of organization (family, species, population and individual) may help elucidate how traits respond to environmental variation and thus, improve trait-based models. For example, (Reich *et al.*, 2014) showed that accounting for ITV in gymnosperm needle longevity with latitude across boreal forests impacted significantly on carbon cycling projections.

A related challenge is to understand how trait covariation changes at different ecological levels (organizational levels and spatial scales) (Levin, 1992; Chave, 2013). Previous work has shown that correlation patterns are not always conserved across scales. For example, several studies have failed to find some of the central LES trade-offs, defined across species means at the global scale, when working at smaller spatial

or organizational scales (Wright & Sutton-Grier, 2012; Laforest-Lapointe *et al.*, 2014; Niinemets, 2015; Messier *et al.*, 2016; Anderegg *et al.*, 2018). This is because traits that appear closely coordinated at certain scales may have different sensitivities to scale-dependant drivers of variation, which can effectively decouple them at finer scales (Messier *et al.*, 2016). These results have important implications for trait-based ecology: if we want to predict species responses to changing environmental conditions, we need to elucidate intraspecific trait covariance structures to understand the adaptive value of trait combinations in different environments. At the same time, we should be cautious when interpreting trait relationships across species as fundamental trade-offs among functions and strategy dimensions. The study of trait correlation networks is a step forward in formalizing multiple factors shaping an integrated plant phenotype (Poorter *et al.*, 2014; Messier *et al.*, 2017) and allowing comparisons across scales.

The complexity of trait variation has usually been condensed in a few easily measured ('soft') traits that are not necessarily good predictors of demographic rates (Poorter *et al.*, 2008; Paine *et al.*, 2015; Yang *et al.*, 2018). For example, leaf mass per area (LMA), one of the most commonly measured traits, is usually weakly associated with growth rate, especially in adult plants (Wright *et al.*, 2010; Gibert *et al.*, 2016). Moving from 'soft' traits to more mechanistic ('hard') traits that have a clearer physiological basis and are likely to be stronger determinants of fitness should improve our capacity to elucidate vegetation dynamics under changing environmental conditions. This is particularly the case for drought-related impacts on forest function and dynamics (Skelton *et al.*, 2015; Sperry & Love, 2015; Brodribb, 2017), which are expected to increase in most regions of the Earth under climate change (Allen *et al.*, 2015).

Several studies have related hydraulic traits to plant performance under drought in terms of growth and mortality rates (Rowland *et al.*, 2015; Anderegg *et al.*, 2016; Choat *et al.*, 2018). Hydraulic traits define the efficiency of the plant water transport system, usually defined in terms of stem-specific hydraulic conductivity (K_S) and its safety against failure under drought stress, typically characterized as the water potential at which 50% stem conductivity is lost due to xylem embolism (P_{50}). In addition, allocation to sapwood cross-sectional area relative to leaf area (the Huber value, Hv) regulates supply capacity per unit of water demand, and it is thus a key component of plant hydraulic architecture (Mencuccini & Bonosi, 2001). It has been shown that plants can respond to drier conditions by increasing the resistance to xylem embolism (e.g.,

Blackman *et al.*, 2014), decreasing the leaf water potential at turgor loss in leaves (Bartlett *et al.*, 2012) and/or increasing their sapwood-to-leaf area ratio (Martínez-Vilalta *et al.*, 2009). Thus , these hydraulic traits can be used to describe the range of plant hydraulic strategies in diverse communities (Skelton *et al.*, 2015) and may provide stronger insights into the drivers of forest dynamics than the more commonly measured 'soft' traits (Brodribb, 2017).

If trait variation across scales in commonly measured 'soft' traits remains poorly understood, knowledge is even more limited regarding hydraulic traits. A recent meta-analysis found that 33% of the variation in P_{50} was contributed by differences within species (Anderegg, 2015). However, part of this variability could be due to methodological aspects (Cochard *et al.*, 2013) and several individual studies have shown low plasticity in embolism resistance across climatically contrasted populations (Maherali & DeLucia, 2000; Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2011, 2014; López *et al.*, 2016). The degree of coordination between leaf economics traits and hydraulic traits is also a leading research subject. A universal 'fast-slow' whole-plant economics spectrum that integrates resource use strategies (for water, carbon and nutrients) across organs has been proposed (Reich, 2014), but the evidence remains mixed (Brodribb *et al.*, 2007; Blonder *et al.*, 2011; Markesteijn *et al.*, 2011; Méndez-Alonzo *et al.*, 2012; Sack *et al.*, 2013; Li *et al.*, 2015).

To address these critical issues, we studied the variability of a set of hydraulic, leaf and stem traits along a water availability gradient in six dominant tree species in Catalonia (NE Spain), focusing on the following questions. (1) How much trait variation is observed and how is it distributed among levels of organization? We hypothesize that differences between families (Pinaceae vs. Fagaceae) will explain the largest part of trait variability in this temperate system, although ITV will be substantial, especially for more integrative traits such as K_L and Hv. (2) How do traits vary along the water availability gradient within and between species? We hypothesize that hydraulic traits will be more closely linked to water availability than other stem and leaf traits. Most of the trait changes along the water availability gradient will entail species substitutions and, thus, the strength of trait–environment relationships will be weaker within than across species, reflecting lower capacity for functional adjustment within species. (3) How are traits coordinated across and within species? Across species, we hypothesize the existence of a general 'fast-slow' strategy at the whole-plant level that

157 combines LES and hydraulic traits (*e.g.*, low LMA will be associated with high Ks and
158 high vulnerability to embolism). At the same time, we expect that intraspecific
159 correlation networks may differ from those across species because relatively weak
160 evolutionary or physiological trade-offs can be reversed due to plasticity within-species.
161

162 **Materials and Methods**

163 *Study site and sampling design*

164 The study area included all the forested territory of Catalonia (NE Spain) that
165 encompasses 1.2 million ha, around 38% of its total land area. Catalonia is very diverse
166 both topographically and climatically: mean annual temperature ranges from 18°C (at
167 the southern coast) to 3°C (in the Pyrenees) and annual rainfall varies from 400 mm to
168 >1,500 mm (CDAC, http://www.opengis.uab.cat/acdc/). We selected six of the most
169 dominant tree species in Catalonia (3 Pinaceae and 3 Fagaceae), accounting for ~75% of
170 the total forest area (Gracia *et al.*, 2004, see also Table S1): *Pinus sylvestris* L, *Pinus*
171 *nigra* J.F.ARNOLD., *Pinus halepensis* MILL., *Fagus sylvatica* L., *Quercus pubescens*
172 WILLD. and *Quercus ilex* L. For each species, 15 plots from the Spanish forest inventory
173 (IFN) were resampled in which the target species was dominant (minimum 50% of the
174 total basal area), maximizing the water availability gradient occupied by each species in
175 the study region. Water availability was quantified as the precipitation to potential
176 evapotranspiration ratio, P/PET, for the spring-summer period (see below). Five plots
177 per species were sampled for each of three species-specific P/PET ranges following a
178 stratified random design (dry, corresponding to P/PET < 33 percentile; wet for P/PET >
179 66 percentile; and mild for the rest) (Fig. S1, S2). Plots with the two highest stoniness
180 levels and those that had been managed during the last 14 years according to previous
181 IFN surveys were discarded.

182 Within each plot, five non-suppressed canopy trees of the target species with
183 diameter at breast height (DBH) > 12.5 cm were randomly selected, all within 25 m of
184 the centre of the plot. All samples and data were collected from May to December 2015.
185 To minimise phenological variation in traits within species, species were sampled
186 sequentially (*P. halepensis*, mid-May to end June; *Q. pubescens*, end June and July; *F.*
187 *sylvatica*, August; *P. sylvestris*; September to mid-October; *Q. ilex*, mid-October to

mid-November; *P. nigra*, mid-November to mid-December). From each tree, two branches (one for leaf measurements and the other for hydraulic measurements) were sampled from the exposed part of the canopy in the top half of the crown. Sampled branches were at least 70 cm long for *Pinus* spp., 150 cm for *Quercus* spp. and 80 cm for *Fagus*, to account for differences in the maximum length of xylem conduits (see below). Branches were transported to the laboratory inside plastic bags under cool and dark conditions and measurements were taken within 24h.

