RESEARCH ARTICLE

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Are leaf, stem and hydraulic traits good predictors of individual tree growth?

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Abstract

1. A major foundation of trait-based ecology is that traits have an impact on individual performance. However, trait–growth relationships have not been extensively assessed in trees, especially outside tropical ecosystems. In addition, measuring traits directly related to physiological processes remains difficult and the differences between inter- and intraspecific relationships are seldom explored.

2. Here, we use individual-level data on a set of hydraulic, leaf and stem traits to assess their ability to predict basal area increment (BAI) and growth efficiency (BAI per unit of tree leaf area, GE) among and within species for six dominant tree species along a water availability gradient under Mediterranean climate (Catalonia, NE Spain). Measured traits include: leaf mass per area (LMA), leaf nitrogen concentration (N), leaf C isotopic composition (δ^{13}C), the leaf water potential at turgor loss (P_{tlp}), stem wood density (WD) and branch-level estimates of the Huber value (Hv), sapwood- and leaf-specific hydraulic conductivity (K_S and K_L) and resistance to xylem embolism (P_{50}).

3. Trait–growth associations were generally weak, particularly for BAI and within species. High values of both growth metrics were associated with 'conservative' leaf and hydraulic traits. In particular, BAI was negatively associated with K_L (and wood density), while GE increased with LMA, allocation to sapwood relative to leaves (Hv) and resistance to xylem embolism (P_{50}). Climate effects on BAI and GE were indirectly mediated by changes in traits, stand structure and tree basal area. Overall, these results suggest that maintaining functionality over extended periods of time may be more important than maximum gas exchange or hydraulic capacity to achieve high radial growth under Mediterranean climates.

4. Our study reveals that widely used 'functional traits' may be poor predictors of tree growth variability along environmental gradients. Moreover, trait effects (when present) do not necessarily conform to simple hypotheses based on our understanding of organ-level processes. An improved understanding of trait coordination along common axes of variation together with a revaluation of the variables

that better reflect whole-tree performance can greatly improve our understanding of trait–growth relationships.

1 | INTRODUCTION

A major challenge in ecology is to understand the link between plant demographic responses and key traits to improve our ability to predict vegetation dynamics and the impacts of climate change on ecosystem structure and functionality. In the last two decades, trait-based approaches have concentrated on investigating the rules that constrain global phenotypic diversity across species, focusing on organ-level spectra such as the leaf economics spectrum (Wright et al., 2004), the wood economics spectrum (Chave et al., 2009) or below-ground traits (Weemstra et al., 2016). The assumption that traits have an impact on plant performance and, thus, can provide a basis to scale up from organisms to ecosystem function and dynamics (Lavorel & Garnier, 2002) has been an important foundation of this research area. However, the relationship between 'functional' traits (sensu Violle et al., 2007) and demographic rates is usually assumed without testing, particularly for large trees, and there is substantial evidence that widely used traits do not predict demographic rates (Yang et al., 2018).

Among the most commonly measured traits, wood density has emerged as a consistent predictor of tree growth and mortality rates, with lower wood densities generally associated with faster growth rates and lower survival. This evidence has been gathered mostly in tropical systems (Iida et al., 2014; Kraft et al., 2010; Poorter et al., 2008), although similar studies exist for temperate biomes (Gleason et al., 2018; Klooster et al., 2007; Martínez-Vilalta et al., 2010). However, easy-to-measure ('soft') traits such as wood density or leaf mass per area (LMA, or its inverse, SLA) frequently explain only a modest proportion of the observed variability in demographic rates (Paine et al., 2015), particularly for adult trees (Gibert et al., 2016; Iida et al., 2014; Wright et al., 2010). We would expect 'soft' traits to be key indicators of overall function and demographic rates if they were associated with plant resistance to several stress factors (the relationship between wood density and mortality likely falls in this category; Chave et al., 2009) or if a strong coordination exists between different traits giving rise to one or a few functional axes at the whole-plant level, both within and across species. Such coordination, reflecting a whole-plant spectrum from conservative to acquisitive plants, has been hypothesized (Reich, 2014), but remains largely untested.

There is growing consensus that hydraulic traits are highly relevant for assessing drought vulnerability and demographic rates under water-limiting conditions (Brodribb, 2017; Choat et al., 2018). However, they are still much less studied than other, easier to measure traits. Plant hydraulic strategies have often been summarized by two main traits that characterize the xylem conductive safety and efficiency. The maximum water transport capacity (conductivity) of the fully hydrated xylem (usually normalized per unit of sapwood area, K_S) is commonly used as a measure of efficiency, while xylem safety is often expressed as the xylem water potential at which 50% of hydraulic conductivity is lost due to embolism (P_{50}). Albeit it is not strictly a hydraulic trait, the leaf water potential at turgor loss (P_{tlp}) has also been used to assess physiological drought tolerance across species (Bartlett et al., 2012), as it is associated with the regulation of plant water loss through stomata (Brodribb et al., 2003; Martin-StPaul et al., 2017). Similarly, traits related to plant allocation and hydraulic architecture, such as the sapwood-to-leaf area ratio (the Huber value, Hv) have been recognized as key components of plant strategies to adjust to changes in water availability (Martínez-Vilalta et al., 2009; Mencuccini & Grace, 1995). The product of K_S by Hv gives the leaf-specific hydraulic conductivity (K_L), a measure of the plant's hydraulic sufficiency.

Usually, studies relating individual traits with tree growth use absolute growth metrics (such as the basal area increment, BAI) or relative metrics that account for overall size (such as the relative growth rate; e.g. Gibert et al., 2016). Although it has received little attention in trait-based studies, growth efficiency (GE), defined here as the ratio of BAI to crown leaf area (Waring, 1983), could be an informative, complementary metric to characterize growth in this context. GE is a physiologically meaningful variable that normalizes overall radial growth (BAI) by the area exchanging carbon and water with the atmosphere. As such, it may be a more precise indicator of physiological performance than other measures of growth, which are strongly affected by allometric scaling (Hérault et al., 2011).

Most studies relating traits with demographic rates have been conducted at the species level, using trait means. This is particularly the case for those relating hydraulic traits and plant performance (Anderegg et al., 2016; Eller et al., 2018; Medeiros et al., 2019; Poorter et al., 2010; Russo et al., 2010). However, an increasing number of studies show the importance of taking into account intraspecific trait variation (Siefert et al., 2015; Violle et al., 2012). The capacity of populations to adjust their traits along environmental gradients results from different processes, including local adaptation and phenotypic plasticity, and a better understanding of these processes is key to forecast species performance under environmental change (Valladares et al., 2014). However, very few studies to date have explored trait–demography relationships at the individual level (but see Liu et al., 2016; Poorter et al., 2018).

In this study, we use individual tree data to explore the ability of traits to predict tree growth along a regional water availability gradient in Catalonia (NE Spain). This gradient encompasses 90 plots dominated by six tree species, and hence we address the relationship between traits and growth at the intra- and interspecific levels. The main question we ask is: are leaf, stem and hydraulic traits good predictors of tree radial growth, either in absolute terms or once growth is normalized by leaf area? We hypothesize that the explanatory power of hydraulic traits will be higher than that of 'soft' traits such as wood density or LMA (Brodribb, 2017). Within this general objective, we also address the following, more specific questions: are trait–growth associations consistent within and across species? To what extent are these associations affected by the environment (climate and stand structure) and tree size?

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

The study area included all the forested territory of Catalonia (NE Spain), which encompasses 1.2 million ha, around 38% of its total land area. Catalonia is very diverse both topographically and climatically: mean annual temperature ranges from 3 to 18°C and annual rainfall varies from 400 to >1,500 mm (Climatic Digital Atlas of Catalonia; www.opengis.uab.cat/acdc). The experimental design and general sampling scheme has been previously outlined in Rosas et al. (2019). Briefly, we selected six of the most dominant tree species in Catalonia (three Pinaceae and three Fagaceae), accounting for ~75% of the total forest area (Gracia et al., 2004): *Pinus sylvestris* L., *Pinus nigra* J.F.Arnold., *Pinus halepensis* Mill., *Fagus sylvatica* L., *Quercus humilis* Mill. and *Quercus ilex* L. These species have different distributions in the study area (Figure S1), largely reflecting their tolerance to drought stress, which increases in the order: *F. sylvatica < P. sylvestris < P. nigra < Q. humilis < Q. ilex < P. halepensis*. Mixed forests are also common, particularly those combining *P. sylvestris*, *P. nigra* and *Q. humilis*; and *Q. ilex* and *P. halepensis*.

For each species, 15 plots from the Spanish forest inventory (IFN) were resampled in which the target species was dominant (accounting for >50% of the total basal area), maximizing the water availability gradient occupied by each species in the study region. Water availability was quantified as the ratio of precipitation to potential evapotranspiration (P/PET) for the spring–summer period (see below). Five plots per species were sampled for each of three species-specific P/PET ranges, following a stratified random design (dry, corresponding to P/PET < 33th percentile; wet, for P/PET > 66th percentile; and mild for the rest; Figure S1). Plots with the two highest stoniness levels and those that had been managed during the last ~15 years according to IFN surveys were discarded.

Within each plot, five non-suppressed canopy trees of the target species with a diameter at breast height (DBH) > 12.5 cm were randomly selected, all within 25 m of the centre of the plot. In total, we sampled 75 individuals (15 plots, 5 trees per plot) per species.

All samples and data were collected from May to December 2015. To minimize phenological variation in traits within species, species were sampled sequentially (*P. halepensis* was sampled from mid-May to end June; *Q. humilis*, end June and July; *F. 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 were sampled from the exposed part of the canopy in the top half of the crown. Branches were transported to the laboratory inside plastic bags under cool and dark conditions and measurements were taken within 24 hr. See Rosas et al. (2019) for additional details on the sampling scheme.