Environmental variables

At each plot, four soil samples (20 cm deep) were taken using a soil core at the four cardinal points at 5 m distance from the centre of the plot. The topsoil (O horizon) was removed to exclude the organic deposit and litterfall, and the four samples were merged. The following variables were measured on each pooled sample: $N\text{-}NO_3$ concentration (colorimetric method; Keeney & Nelson, 1982), phosphorus content (available phosphorous-Olsen phosphorous; Olsen & Sommers, 1982), soil humidity (gravimetric soil water content; Gardner, 1986), organic matter fraction (organic carbon content estimated with acid dichromate oxidation method; Nelson & Sommers, 1982) and soil texture classes defined by the USDA system (sedimentation-Robinson pipette; Gee & Or, 2002). To integrate the different components of soil texture into one single variable, the exponent of the Saxton equation (Saxton *et al.*, 1986) was calculated as follows:

$$b = -3.140 - 0.00222\ (\%\ clay)^2 - 3.484 \cdot 10^{-5}\ (\%\ sand)^2\ (\%\ clay) \quad \text{(Equation 1)}$$

where less negative values of *b* indicate sandy soils with lower soil water retention capacity.

Forest structure data for each plot were also available from the last Spanish forest inventory (IFN4) that was conducted over the same time period as our sampling. Forest structural data included total plot basal area, stand density, mean diameter at breast height and the 90^{th} percentile for height of all trees in the plot. Climate data were obtained from the Climatic Digital Atlas of Catalonia (Ninyerola *et al.*, 2005), a collection of digital maps at 200 x 200 m resolution including average annual radiation,

mean annual temperature, minimum annual temperature, and annual precipitation for the period 1951-2010. PET values were calculated according to the Hargreaves-Samani method (Hargreaves & Samani, 1982) and used to estimate P/PET for the spring-summer period and P/PET for the summer period.

Leaf traits and wood density

Standard protocols (Pérez-Harguindeguy *et al.*, 2013) were followed for all trait measurements. Previous-year needles (conifers) and current-year leaves (broadleaves) were selected to measure fully expanded leaves. Twigs with leaves were cut under water and placed into flasks with the cut end submerged in deionized water in the dark overnight before measurements.

Leaf mass per area (LMA) is a measure of biomass investment in leaves per unit light interception and gas exchange (Poorter *et al.*, 2009). For LMA determinations, twenty leaves were randomly selected, scanned and their areas were measured with ImageJ software (Wayne Rasband-National Institute of Health, Bethesda, USA). Afterwards, samples were oven-dried at 60 °C and weighed, and LMA was calculated as leaf dry mass/ fresh area.

The Huber value is the ratio of cross-sectional sapwood area to subtended leaf area, and can be viewed therefore as the ratio of hydraulic and mechanical investment costs over the expected gains obtained by leaf display. Leaves from terminal branches (65 cm long from the tip) were oven dried and weighted, and LMA was used to convert the total dry weight of the distal leaves of each branch into total branch leaf area. In order to calculate branch level Hv, and to make values comparable across species, maximum leaf area was estimated taking into account species phenology and the time of sampling. Sapwood area was obtained through measuring total xylem area on digital images of stained (safranin-astra blue) 15-20 micrometer thin sections in ImageJ (v 1.440 - Wayne Rasband, USA).

We used leaf carbon isotope composition ($\delta^{13}C$) and leaf nitrogen concentrations (N) to further characterize leaf functioning. Less negative $\delta^{13}C$ values suggesting lower discrimination against the heavier ^{13}C are indicative of greater stomatal control and

water-use efficiency (Farquhar *et al.*, 1989), whereas higher leaf N concentrations are usually associated to higher photosynthetic capacity because of the high N content of photosynthetic machinery (Evans, 1989). Leaf $\delta^{13}C$ and N were determined using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the UC-Davis Stable Isotopes Facility (California, USA). Samples were previously oven-dried at 60º C for four days, grounded with a Retsch MM400 ball mill (Verder Group, Netherlands) and placed in tin capsules for analysis. Carbon stable isotope concentrations were expressed in relation to the Pee-Dee Belemnite (PDB) standard.

Leaf osmotic potential (ψ_0) was measured with a VAPRO 5500 vapor pressure osmometer. Leaves were wrapped in foil to limit condensation and evaporation, were submerged in liquid nitrogen for two minutes and were sealed in a plastic zip bag at ambient conditions. After letting them defrost, they were put inside a syringe and squeezed until 10 µl of sap were obtained. Finally, ψ_0 was used to predict the leaf water potential at which leaf cells lose turgor closing their stomata and ceasing gas exchange and growth (P_{tlp}) (Brodribb *et al.*, 2003) following the equation described in Bartlett *et al.* (2012):

$$P_{tlp} = 0.832\ \psi_0 - 0.631 \qquad \text{(Equation 2)}$$

Wood density (WD) is considered a central trait shaping the wood economics spectrum (Chave *et al.*, 2009). We measured WD on one stem core per individual extracted using a hand increment borer (5 mm diameter; Suunto, Vantaa, Finland). The core was sealed in plastic tubes upon collection and taken to the laboratory under cold conditions. Fresh core volume of all wood was calculated after removing the bark by the dimensional method, measuring its total length and its diameter using a caliper. Cores were then oven dried at 100 ° C for 48 h and weighed. Wood density was calculated as the oven-dry mass divided by fresh volume.

Hydraulic traits

Prior to hydraulic measurements, maximum vessel length was estimated using the air infiltration technique (Ewers & Fisher, 1989) on eight 2 m branches per species. We flowed compressed air (~0.15 MPa) through the branches with their basal end

immersed in water and successively shortened the stem until bubbling was observed. Because compressed air at low pressures cannot pass through vessel end walls, the bubbling indicated the presence of open xylem conduits. The resulting estimates of maximum conduit length were used to decide the minimum length of the sampled branches (see *Study site and sampling design* section above).

Vulnerability curves were established by measuring the hydraulic conductivity of stem segments at different water potentials, using a variation of the bench dehydration method (Sperry & Tyree, 1988; Cochard *et al.*, 2013; Choat *et al.*, 2015). Hydraulic conductivity was measured using a commercial XYL'EM apparatus (Bronkhorst, Montigny-les-Cormeilles, France) as the ratio between the flow through the stem segment and the pressure gradient (5 kPa). The initial hydraulic conductivity (K_i) was measured in three subsamples (segments) per branch that were excised underwater at the terminal part of the shoots (Martin-StPaul *et al.*, 2014). An initial cut was applied to allow xylem tension in the branch segment to relax before measurements, avoiding artefacts associated with the cutting under tension (Wheeler *et al.*, 2013). After the segments were cut again to their final size (~2 cm in length), their proximal ends were connected to the tubing system of the XYL'EM, which was filled with deionized filtered water with 10 mM KCl and 1 mM $CaCl_2$ that had been previously degassed using a membrane contactor (Liqui-Cell Mini-Module membrane 1.7x5.5, Charlotte, USA). After measuring the initial conductivity, the segments were flushed once at 0.15 MPa for 10 minutes (for *Quercus spp*. and *F. sylvatica*) or held in the solution under partial vacuum during 48h (for *Pinus spp.,* as flushing conifer segments often results in the pit membranes being permanently pushed against tracheid cells walls) in order to measure their maximal conductivity (K_{max}) as above. The values of K_i and K_{max} were used to compute the percent loss of hydraulic conductivity (PLC). The previous measurements were repeated a second time on a different set of stem segments after branches had been dehydrated on the bench to obtain PLC estimates at lower water potentials. The timing of this second measurement was adjusted for different species and branches (between two and eight days) to cover a wide range of PLC values. The tubing system was regularly cleaned using 10% bleach solution for at least 20 min to prevent microorganism's growth and, afterwards, flushed with a degassed solution. Additionally, we used the apical part of each measured twig segment

311 to measure water potential (Ψ) with a Scholander pressure chamber (Solfranc
312 Tecnologias, Tarragona, Spain).