2.2 | Individual trait data

For each of the target trees, nine traits were measured (Table S1): leaf mass per area (LMA) and nitrogen concentration (N) as proxies for the leaf economics spectrum (Wright et al., 2004); leaf C isotopic composition ($\delta^{13}C$) as a measure of water-use efficiency (Farquhar et al., 1989); stem wood density (WD) as a central trait defining the wood economics spectrum (Chave et al., 2009); the Huber value at the branch level (Hv), defined as the ratio of cross-sectional sapwood area to subtended (projected) leaf area; the sapwood-specific (K_S) and leaf-specific hydraulic conductivity (K_L) of branch segments as a measure of xylem transport efficiency and sufficiency, respectively; the water potential causing 50% loss of hydraulic conductivity (P_{50}) in branch segments as a proxy for xylem safety; and the leaf water potential at turgor loss (P_{tlp}) as a measure of stomatal sensitivity (Brodribb et al., 2003). Standard protocols (Pérez-Harguindeguy et al., 2013) were followed for all trait measurements. Leaf measurements were conducted on previous-year needles (conifers) and current-year leaves (broadleaves) to ensure leaves were fully expanded. See Rosas et al. (2019) for a complete description of the methods used to measure individual traits.

2.3 | Growth data

The data on individual tree growth were obtained from the third and fourth Spanish National Forest Inventories (IFN3 and IFN4), the latter conducted over the same time period as our sampling. Spanish National Forest Inventory plots are circular with variable radius (5–25 m) depending on the diameter of the measured trees. The time interval between inventories varied between 13.9 and 15.4 years depending on the plot. We calculated individual tree BAI as the difference between final and initial basal area (over-bark), divided by the plot-specific time interval between surveys. Because not all trees where traits were measured had been measured at the IFN3 (due to the variable plot radius) tree growth data were missing for 98 of 450 measured trees.

Total tree leaf area (projected) was estimated from the diameter of all primary branches, branch-level ratios between leaf biomass and diameter (two to eight branches per tree) and tree-level LMA,

as explained in Rosas et al. (2019). In order to make values comparable across species, seasonal maximum leaf area was estimated, taking into account species phenology and the time of sampling. Individual GE was calculated as the ratio between individual BAI (per year) and total (projected) tree leaf area. In a supplementary analysis, GE was also estimated per unit leaf surface area, assuming that, for a given projected leaf area, total surface area is 50% higher in pines than in broadleaves (Johnson, 1984). Note, however, that GE comparisons between broadleaf and needleleaf species may be problematic.

2.4 | Climatic data

To estimate P/PET as a measure of water availability for each study plot, climate data were obtained from the Climatic Digital Atlas of Catalonia, a collection of digital maps at approximately 200×200 m resolution including average annual radiation, mean, maximum and minimum annual temperature and annual precipitation for the period 1951–2010. PET values were calculated according to the Hargreaves–Samani method and used to estimate P/PET for the spring–summer period (April–September) for each sampled plot.

2.5 | Statistical analyses

All variables were checked for normality and natural-log transformed whenever required. First, Pearson correlation coefficients were used to quantify the association between traits and growth rates (BAI and GE). Second, to separate the intraspecific from the interspecific component of trait–growth relationships, we fitted two linear mixed effects models for each trait, with either BAI or GE as the response variable. In these models, two variables were included as non-interacting explanatory factors: the mean trait value at the species level and the species-centred trait value for each tree. The latter was calculated as the difference between the trait value for a given tree and the average value of the corresponding species. Including both variables allows isolating the relative importance of among-versus within-species effects on growth (cf. Rosas et al., 2019). We included plot nested in species as random effects on the intercept of each model. Preliminary analyses showed that including a random species effect on the slope did not improve model fit. The residuals of all models showed no obvious pattern and were approximately normally distributed. Linear mixed effects models were fit using the LME4 R package (Bates et al., 2015).

To summarize studied traits into overall axes of variation, a principal component analysis (PCA) was performed on the nine traits considered in the study. The first two axes of the PCA, which together explained 73% of the variability in the trait data, were retained. To separate the interspecific from the intraspecific component, we also computed the mean of each PCA score at the species level and the species-centred score value for each of the two

axes, which resulted in a total of four variables. As before, centred values were calculated as the difference between individual PCA score values and the average value of the corresponding species. The resulting four variables were used as explanatory factors in two linear mixed effects models to evaluate how trait coordination determined BAI and GE. To confirm that the previous PCA axes, which were driven by trait variability both within and among species, also reflected the main axes of variation at the intraspecific level, a second PCA was performed directly on centred trait values at the species level (Figure S2).

Finally, to evaluate the direct and indirect effects of climate (P/PET), stand structure (initial plot basal area at IFN3), tree size (initial tree basal area at IFN3) and trait covariation (PCA axes) on growth rates, two different piecewise structural equation models (piecewise SEM) were fitted, one for BAI and one for GE. In each case we started with the 'saturated' model including all possible directional effects of the two trait (PCA) axes, P/PET, stand structure and tree size on growth rate, as well as directional effects of P/PET on stand structure, tree size and traits (PCA axes), plus all possible covariations among them. In addition, alternative models were fit in which tree height was used as a measure of tree size instead of individual basal area. Piecewise SEM allows piecing multiple individual linear mixed models together into a single causal network, taking into account the hierarchical structure of the data (Lefcheck, 2016). Thus, we included plot nested in species as random effects on the intercept in all SEM sub-models. The overall SEM fit was evaluated using Shipley's test of d-separation (Shipley, 2013) and Akaike information criterion (AIC). Models were simplified stepwise by removing the least significant path until a minimal adequate model with the lowest AIC was obtained. Models within two AIC units were considered equivalent in terms of fit and the simplest one was selected. Marginal and conditional R^2 values were computed following Nakagawa and Schielzeth (2013). SEM models were fitted with the R package PIECE-WISESEM (Lefcheck, 2016). All statistical analyses were carried out using R statistical software v.3.3.2.

3 | RESULTS

3.1 | Trait–growth associations

Our sampling scheme covered a large gradient of water availability both within and across species, with spring–summer P/PET ranging from 0.29 (a *Pinus halepensis* plot) to 1.33 (a *Fagus sylvatica* plot; Figure 1e). Individual growth rates (Figure 1a,b) and tree sizes (Figure 1d) also varied substantially, as well as stand characteristics, with plot basal areas ranging from 6.2 m^2/ha (a *Quercus humilis* plot) to 49.9 m^2/ha (a *Fagus sylvatica* plot; Figure 1c).

Individual-level correlations between trait values and GE were stronger than trait–BAI associations, the highest value corresponding to the LMA-GE relationship ($r = 0.62$; Figure S3). In our models of trait–growth relationships, a substantial percentage of the variance was explained by differences among species and plots (high

FIGURE 1 Boxplot of (a) basal area increment (BAI), (b) growth efficiency (basal area increment per unit of total tree leaf area, GE), (c) plot basal area, (d) tree basal area and (e) precipitation to potential evapotranspiration ratio (P/PET) as a function of species and family (Pinaceae vs. Fagaceae). The limits of boxes indicate the first and third quartiles, and the horizontal line within each box corresponds to the median. The upper whisker extends to the highest value within $1.5 \times$ IQR (interquartile range) of the third quartile. The lower whisker extends to the lowest value within $1.5 \times$ IQR of the first quartile. Abbreviations: Fs, *Fagus sylvatica*; Ph, *Pinus halepensis*; Pn, *Pinus nigra*; Ps, *Pinus sylvestris*; Qh, *Quercus humilis*; Qi, *Quercus ilex*
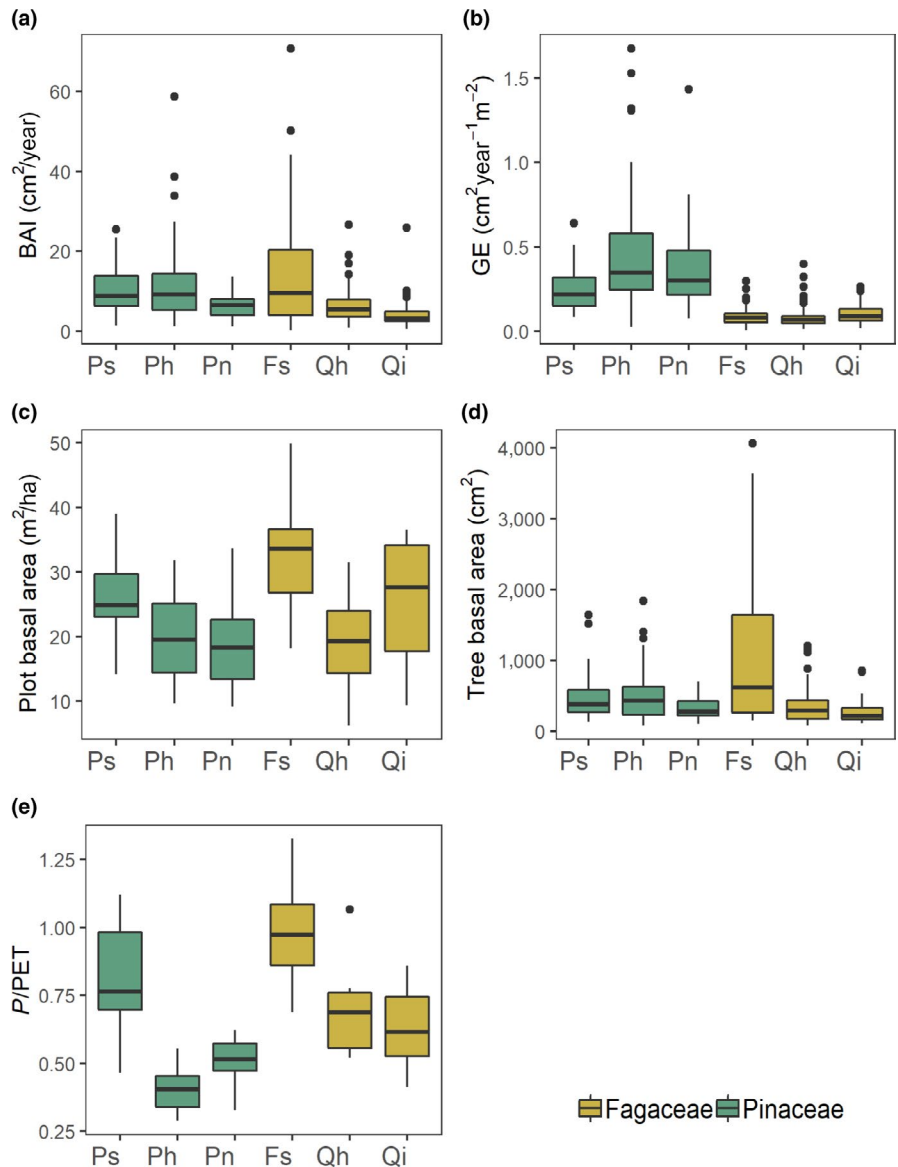
difference between conditional and marginal R^2 in our mixed models), especially for BAI (Tables S2 and S3). K_L and WD were the only traits that showed a significant relationship with BAI across species, whereby higher BAI was associated with lower WD and K_L values (Figure 2; Table S2). Within species, only $\delta^{13}C$ showed a significant (positive) effect on BAI (Figure 2; Table S2).