313 To fit vulnerability curves to each set of PLC and water potential measurements,
314 the following sigmoid function was used (Pammenter & Willigen, 1998):

315 $$PLC = 100/(1 + \exp(a(\Psi - P_{50}))) \quad \text{(Equation 3)}$$

316 where Ψ is the water potential, *a* is the slope of the curve and thus determines the rate at
317 which conductivity is lost as water potential declines, and P_{50} determines the position of
318 the curve on the abscissa and gives the pressure causing 50% loss of conductivity.
319 Parameters were estimated by fitting a separate nonlinear mixed model for each species,
320 using the *nlme* R package (Pinheiro *et al.*, 2018). The model accounted for individual
321 nested in plot as a random effect on coefficient P_{50}. Preliminary analyses confirmed that
322 this model structure provided the best fit to the data.

323 In addition, all distal leaves of each segment were removed to determinate their
324 area as explained above. Leaf-specific hydraulic conductivity (K_L) was calculated as
325 K_{max} divided by the distal leaf area supported. Similarly, stem-specific hydraulic
326 conductivity (K_S) was calculated as K_{max} divided by cross-sectional sapwood area.

327

328 *Statistical analyses*

329 To assess trait variability, the quartile coefficient of dispersion (QCD) was
330 calculated for each trait as the ratio between half the interquartile range ((Q3-Q1)/2) and
331 the average of the quartiles ((Q1+Q3)/2). QCD was used as a more robust measure of
332 dispersion than the coefficient of variation (CV), as the latter is not appropriate for
333 datasets including isotopic measurements (Brendel, 2014) or log-transformed data
334 (Canchola *et al.*, 2017) (see also the Supporting Information Table S2). To understand
335 the distribution of variability for each trait, we used different sets of linear mixed
336 models, always fitting separate models for each trait. In the first ones, family, species
337 and population were introduced as nested random factors to assess how trait variability
338 was distributed among these different levels of organization. In the second ones, models
339 were fit separately for each family, and included only species and population (nested) to
340 assess trait variability among- and within-species (within each family). All variables

were checked for normality and natural-log transformed whenever required to ensure normality.

Before exploring the effect of environmental factors on trait variation, three separate principal components analyses (PCAs) were performed to summarize soil, forest structure and climate data (Supporting Information Fig. S3). As before, all variables were checked for normality and natural-log transformed if required. For further analyses, the two most orthogonal variables showing the highest axes loading in each PCA were selected as integrated measures of environmental predictors. Coefficient b from Saxton equation (Eqn.1) and soil P were selected to describe soil characteristics, the mean tree diameter at breast height and total plot basal area to describe forest structure, and spring-summer P/PET and annual radiation to describe the climate. A first mixed model for each trait was fit starting with the 'saturated' model including all six environmental variables as fixed explanatory variables (without interactions). We included plot nested in species as random effects on the intercept of the model. Preliminary analyses showed that including a random species effect on the slopes did not improve model fit. This model was simplified stepwise removing the least significant term until a minimal adequate model with the lowest AIC (Akaike information criterion) was obtained. Models within 2 AIC units were considered equivalent in terms of fit and the simplest one was selected (Zuur *et al.*, 2009).

To explore specifically the variability of each trait along the P/PET gradient imposed by our sampling design, a second mixed model was fit for each trait. To separate the intraspecific from the interspecific component of trait responses to P/PET, we split P/PET into two additive variables which were included as separate fixed factors in the model: mean P/PET at the species level and centred P/PET. The latter variable was calculated as the difference between plot P/PET and the average P/PET for the corresponding species. We also included plot nested within species as a random effect on the intercept. As before, preliminary analyses showed that including a random species effect on the slope did not improve model fit. Model selection was carried out as described above. In all cases, the residuals of the selected models showed no obvious pattern and were approximately normally distributed. Linear mixed effects models were fit using the 'lme4' package (Bates *et al.*, 2015).

Finally, to characterize trait coordination within- and between-species, statistically significant correlations among traits were graphically represented using trait covariation networks with the *igraph* package (Csardi & Nepusz, 2006). Traits were represented as nodes and their correlation as the edges linking them. Two indicators of network centrality were calculated for each trait: the degree (D), defined as the number of edges of a node and the weighted degree (Dw), defined as the sum of all significant coefficients of correlation of a node (Supporting Information Table S5). In these latter analyses, all traits were natural-log transformed to improve the linearity of relationships. All analyses were carried out with R Statistical Software version 3.3.2 (R Core Team, 2017).

Results

Magnitude and distribution of trait variability

Most trait variation occurred between families (Pinaceae vs Fagaceae), with the exception of K_L and P_{tlp} for which the contribution of family was close to zero (Fig. 1b). Pinaceae tended to have higher LMA, Hv and $\delta^{13}C$ than Fagaceae, whereas the opposite was true for leaf N, WD, Ks and P_{50} (Figure S4). Overall, the proportion of variance explained at the intraspecific level (among and within populations) was on average 23.11% (Fig.1b). Within Pinaceae, K_S, K_L, Hv, WD and $\delta^{13}C$ showed a higher variability within than among species, while in Fagaceae this was only the case for Hv (Fig. S5). Other traits, such as P_{50}, showed substantial variability within families (4.51 MPa range within Pinaceae and 3.84 MPa range within Fagaceae) but most of this variance occurred across species (Table S2 and Fig. S5). K_S, K_L, LMA and Hv were the most variable traits, while $\delta^{13}C$, P_{tlp} and WD showed the least variation (Fig. 1a).

Trait responses along a water availability gradient

Traits responded differently to environmental factors (Table 2). Regarding soil properties, only soil phosphorus concentration showed a significant effect (positive) on LMA. As for stand structure, mean DBH had the strongest predictive effect across all models. Plots with larger trees on average were associated with lower LMA, lower WD, lower Hv and lower K_L. Stand basal area did not have significant effects on any trait. Finally, regarding climatic variables, high annual radiation was associated with leaves

with high LMA and high (less negative) $\delta^{13}C$. Plots with higher P/PET values had trees with more negative $\delta^{13}C$, lower Hv and less negative P_{tlp}. Overall, environmental variables at the plot level were not strong predictors of trait variation, as showed by relatively low values of the marginal R^2 (variation explained by the fixed effects) (Table 2). The fact that conditional R^2 values (Table 2) were normally much higher indicates that a large proportion of the variance in all traits is explained by differences among species and plots not captured by the environmental variables included in our analysis. Similar results were obtained if we used PCA axes as fixed factors describing environmental variation in models instead of individual variables (Table S3).

When we specifically explored the variability of each trait along the water availability (P/PET) gradient, considering both species means and plot-scale deviations from the means (centred values), higher marginal R^2 values and generally stronger effects were obtained (cf., Supporting Information Table S4). Significant relationships between P/PET and traits across species were consistent with the results reported in the previous paragraph, but we also found a positive relationship between P/PET and P_{50} (which was only marginally significant in the previous analysis) and a positive relationship with leaf N concentrations (Fig. 2). Importantly, trait-environment relationships were scale dependent and when these patterns were analysed within species, we only found significant relationships between centred P/PET and Hv and P_{tlp}. In these two cases, the relationships had the same (negative) sign but shallower slopes than the corresponding relationships across species (Fig. 2 and Supporting Information Table S4). Similar results were obtained when the mean DBH, the strongest explanatory variable in the initial mixed model (cf. previous paragraph), was included as a fixed factor in this latter model (not shown).

Trait correlation networks

Trait coordination differed within- and among- species (Fig. 3). When species means were considered, LMA and Hv were the traits showing highest values of centrality across species (Supporting Information Table S5). These two traits were positively related to each other and tightly linked to leaf N, $\delta^{13}C$ and P_{50}, so that higher allocation to sapwood area relative to leaf area was correlated with a greater construction cost per unit leaf area, lower N, higher water use efficiency (less negative

436 $\delta^{13}C$ values) and higher cavitation resistance (more negative P_{50}). P_{tlp} and K_L also
437 showed a positive relationship. Surprisingly, K_L and K_S were unrelated across species,
438 although a consistent, positive relationship appeared when species were analysed
439 separately (Fig. 3).