Species with higher GE were characterized by high LMA and low N, high water-use efficiency (less negative $\delta^{13}C$) and low vulnerability to xylem embolism (more negative P_{50}; Figure 3; Table S3). Species GE also showed a positive relationship with Hv and a negative one with K_S that resulted in a non-significant relationship with K_L across species (Figure 3; Table S3). However, when trait–GE relationships were assessed within species, significant (positive) relationships were only found for K_L, Hv and LMA (Figure 3; Table S3). For the latter two variables, the intraspecific slopes were shallower than the corresponding interspecific slopes. All results remained similar if GE was estimated per unit leaf surface area (Table S4).

3.2 | Associations between growth and composite trait metrics

Trait data showed two orthogonal axes of variation that explained 49% and 24% of the total variance respectively. The first axis was interpreted in terms of conservative leaf resource use and drought resistance strategies, since high LMA, low N, high resistance to embolism (more negative P_{50}) and high water-use efficiency (less negative $\delta^{13}C$) were all associated with positive loadings (Figure 4). The second axis was associated with high values of K_L (and to a lower extent K_S, wood density and P_{tlp}) and, thus, it was interpreted as a proxy for hydraulic sufficiency (Figure 4). Associations between these trait axes, representing trait covariation, and growth metrics were generally in line with the individual trait–growth relationships reported in the previous section. When we explored the effect of trait PCA axes on BAI, we found a negative relationship with the hydraulic sufficiency axis both within and among species (Table S5). An association between BAI and conservative leaf resource use and drought resistant strategies (PCA
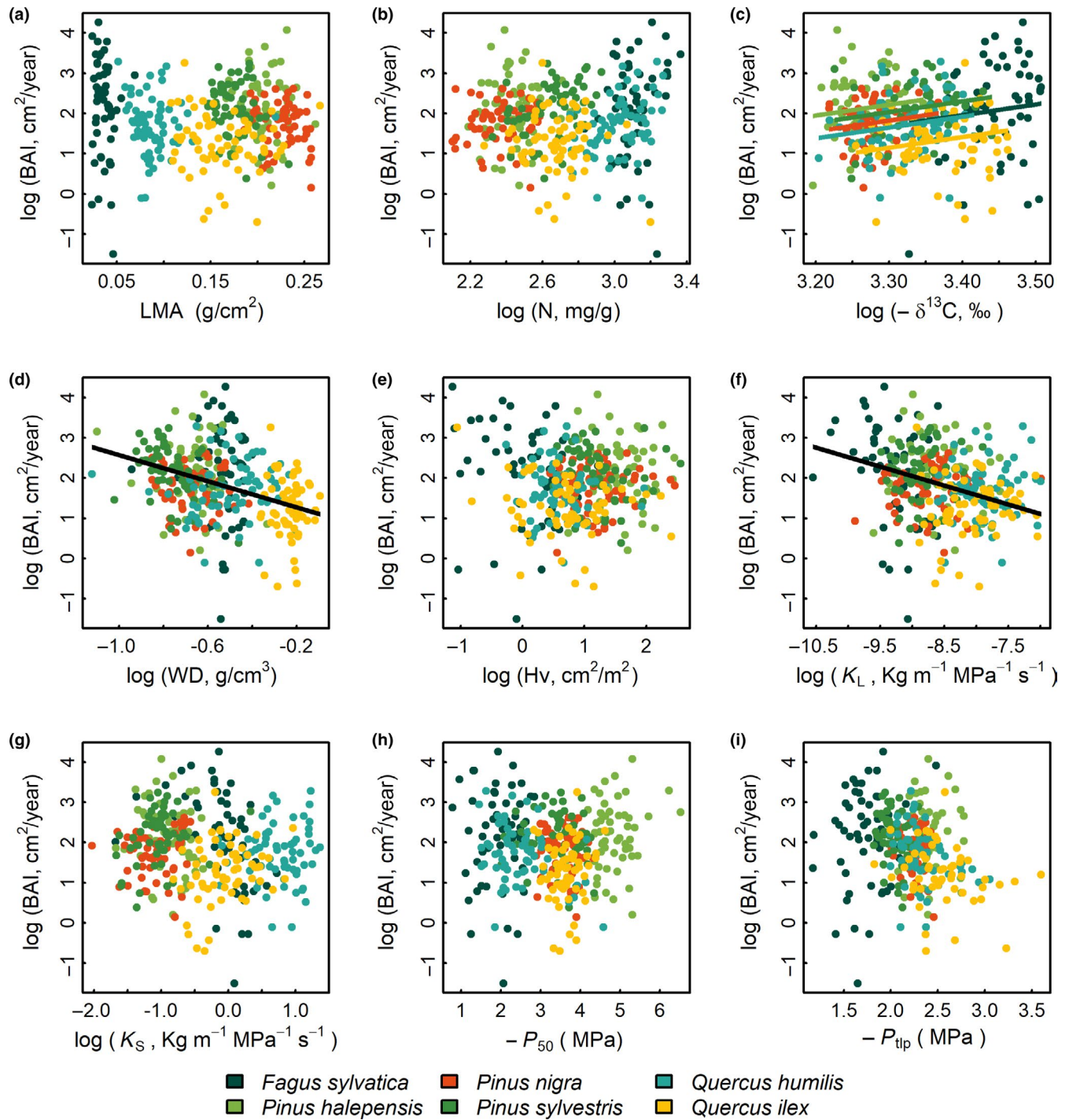
FIGURE 2 Relationship between basal area increment (BAI) and studied traits at the individual tree level. The black regression lines give the overall among-species relationships ($n = 6$ species), and the coloured lines the corresponding within-species relationships ($n = 53–65$ trees per species), when significant ($p < 0.05$). Variables were natural-log transformed whenever required to satisfy normality assumptions. See Table S1 for definition of variable abbreviations

axis 1) was found only at the intraspecific level (Table S5). For GE, more conservative leaf resource use and drought resistance strategies (PCA axis 1), as well as lower hydraulic sufficiency (PCA axis 2) were associated with higher GE, but only across species (Table S5). Models accounting for trait coordination (PCA axes) explained a higher proportion of growth variance than individual trait models (14% and 52% of BAI and GE respectively; Table S5).

3.3 | Effects of trait axes, environment and tree size on plant growth

Structural equation models showed that P/PET was positively associated with initial tree and plot basal areas. At the same time, P/PET had a negative effect on both PCA axes, whereby higher values were related with traits associated with more acquisitive leaf resource use
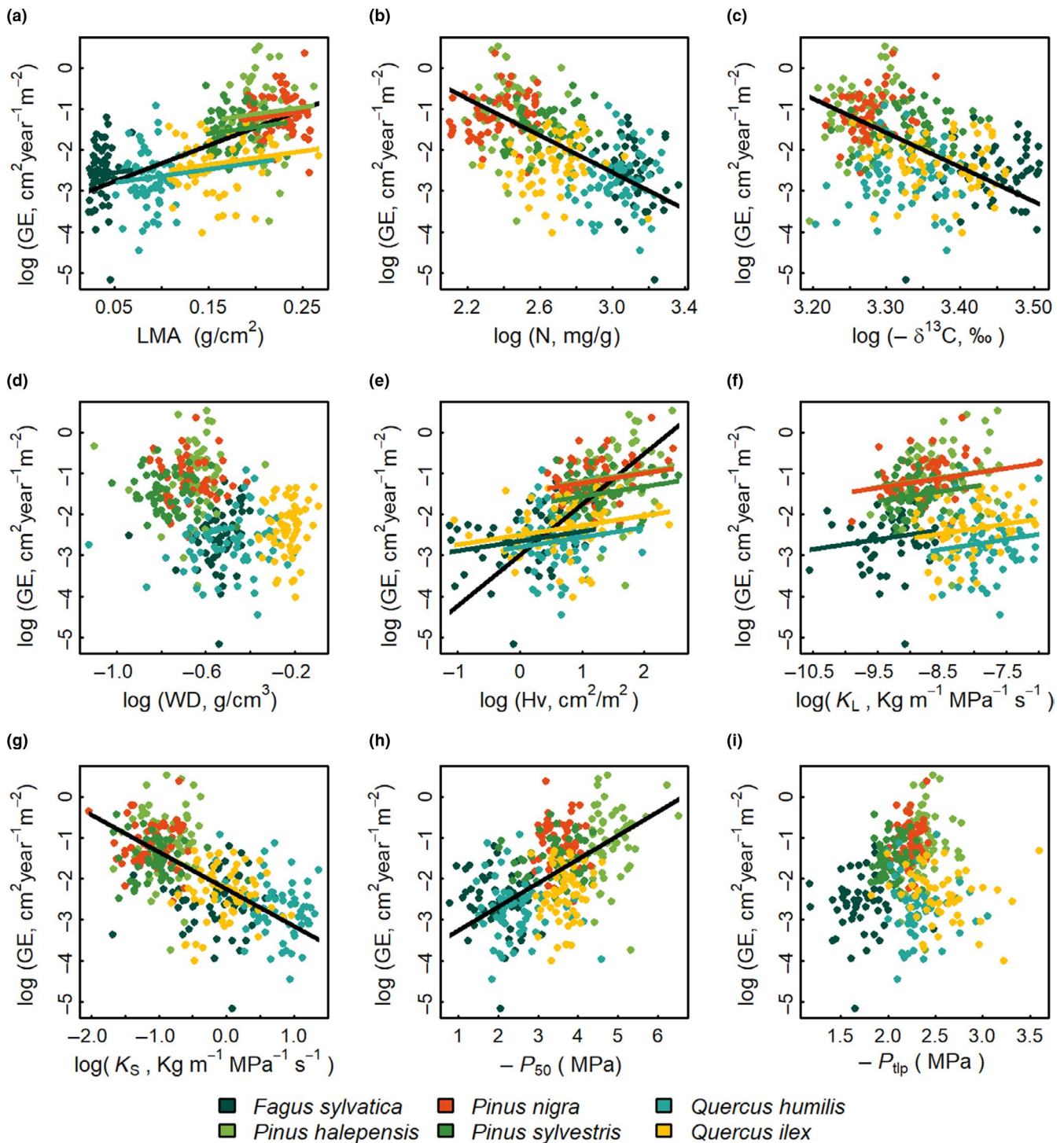
FIGURE 3 Relationship between growth efficiency (basal area increment per unit of total tree leaf area, GE) and studied traits at the individual tree level. The black regression lines give the overall among-species relationships ($n = 6$ species), and the coloured lines the corresponding within-species relationships ($n = 53$–65 trees per species), when significant ($p < 0.05$). Variables were natural-log transformed whenever required to satisfy normality assumptions. See Table S1 for definition of variable abbreviations