440 When analysing trait coordination within species, the strong LMA-Hv
441 relationship observed across species was only significant in one species (*Q. ilex*). At the
442 intraspecific level, the negative correlation between LMA and $-\delta^{13}C$ and the positive
443 correlation between K_S and K_L were the only relationships present in all cases (Fig. 3).
444 K_L showed the highest centrality in two out of the three measured gymnosperms, while
445 it was never central in angiosperms. On the other hand, LMA was the trait with the
446 highest centrality in two out of three studied angiosperms species. However, caution is
447 needed when considering these results due to the limited number of species sampled
448 within each family. When centrality was expressed as simple count of number of
449 significant correlations (degree), $\delta^{13}C$ and P_{tlp} appeared also particularly important,
450 especially in Fagaceae (Table S5). Finally, taking into account the overall network, *P.*
451 *sylvestris, F. sylvatica,* and *Q. ilex* were the species showing more correlations among
452 traits and the highest weighted degree (Table S5).

453

454 **Discussion**

455 We found that traits varied primarily between tree families but that ITV also accounted
456 for a relevant amount of total variation, especially in more integrative traits (K_L, Hv).
457 Most study traits responded to water availability, with increasing N, P_{50} and P_{tlp} and
458 decreasing LMA, $\delta^{13}C$ and Hv with P/PET across species. However, at the intraspecific
459 level we only found trait variation along the water availability gradient for Hv and P_{tlp}.
460 Finally, trait coordination was scale-dependent and we did not find clear evidence of a
461 single, dominant axis of variation reflecting a fast–slow, whole-plant economics
462 spectrum.

463

464 *Magnitude and distribution of trait variability*

465 Our results show that traits differ substantially in their variability along the same
466 environmental gradient, with an order of magnitude difference in the quartile coefficient

of dispersion between the most variable (K_S and K_L) and the least variable traits ($\delta^{13}C$ and P_{tlp}). The high variability of K_S and K_L agrees with previous studies across species (Maherali *et al.*, 2004; Martínez-Vilalta *et al.*, 2004; Gleason *et al.*, 2015), and may be caused by their high sensitivity to small differences in wood anatomy (particularly conduit diameter), which varies substantially across and within species (Tyree et al., 1994; Sperry et al., 2008). The higher variability of K_S relative to K_L likely reflects that the latter is normalized by water demand in terms of leaf area. More generally, however, the ecological implications of this high variability in xylem transport capacity, both within and among species, remains to be elucidated, particularly considering that in our study K_S and K_L did not respond consistently to water availability. On the other hand, P_{tlp} showed very low variability in comparison with other hydraulics traits, also in agreement with previous findings (Mencuccini *et al.*, 2015; Bartlett *et al.*, 2016).

Not surprisingly, trait variability was mostly distributed across families, reflecting the contrasting trait syndromes between angiosperm and gymnosperm clades (Wright *et al.*, 2004; Chave *et al.*, 2009; Carnicer *et al.*, 2013). Our results also confirm previous findings for hydraulic traits, with higher Hv, lower K_S and higher resistance to embolism in conifers relative to angiosperm trees (Becker *et al.*, 1999; Choat *et al.*, 2012; Gleason *et al.*, 2015). The high proportion of variation attributed to the family level for K_S is explained by xylem conduit properties, as unicellular conifer tracheids are substantially narrower and more than an order of magnitude shorter than angiosperm vessels (Sperry et al., 2006). Besides the direct effect of these different dimensions on K_S, the fact that we measured relatively short length segments implies that our K_S estimates corresponded mostly to lumen conductivity for the Fagaceae and to total conductivity (lumen and end-wall) for Pinaceae species. Interestingly, the family effect disappeared when xylem conductivity was normalized by leaf area (K_L) because conifers also tend to have more sapwood per unit of leaf area (higher Hv, Fig. S4) (see also Becker *et al.*, 1999).

ITV contributed to a substantial amount of the total variance (from 6 to 42% depending on the trait). This is consistent with a growing body of evidence showing that ITV is relevant (Albert *et al.*, 2012; Laforest-Lapointe *et al.*, 2014), especially when we move from organ-specific traits (leaves, stems or roots) to more integrative traits involving several organs (e.g. K_L, Hv) (Siefert et al., 2015). Studies addressing ITV in hydraulic traits are less frequent (but see Martínez-Vilalta *et al.*, 2009; Wortemann *et*

al., 2011; Lamy *et al.*, 2014; Hajek *et al.*, 2016). In line with our results, Hv and K_L have been reported to be among the most plastic hydraulic properties in pines (DeLucia *et al.*, 2000; Martínez-Vilalta *et al.*, 2009) while other traits such as P_{50} usually show low plasticity (Maherali & DeLucia, 2000; Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2014; López *et al.*, 2016). Further studies are needed to investigate whether these patterns are generalizable across other plant families**.** It should also be noted that we probably underestimated the magnitude of ITV because we did not cover the whole species distribution range, species were sampled sequentially to minimise phenological variation within species, and we always selected healthy-looking mature trees with sun-exposed branches according to standard trait sampling protocols (Pérez-Harguindeguy et al., 2013). These factors, however, would also affect total trait variation and it remains unclear what their impact would be on the percentage contribution of ITV.

Trait responses along a water availability gradient

In agreement with findings reported in others studies (Vilà-Cabrera *et al.*, 2015; Anderegg *et al.*, 2018), trait-environment relationships were not very tight, suggesting that unaccounted species-specific differences and/or other plot variables not included in our study were stronger drivers of trait variability. Mean DBH was the strongest determinant of trait variation. Specifically, plots with larger trees on average tended to have lower LMA, WD, Hv and K_L, in line with previous findings (Laforest-Lapointe *et al.*, 2014; Gleason *et al.*, 2018). The effect of P/PET, our target environmental factor, was significant or marginally significant for $\delta^{13}C$, Hv, P_{tlp} and P_{50}, but not for LMA, N or WD when controlling for the effect of other environmental factors. This indicates that hydraulic and water related traits responded more strongly to water availability than LES or other stem traits, as hypothesized.

When we assessed the overall response of each trait to P/PET, without accounting for the effect of other environmental variables that co-varied along the environmental gradient studied, a higher proportion of trait variance was explained, because species means were explicitly included in the model (Table S4). In this broader assessment, LMA and N were also related to water availability, besides the hydraulic/water relations variables identified in the previous analysis. Wetter sites were associated with species with leaf traits related to acquisitive resource strategies (low LMA and high N). Several studies have shown that LMA tends to be higher at drier

sites as a result of water stress adaptation through increasing wilting resistance (Schulze *et al.*, 1998; Cunningham *et al.*, 1999). Regarding the relationship between N and water availability, contrasting results have been reported. While some studies have reported that species from drier sites present higher N leaf concentration to enhance water conservation during photosynthesis (Wright & Westoby, 2002), others have found no general relationship (Killingbeck & Whitford, 1996; Vilà-Cabrera *et al.*, 2015).

Vulnerability to xylem embolism was lower (more negative P_{50}) in species occupying drier sites, consistent with the notion that cavitation resistance is a key determinant of species distributions (Maherali *et al.*, 2004; Jacobsen *et al.*, 2007; Martínez-Vilalta *et al.*, 2012; Choat *et al.*, 2012; Blackman *et al.*, 2014; Trueba *et al.*, 2017; Li *et al.*, 2018; Skelton *et al.*, 2018). Similarly, another key drought tolerance trait, P_{tlp}, also showed a significant relationship with P/PET across species, with lower (more negative) P_{tlp} associated with drier habitats, allowing the maintenance of leaf turgor and gas exchange under drier conditions (Brodribb *et al.*, 2003; Lenz *et al.*, 2006; Bartlett *et al.*, 2012). This did not prevent, however, an increase in water use efficiency (less negative $\delta^{13}C$ values) and increased allocation to sapwood area relative to leaf area (Hv) at drier sites, consistent with previous reports (Warren *et al.*, 2001; Martínez-Vilalta *et al.*, 2004, 2009; Gebrekirstos *et al.*, 2011). Interestingly, species hydraulic efficiency (K_S, K_L) did not vary consistently along the water availability gradient. Overall, our results across species suggest that increasing tolerance to hydraulic dysfunction in drier sites implies increasing carbon costs per unit leaf area in terms of leaf and sapwood construction.