strategies, lower drought tolerance and lower hydraulic sufficiency (Figure 5). Tree basal area had a strong positive effect on BAI, while a weaker and opposite effect was found for GE (Figure 5). Plot basal area only showed a significant (negative) relationship with BAI. Relationships between trait PCA axes and growth were relatively weak when accounting for climate, stand structure and tree size. BAI

was negatively associated with hydraulic sufficiency (PCA axis 2; Figure 5a), while a positive effect on GE was found for traits related to conservative leaf resource use and drought resistance strategies (PCA axis 1; Figure 5b). Overall, the model accounted for 58% of the total variability on BAI and 64% on GE, but the variance explained by the fixed factors was relatively low (40% for BAI and 10% for GE).
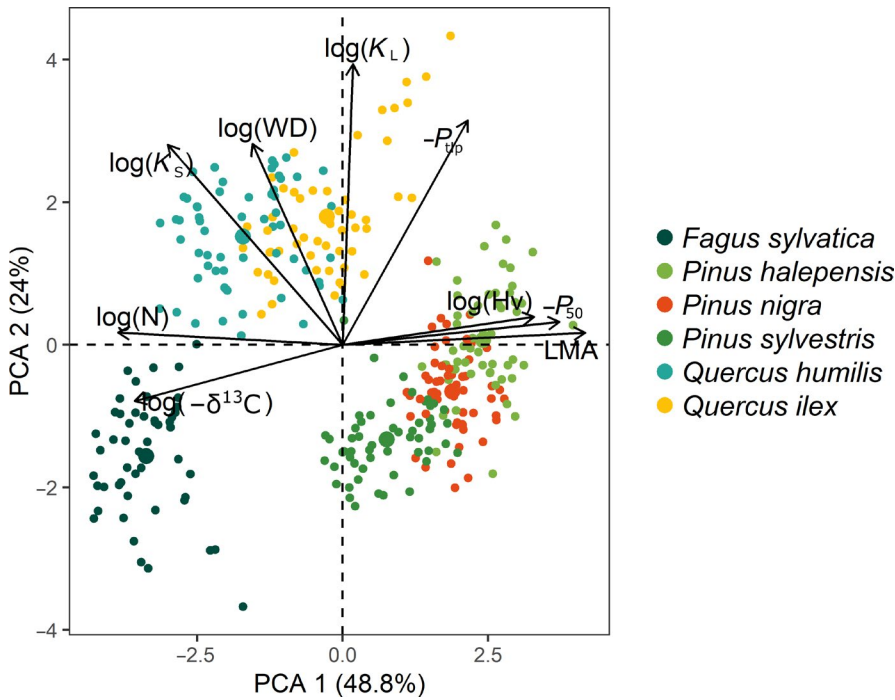
FIGURE 4 Principal component analysis (PCA) summarizing trait variability across individual sampled trees. The first two PCA axes with the percentage of explained variance (in brackets) are shown. Variables were natural-log transformed whenever required to satisfy the normality assumptions. See Table S1 for definition of variable abbreviations
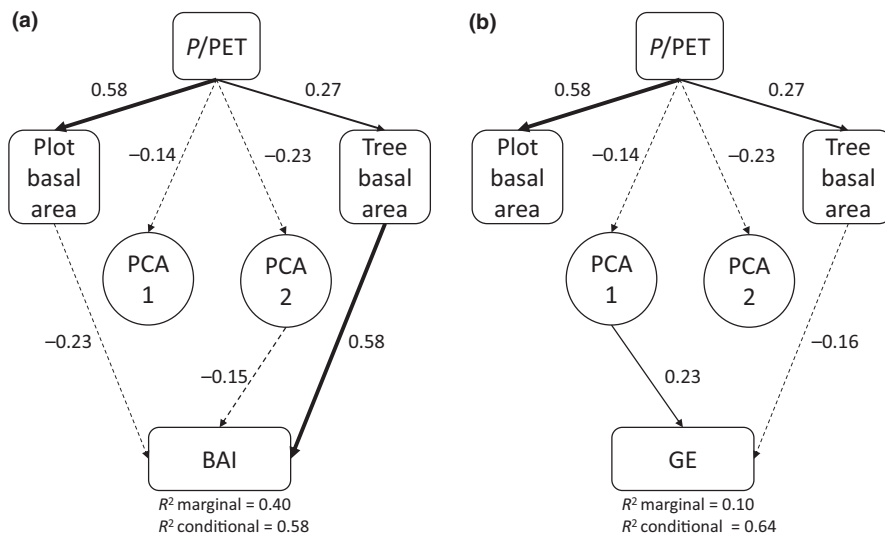