Importantly, trait-environment relationships were scale dependent (Anderegg *et al.*, 2018) and, as hypothesized, relationships within species were generally less strong than across species. Hv and P_{tlp}, two of the three traits with higher %ITV, were the only traits that responded to P/PET within species. These two intraspecific relationships had the same sign but shallower slopes than the corresponding relationships with P/PET among species, which likely reflects lower capacity for hydraulic adjustment within than among species due to relatively fixed drought response strategies at the species level. This result highlights the importance of Hv and P_{tlp} in shaping plastic responses along water availability gradients. Lower leaf area per unit of sapwood (which reduced water demand) and osmotic adjustment may be needed to balance water and carbon costs under reduced water availability in the context of relatively constant hydraulic

safety thresholds within species, measured here as stem P_{50}. This is consistent with the view that P_{50} is an (evolutionarily) canalized trait buffered against genetic and environmental variation (Lamy *et al.*, 2014). Overall, adjustments along the water availability gradient in the six species studied rely more on changes in stomata closure and resource allocation between sapwood and leaf area than changes in hydraulic safety and efficiency, consistent with previous results comparing pine populations (Mencuccini & Grace, 1995; Mencuccini & Bonosi, 2001; Poyatos *et al.*, 2007; Martínez-Vilalta *et al.*, 2009).

Trait correlation networks

To our knowledge, our study is the first attempt to test simultaneously the covariation between traits related to leaf economics (LMA, N), xylem hydraulics in terms of safety and efficiency (P_{50}, K_S), allocation (K_L, HV) and traits related to leaf gas exchange ($\delta^{13}C$, P_{tlp}), both at the interspecific and intraspecific levels. We found weak evidence for the existence of a unique coordination between hydraulics and more standard leaf and stem traits, which would be required for the existence of universal, resource use strategies at the whole plant-level (our last hypothesis, cf. (Reich, 2014). In our study, species with conservative leaf economic strategies (i.e., higher LMA) presented a safer xylem (lower P_{50}), possibly to support longer leaf lifespans (Wright *et al.*, 2004). However, this interpretation should also consider that species occupying drier sites are also likely to be exposed to lower water potentials, which would affect their hydraulic safety margins and possibly result in higher hydraulic risk in drier locations. On the other hand, although higher LMA species showed also higher Hv, this pattern did not result in any relationship with xylem transport efficiency (either K_S or K_L). This lack of a universal 'fast-slow' whole-plant economics spectrum is reinforced when we assess trait covariation at the intraspecific level. We provide evidence that rather than a single dominant axis of 'fast–slow' plant economics spectrum, multiple combinations of traits are possible depending on the species and the environment. Caution is thus needed when interpreting the comparatively simple trait covariation structures revealed in global studies using relatively few traits (Díaz *et al.*, 2016), and comprehensive assessments including wider sets of traits may improve our ability to represent the patterns underlying the huge diversity in plant form and function.

The increase in water use efficiency (estimated from $\delta^{13}C$) with increasing LMA was the only correlation present in all studied trait networks. This relationship is commonly reported (Körner *et al.*, 1991; Hultine & Marshall, 2000) and it is probably due to an increase in length in the internal diffusion pathway from the stomata to the chloroplasts reducing carbon dioxide supply at the site of carboxylation (Evans *et al.*, 1986). We did not find support for a trade-off between hydraulic safety and efficiency across species and only in two cases within species, consistent with a recent global synthesis that found that many species presented low safety and low efficiency (Gleason et al., 2015). At the intraspecific level, of the two traits that responded to water availability at the intraspecific level, Hv was typically loosely linked to the rest of the trait network (except in *Q. ilex*), whereas P_{tlp} retained a more central role. Higher leaf tolerance to low water potentials (more negative P_{tlp}) was associated to higher water use efficiency (less negative $\delta^{13}C$) and to higher leaf construction costs (higher LMA) in most species, suggesting an adaptation to drier and hotter conditions (Wright *et al.*, 2005). It should be noted, however, that our results on trait coordination across species should be considered with caution, as only six species were measured. In addition, our experimental design does not allow disentangling associations resulting from fundamental constraints from those arising from indirect relationships through third variables (in our case driven by changing water availability), which should constitute a priority for future research.

Conclusion

Our study shows that plant adjustment along a water availability gradient involve many different suites of traits, and highlight the importance of ITV for understanding the capacity of plants to buffer against environmental changes. Availability of individual/plot level trait data coupled with environmental and site information will allow more accurate model parameterization and, therefore, better predictions of species responses to global change (Moran *et al.*, 2016). We show that, within species, plant adjustments along a water availability gradient rely more on changes in allocation (Hv) and leaf tolerance to low water potentials (P_{tlp}) than on changes in xylem safety or efficiency. Finally, we show that the use of trait networks could accommodate the intricate, multivariate relationships shaping plant strategies to a much greater degree than approaches based on bivariate relationships (Poorter *et al.*,

2014; Messier *et al.*, 2017). Scale-dependent trait covariation networks can provide powerful insights when assessing the architecture of plant plasticity and its limits under changing environmental conditions.

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Author Contribution

J. M.-V., M.M and T. R. planned and designed the research, T.R and J.B performed the measurements with contributions from H.C., M.M and J. M.-V., T.R. analyzed the data and T.R. wrote the first draft with contributions from J. M.-V., M.M, S. S.-M., J.B and H.C.

References

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-mukherjee J. **2014**. Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences* **111**: 740–745.

Albert CH, de Bello F, Boulangeat I, Pellet G, Lavorel S, Thuiller W. **2012**. On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* **121**: 116–126.

Allen CD, Breshears DD, McDowell NG. **2015**. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**: 1–55.

Anderegg WRL. **2015**. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**: 1008–1014.

Anderegg LDL, Berner LT, Badgley G, Sethi ML, Law BE, HilleRisLambers J. **2018**. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* **21**: 734–744.

Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S. **2016**. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences* **113**: 5024–5029.

Bartlett MK, Klein T, Jansen S, Choat B, Sack L. **2016**. The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences* **113**: 13098–13103.

Bartlett MK, Scoffoni C, Sack L. **2012**. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology letters* **15**: 393–405.

Bates D, Mächler M, Bolker B, Walker S. **2015**. Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software* **67**: 1–48.

Becker P, Tyree MT, Tsuda M. **1999**. Hydraulic conductances of angiosperms versus conifers: Similar transport sufficiency at the whole-plant level. *Tree Physiology* **19**: 445–452.

Blackman CJ, Gleason SM, Chang Y, Cook AM, Laws C, Westoby M. **2014**. Leaf hydraulic vulnerability to drought is linked to site water availability across a broad range of species and climates. *Annals of Botany* **114**: 435–440.

Blonder B, Violle C, Bentley LP, Enquist BJ. **2011**. Venation networks and the origin of the leaf economics spectrum. *Ecology Letters* **14**: 91–100.

Van Bodegom PM, Douma JC, Witte JPM, Ordoñez JC, Bartholomeus RP, Aerts R. **2012**. Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: Exploring the merits of traits-based approaches. *Global Ecology and Biogeography* **21**: 625–636.

Bradshaw AD. **1965**. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**: 115–155.

689 **Bradshaw AD**. **2006**. Unravelling phenotypic plasticity - Why should we bother? *New*
690 *Phytologist* **170**: 644–648.

691 **Brendel O**. **2014**. Is the coefficient of variation a valid measure for variability of stable
692 isotope abundances in biological materials? *Rapid Communications in Mass*
693 *Spectrometry* **28**: 370–376.

694 **Brodribb TJ**. **2017**. Progressing from 'functional' to mechanistic traits. *New*
695 *Phytologist* **215**: 9–11.

696 **Brodribb TJ, Feild TS, Jordan GJ**. **2007**. Leaf maximum photosynthetic rate and
697 venation are linked by hydraulics. *Plant Physiology* **144**: 1890–1898.

698 **Brodribb TJ, Holbrook NM, Edwards EJ, Gutiérrez M V. 2003**. Relations between
699 stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees.
700 *Plant, Cell and Environment* **26**: 443–450.

701 **Canchola JA, Tang S, Hemyari P, Paxinos E, Marins E**. **2017**. Correct use of percent
702 coefficient of variation (% CV) formula for log-transformed data. *MOJ Proteomics &*
703 *Bioinformatics* **6**: 00200.

704 **Carnicer J, Barbeta A, Sperlich D, Coll M, Peñuelas J**. **2013**. Contrasting trait
705 syndromes in angiosperms and conifers are associated with different responses of tree
706 growth to temperature on a large scale. *Frontiers in Plant Science* **4**: 1–19.

707 **Chave J**. **2013**. The problem of pattern and scale in ecology: What have we learned in
708 20 years? *Ecology Letters* **16**: 4–16.

709 **Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE**. **2009**. Towards a
710 worldwide wood economics spectrum. *Ecology Letters* **12**: 351–366.

711 **Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE**. **2018**.
712 Triggers of tree mortality under drought. *Nature* **558**: 531–539.

713 **Choat B, Creek AD, Lo Gullo MA, Nardini A, Oddo E, Raimondo F, Torres-Ruiz**
714 **JM, Triiflo P, Vilagrosa A**. **2015**. Quantification of vulnerability to xylem embolism -
715 bench dehydration. *Prometheus Wiki*.

716 **Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild**

TS, Gleason SM, Hacke UG, *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–5.

Cochard H, Badel E, Herbette S, Delzon S, Choat B, Jansen S. **2013**. Methods for measuring plant vulnerability to cavitation: A critical review. *Journal of Experimental Botany* **64**: 4779–4791.

Csardi G, Nepusz T. **2006**. The igraph software package for complex network research. *InterJournal* **Complex Sy**: 1695.

Cunningham SA, Summerhayes B, Westoby M. **1999**. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecology* **69**: 569–588.

DeLucia EH, Maherali H, Carey E V. 2000. Climate-driven changes in biomass allocation in pines. *Global Change Biology* **6**: 587–593.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, *et al.* 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Evans JR. **1989**. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* **78**: 9–19.

Evans J, Sharkey T, Berry J, Farquhar G. **1986**. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. *Australian Journal of Plant Physiology* **13**: 281–292.

Ewers FW, Fisher JB. **1989**. Techniques for measuring vessel lengths and diameters in stems of woody plants. *American Journal of Botany* **76**: 645–656.

Farquhar GD, Hubick KT, Condon AG, Richards RA. **1989**. Carbon isotope fractionation and plant water-use efficiency. Stable isotopes in ecological research. New York, USA: Springer New York, 21–40.

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J. **2017**. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews* **92**: 1156–1173.

Gardner WR. **1986**. Water content. In: Klute A, ed. Methods of soil analysis: Part 1. Physical and mineralogical methods. Madison: American Society of Agronomy, Soil Science Society of America.63–73.

Gebrekirstos A, van Noordwijk M, Neufeldt H, Mitlöhner R. **2011**. Relationships of stable carbon isotopes, plant water potential and growth: An approach to asses water use efficiency and growth strategies of dry land agroforestry species. *Trees - Structure and Function* **25**: 95–102.

Gee G., Or D. **2002**. Particle size analysis. In: Dane J, In: Topp G, eds. Methods of soil analysis. Part 4. Physical methods. Madison: Soil Science Society of America.383–411.

Gibert A, Gray EF, Westoby M, Wright IJ, Falster DS. **2016**. On the link between functional traits and growth rate: meta-analysis shows effects change with plant size, as predicted. *Journal of Ecology* **104**: 1488–1503.

Gleason SM, Stephens AEA, Tozer WC, Blackman CJ, Butler DW, Chang Y, Cook AM, Cooke J, Laws CA, Rosell JA, *et al.* 2018. Shoot growth of woody trees and shrubs is predicted by maximum plant height and associated traits. *Functional Ecology* **32**: 247–259.

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Bhaskar R, Brodribb TJ, Bucci SJ, Cao K, *et al.* 2015. Weak tradeoff between xylem safety and xylem- specific hydraulic efficiency across the world's woody plant species . *New Phytologist* **209**: 123–136.

Gracia C, Burriel JA, Ibàñez JJ, Mata T, Vayreda J. **2004**. *Inventari ecològic i forestal de Catalunya. Catalunya,10 volumes.* Bellaterra, Spain: CREAF.

Hajek P, Kurjak D, von Wühlisch G, Delzon S, Schuldt B. **2016**. Intraspecific variation in wood anatomical, hydraulic, and foliar traits in ten european beech provenances differing in growth yield. *Frontiers in Plant Science* **7**: 1–14.

Hargreaves GH, Samani ZA. **1982**. Estimating potential evapotranspiration. *Journal of the Irrigation & Drainage Division - ASCE* **108**: 225–230.

Harper AB, Cox PM, Friedlingstein P, Wiltshire AJ, Jones CD, Sitch S, Mercado LM, Groenendijk M, Robertson E, Kattge J, *et al.* 2016. Improved representation of

plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4.2) using plant trait information. *Geoscientific Model Development* **9**: 2415–2440.

Hultine KR, Marshall JD. **2000**. Altitude trends in conifer leaf morphology and stable carbon isotope composition. *Oecologia* **123**: 32–40.

Jacobsen AL, Pratt RB, Davis SD, Ewers FW. **2007**. Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell and Environment* **30**: 1599–1609.

Keeney D, Nelson D. **1982**. Nitrogen-inorganic forms. In: Page A, ed. Methods of soil analysis. Part 2: Chemical and microbiological properties. Madison: American Society of Agronomy, Soil Science Society of America.643–698.

Killingbeck KT, Whitford WG. **1996**. High foliar nitrogen in desert shrubs: An important ecosystem trait or defective desert doctrine? *Ecology* **77**: 1728–1737.

Körner C, Farquhar GD, Wong SC. **1991**. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia* **88**: 30–40.

Laforest-Lapointe I, Martínez-Vilalta J, Retana J. **2014**. Intraspecific variability in functional traits matters: Case study of Scots pine. *Oecologia* **175**: 1337–1348.

Lamy JB, Bouffier L, Burlett R, Plomion C, Cochard H, Delzon S. **2011**. Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. *PLoS ONE* **6**: e23476.

Lamy JB, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C. **2014**. Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *New Phytologist* **201**: 874–886.

Laughlin DC. **2014**. The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* **102**: 186–193.

Lavorel S, Garnier E. **2002**. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545–556.

Lenz TI, Wright IJ, Westoby M. **2006**. Interrelations among pressure-volume curve traits across species and water availability gradients. *Physiologia Plantarum* **127**: 423–433.

Levin SA. **1992**. The problem of pattern and scale in ecology. *Ecology* **73**: 1943–1967.

Li X, Blackman CJ, Choat B, Duursma RA, Rymer PD, Medlyn BE, Tissue DT. **2018**. Tree hydraulic traits are co-ordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant, Cell & Environment* **41**: 646–660.

Li L, McCormack ML, Ma C, Kong D, Zhang Q, Chen X, Zeng H, Niinemets Ü, Guo D. **2015**. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecology Letters* **18**: 899–906.

López R, Cano FJ, Choat B, Cochard H, Gil L. **2016**. Plasticity in vulnerability to cavitation of pinus canariensis occurs only at the driest end of an aridity gradient. *Frontiers in Plant Science* **7**: 769.

Maherali H, DeLucia EH. **2000**. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiology* **20**: 859–867.

Maherali H, Pockman WT, Jackson RB. **2004**. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* **85**: 2184–2199.

Markesteijn L, Poorter L, Bongers F, Paz H, Sack L. **2011**. Hydraulics and life history of tropical dry forest tree species: Coordination of species' drought and shade tolerance. *New Phytologist* **191**: 480–495.

Marks CO. **2007**. The causes of variation in tree seedling traits: the roles of environmental selection versus chance. *Evolution* **61**: 455–469.

Martin-StPaul NK, Longepierre D, Huc R, Delzon S, Burlett R, Joffre R, Rambal S, Cochard H. **2014**. How reliable are methods to assess xylem vulnerability to cavitation? The issue of 'open vessel' artifact in oaks. *Tree physiology* **34**: 894–905.

Martínez-Vilalta J, Cochard H, Mencuccini M, Sterck F, Herrero A, Korhonen JFJ, Llorens P, Nikinmaa E, Nolè A, Poyatos R, *et al.* 2009. Hydraulic adjustment of Scots pine across Europe. *New Phytologist* **184**: 353–364.

Martínez-Vilalta J, Mencuccini M, Álvarez X, Camacho J, Loepfe L, Piñol J, Cochard H, Sterck F, Herrero A, Korhonen JFJ, *et al.* 2012. Spatial distribution and packing of xylem conduits. *American Journal of Botany* **99**: 1189–1196.

Martínez-Vilalta J, Sala A, Piñol J. **2004**. The hydraulic architecture of Pinaceae –a review. *Plant Ecology* **171**: 3–13.

McGill BJ, Enquist BJ, Weiher E, Westoby M. **2006**. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**: 178–185.

Mencuccini M, Bonosi L. **2001**. Leaf/sapwood area ratios in Scots pine show acclimation across Europe. *Canadian Journal of Forest Research* **31**: 442–456.

Mencuccini M, Grace J. **1995**. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology* **15**: 1–10.

Mencuccini M, Minunno F, Salmon Y, Martínez-Vilalta J, Hölttä T. **2015**. Coordination of physiological traits involved in drought-induced mortality of woody plants. *New Phytologist* **208**: 396–409.

Méndez-Alonzo R, Paz H, Cruz RZ, Rosell JA, Olson ME. **2012**. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* **93**: 2397–2406.

Messier J, Lechowicz MJ, Mcgill BJ, Violle C, Enquist BJ. **2017**. Interspecific integration of trait dimensions at local scales: The plant phenotype as an integrated network. *Journal of Ecology* **105**: 1775–1790.

Messier J, Mcgill BJ, Enquist BJ, Lechowicz MJ. **2016**. Trait variation and integration across scales: Is the leaf economic spectrum present at local scales? *Ecography* **40**: 685–697.

Messier J, McGill BJ, Lechowicz MJ. **2010**. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838–848.

Moran E V., Hartig F, Bell DM. **2016**. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* **22**: 137–150.

Nelson DW, Sommers LE. **1982**. Total carbon, organic carbon, and organic matter. In: Page A, ed. Methods of soil analysis. Part 2. Chemical and microbiological properties. Madison: American Society of Agronomy, Soil Science Society of America.961–1010.

Niinemets Ü. **2015**. Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll Quercus ilex. *New Phytologist* **205**: 79–96.

Ninyerola M, Pons X, Roure J. **2005**. Atlas climático digital de la Península Ibérica. Metodologías y aplicaciones en bioclimatología y geobotánica. Metodología y aplicaciones en bioclimatología y geobotánica. Bellaterra, Spain: Universidad Autónoma de Barcelona

Olsen SR, Sommers LE. **1982**. Phosphorous. In: Page A, ed. Methods of soil analysis. Part 2. Chemical and microbiological properties. Madison: American Society of Agronomy, Soil Science Society of America.403–430.

Paine CET, Amissah L, Auge H, Baraloto C, Baruffol M, Bourland N, Bruelheide H, Daïnou K, de Gouvenain RC, Doucet JL, *et al.* 2015. Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology* **103**: 978–989.

Pammenter NW, Willigen C V. **1998**. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology* **18**: 589–593.

Pérez-Harguindeguy N, Díaz S, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, *et al.* 2013. New Handbook for standardized measurment of plant functional traits worldwide. *Australian Journal of Botany* **23**: 167–234.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. **2018**. {nlme}: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137, https://CRAN.R-project.org/package=nlme.

Poorter H, Lambers H, Evans JR. **2014**. Trait correlation networks - a whole-plant perspective on the recently criticized leaf economic spectrum. *New Phytologist* **201**: 378–382.

Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R, Niinemets U, Poorter L, Wright IJ, Villar R. **2009**. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New phytologist* **182**: 565–588.

Poorter L, Wright SJ, Paz H, Ackerly DD, Condit R, Ibarra-Manríquez G, Harms KE, Licona JC, Martínez-Ramos M, Mazer SJ, *et al.* 2008. Are Functional Traits Good Predictors of Demographic Rates? Evidence From Five Neotropical Forests. *Ecology* **89**: 1908–1920.

Poyatos R, Martínez-Vilalta J, Čermák J, Ceulemans R, Granier A, Irvine J, Köstner B, Lagergren F, Meiresonne L, Nadezhdina N, *et al.* 2007. Plasticity in hydraulic architecture of Scots pine across Eurasia. *Oecologia* **153**: 245–259.

R Core Team. **2017**. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Reich PB. **2014**. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology* **102**: 275–301.

Reich PB, Rich RL, Wang Y, Lu X, Oleksyn J. **2014**. Biogeographic variation in evergreen conifer needle longevity and impacts on boreal forest carbon cycle projections. *Proceedings of the National Academy of Sciences* **111**: 13703–13708.

Reich PB, Walters MB, Ellsworth DS. **1997**. From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences* **94**: 13730–13734.

Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS, *et al.* 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* **528**: 119–122.

Sack L, Scoffoni C, John GP, Poorter H, Mason CM, Mendez-Alonzo R, Donovan LA. **2013**. How do leaf veins influence the worldwide leaf economic spectrum? Review and synthesis. *Journal of Experimental Botany* **64**: 4053–4080.

Saxton KE, Rawls WJ, Romberger JS, Papendick RI. **1986**. Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal* **50**:

1031.

Schulze E, Williams R, Farquhar G, Schulze W, Langridge J, JM M, BH W. **1998**. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* **25**: 413–425.

Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB. **2016**. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* **180**: 923–931.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso M V., *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406–1419.

Skelton RP, Dawson TE, Thompson SE, Shen Y, Weitz AP, Ackerly D. **2018**. Low vulnerability to xylem embolism in leaves and stems of north american oaks. *Plant Physiology* **177**: 1066–1077.

Skelton RP, West AG, Dawson TE. **2015**. Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences* **112**: 5744–9.

Sperry JS, Hacke UG, Pittermann J. **2006**. Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany* **93**: 1490–1500.

Sperry JS, Love DM. **2015**. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* **207**: 14–27.

Sperry JS, Meinzer FC, McCulloh KA. **2008**. Safety and efficiency conflicts in hydraulic architecture: Scaling from tissues to trees. *Plant, Cell and Environment* **31**: 632–645.

Sperry JS, Tyree MT. **1988**. Mechanism of water stress-induced. *Plant physiology* **88**: 581–587.

Trueba S, Pouteau R, Lens F, Feild TS, Isnard S, Olson ME, Delzon S. **2017**. Vulnerability to xylem embolism as a major correlate of the environmental distribution

946 of rain forest species on a tropical island. *Plant Cell and Environment* **40**: 277–289.

947 **Tyree MT, Davis SD, Cochard H**. **1994**. Biophysical perspectives of xylem evolution:
948 Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA*
949 *Journal* **15**: 335–360.

950 **Vilà-Cabrera A, Martínez-Vilalta J, Retana J**. **2015**. Functional trait variation along
951 environmental gradients in temperate and Mediterranean trees. *Global Ecology and*
952 *Biogeography* **24**: 1377–1389.

953 **Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier**
954 **J**. **2012**. The return of the variance: intraspecific variability in community ecology.
955 *Trends in Ecology and Evolution* **27**: 244–252.

956 **Warren CR, McGrath JF, Adams MA**. **2001**. Water availability and carbon isotope
957 discrimination in conifers. *Oecologia* **127**: 476–486.

958 **Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ**. **2002**. Plant ecological
959 strategies: some leading dimensions of variation between species. *Annual Review of*
960 *Ecology and Systematics* **33**: 125–159.

961 **Westoby M, Wright IJ**. **2006**. Land-plant ecology on the basis of functional traits.
962 *Trends in Ecology and Evolution* **21**: 261–268.

963 **Wheeler JK, Huggett BA, Tofte AN, Rockwell FE, Holbrook NM**. **2013**. Cutting
964 xylem under tension or supersaturated with gas can generate PLC and the appearance of
965 rapid recovery from embolism. *Plant, Cell and Environment* **36**: 1938–1949.

966 **Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducousso A, Gomory**
967 **D, Roeckel-Drevet P, Cochard H**. **2011**. Genotypic variability and phenotypic
968 plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology*
969 **31**: 1175–1182.

970 **Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R,**
971 **Dalling JW, Davies SJ, Díaz S, *et al.* 2010**. Functional traits and the growth —
972 mortality trade-off in tropical trees. *Ecology* **91**: 3664–3674.

973 **Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Groom PK, Hikosaka K, Lee**
974 **W, Lusk CH, Niinemets Ü, Oleksyn J, *et al.* 2005**. Modulation of leaf economic traits

and trait relationships by climate. *Global Ecology and Biogeography* **14**: 411–421.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornellssen JHC, Diemer M, *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Wright JP, Sutton-Grier A. **2012**. Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology* **26**: 1390–1398.

Wright IJ, Westoby M. **2002**. Leaves at low versus high rainfall: Coordination of structure, lifespan and physiology. *New Phytologist* **155**: 403–416.

Yang J, Cao M, Swenson NG. **2018**. Why functional traits do not predict tree demographic rates. *Trends in Ecology & Evolution* **33**: 1–11.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith G. **2009**. Mixed effects models and extensions in ecology with R. New York, USA: Springer Science

Supporting Information

Additional supporting information may be found in the online version of this article.

Figure S1. Map of study area showing the distribution of sampling plots along the water availability gradient.

Figure S2. Distribution of the precipitation to potential evapotranspiration ratio (P/PET) plot values for each sampled species.

Figure S3. Principal component analysis (PCA) conducted to summarize environmental variables at the plot level (climate, forest structure and soil characteristics).

Figure S4. Distribution of each trait as a function of species and family.

Figure S5. Variance partitioning within (a) Pinaceae and (b) Fagaceae families.

Table S1. Characterization of the dominant species in the study plots.

Table S2. Statistical descriptors of studied traits.

Table S3. Results of the linear mixed models examining the relationships between environmental variables using the PCA axis and traits.

Table S4. Results of the linear mixed models examining the effect of precipitation to potential evapotranspiration ratio (P/PET) on each trait within and among species.

Table S5. Descriptors of trait networks across species and for each studied species separately.

1008 **Table 1. Traits measured in this study**

Trait	Symbol	Units
Leaf mass per area	LMA	g cm^{-2}
Leaf nitrogen concentration	N	mg g^{-1}
Leaf carbon isotope composition	$\delta^{13}C$	‰
Wood density (stem)	WD	g cm^3
Huber value, sapwood to leaf area ratio (branch)	Hv	cm^2 m^{-2}
Leaf-specific xylem hydraulic conductivity (branch)	K_L	kg m^{-1} s^{-1} MPa^{-1}
Stem-specific xylem hydraulic conductivity (branch)	K_S	kg m^{-1} s^{-1} MPa^{-1}
Pressure causing 50% xylem embolism (branch)	P_{50}	MPa
Leaf water potential at turgor loss point	P_{tlp}	MPa

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Table 2. Results of the linear mixed models examining the relationships between traits and environmental variables characterizing the soil, the climate and the stand structure. A different mixed effects model including all environmental variables in the fixed part and plot nested within species in the random part was fit for each trait.

	LMA	**log (N)**	**log(-δ^{13}C)**	**log (WD)**	**Hv**	**K_L**	**K_S**	**-P_{50}**	**-P_{tlp}**
Fixed Parts									
soil P	**0.08**	-0.08	n.i.	0.08	n.i.	n.i.	n.i.	n.i.	n.i.
	(0.02 – 0.13)*	(-0.17 – 0.01)		(-0.00 – 0.17)					
log (b.Saxton)	n.i.	n.i.	n.i.	0.05	n.i.	n.i.	n.i.	n.i.	-0.03
				(-0.01 – 0.12)					(-0.13 – 0.07)
log (DBH mean)	**-0.07**	0.09	0.12	**-0.11**	**-0.14**	**-0.14**	-0.08	n.i.	n.i.
	(-0.12 – -0.01)*	(-0.00 – 0.17)	(0.00 – 0.24)	**(-0.19 – -0.03)****	**(-0.26 – -0.01)***	**(-0.24 – -0.03)***	(-0.16 – -0.00)		
Basal Area	-0.05	n.i.	n.i.	0.01	n.i.	n.i.	n.i.	0.08	n.i.
	(-0.10 – 0.01)			(-0.06 – 0.09)				(-0.03 – 0.20)	
Annual radiation	**0.06**	n.i.	**-0.23**	n.i.	0.09	0.07	n.i.	n.i.	n.i.
	(0.01 – 0.10)*		**(-0.33 – -0.13)*****		(-0.01 – 0.20)	(-0.02 – 0.17)			
log (P/PET)	n.i.	n.i.	**0.25**	n.i.	**-0.27**	n.i.	n.i.	-0.18	**-0.36**
			(0.09 – 0.41)**		**(-0.44 – -0.10)****			(-0.35 – -0.02)	**(-0.53 – -0.20)*****
Random Part									
σ2	0	0.009	0.001	0.009	0.178	0.153	0.087	0.071	0.024
τ00, PLOT:SP	0	0.009	0.001	0.002	0.065	0.039	0.036	0.193	0.017
τ00, SP	0.005	0.084	0.002	0.035	0.134	0.216	0.521	0.775	0.053
R^2 marginal	0.02	0.01	0.22	0.01	0.14	0.03	0	0.02	0.14
R^2 conditional	0.94	0.91	0.84	0.8	0.59	0.64	0.86	0.93	0.78
Observations	444	444	444	444	439	444	444	444	425

The model's standardized coefficients including confidence intervals (in brackets) are shown. Significant correlations (* P<0.05, ** P<0.01, *** P<0.001) are shown in bold. Information on the random effect variances (σ2, total; τ00, PLOT:SP, within-species; and τ00, SP, cross-species), the proportions of explained variance by fixed effects (R^2 marginal) and explained variance by fixed and random effects (R^2 conditional) is also provided. DBH mean, plot mean diameter at the breast height; b.Saxton, b Saxton coefficient; soil P, soil phosphorus content; P/PET, precipitation to potential evapotranspiration ratio; n.i., not included in the best model. See Table 1 for definition of symbols.

Figure Legends

Fig. 1 (a) Quartile coefficient of dispersion of the studied traits across all measurements of the study and (b) variance partitioning across different ecological levels of organization. 'Within' denotes variance between individuals of the same population. Traits are ordered (left to right) from higher to lower total variation in panel (a), and from higher to lower % variation within species in panel (b). See Table 1 for definition of symbols.

Fig. 2 Relationship between water availability (in terms of the precipitation to potential evapotranspiration ratio, P/PET) and studied traits. The black regression lines give the overall cross-species relationships, and the coloured lines the corresponding within-species relationships, when significant ($P<0.05$). Variables were natural-log transformed whenever required to satisfy normality assumptions. See Table 1 for definition of symbols.

Fig. 3 (a) Trait correlation networks across species (n=6) and for each studied species separately (b-g). Solid black and grey dashed edges show positive and negative correlations, respectively. Correlation strength is represented by edge thickness. Only significant correlations are shown ($P<0.05$). Traits identified by red circles show the highest centrality value in terms of weighted degree (the sum of all the significant coefficients of correlation of a node). All traits were natural-log transformed before analysis. See Table 1 for definition of symbols.