FIGURE 5 Piecewise structural equation models relating climate (in terms of precipitation over potential evapotranspiration ratio, P/PET), forest structure (in terms of initial plot basal area), tree size (in terms of initial tree basal area) and traits (using the first and second PCA components: PCA1 and PCA2 respectively; Figure 4). Panel (a) shows the results for basal area increment (BAI) and panel (b) for growth efficiency (basal area increment per unit of total tree leaf area, GE). Arrows indicate significant links between variables. Solid and dashed lines indicate positive and negative relationships respectively. Standardized path coefficients, as well as the marginal and conditional R^2 values, are shown

Results remained largely consistent when tree height was used as a measure of tree size instead of individual basal area (Figure S4). In the corresponding structural models, the main difference was that tree height was unrelated to P/PET and explained a larger proportion of BAI variance than tree basal area (explained variance remained similar for GE). As a result, a direct effect of P/PET on BAI was detected, which turned the link between hydraulic sufficiency (PCA axis 2) and BAI non-significant ($p = 0.29$). Interestingly, tree height was unrelated to the PCA axes describing trait variability ($p \geq 0.1$).

4 | DISCUSSION

4.1 | 'Functional' traits are weak predictors of individual radial growth

Only one of the measured traits was predictive of BAI within species ($\delta^{13}C$) and two across species (WD, K_L), and even in these cases relationships were weak. This is noteworthy considering that all measured traits, and particularly those describing the leaf economics

spectrum (LMA, N), are considered key functional traits and are usually assumed to be good proxies for growth and performance. As we hypothesized, the predictive power of traits increased for GE, although relationships were still weak. Even if GE is affected by the distribution of canopy leaf area and by light conditions (Gersonde & O'Hara, 2005; Waring, 1983), it is more closely linked to physiological performance in terms of carbon and water economies than other measures of growth. It is clear, however, that different growth metrics characterize different dimensions of whole-plant growth (e.g. Gibert et al., 2016; Kleinschmidt et al., 2020), thus a key question remains to determine which of them is the best proxy for fitness in a given ecological context. Regardless of this, our study adds to the evidence showing that 'functional' traits, including 'mechanistic', hydraulic traits (sensu Brodribb, 2017), are not necessarily good predictors of demographic rates, at least for mature trees (Gibert et al., 2016; van der Sande et al., 2015; Yang et al., 2018).

Interestingly, the trait–growth relationships we did find were frequently counterintuitive. For instance, we observed a negative relationship between hydraulic sufficiency (K_L) and BAI across species, in addition to the expected negative effect of WD on BAI. The latter has been interpreted to result from the lower sapwood hydraulic efficiency of denser wood (Chave et al., 2009). However, we observed a positive relationship between wood density and hydraulic efficiency, which likely reflects the particular mixture of species in our study and the fact that angiosperm wood tends to be both denser and more conductive than that of gymnosperms (Sperry et al., 2006; see also Figure 4). In addition, no WD-BAI relationship was detected within species, in agreement with Fajardo (2016) and Poorter et al. (2018).

Trait associations with GE were even more unexpected, as this growth metric increased with leaf traits related to conservative resource use strategies across species (high LMA and low N). Again, these relationships have to be interpreted in the context of the specific set of species studied here, but also considering that photosynthetic capacity per unit leaf area (the relevant comparison here) is weakly related with LMA both across (Wright et al., 2004) and within species (Poorter et al., 2009). In our study, LMA and N per unit area (the latter calculated by combining mass-based N and the corresponding, tree-level LMA) were positively related ($p < 0.001$), and the effect of mean species N on GE turned from significantly negative when N was expressed per unit mass (Figure 3) to marginally positive when N was expressed per unit area ($p = 0.09$; data not shown). Previous studies have found that LMA can be positively related to growth, even without normalizing it by leaf area, under water- or nutrient-limited conditions in the tropics (Poorter et al., 2018; van der Sande et al., 2018).

As hypothesized, trait–growth relationships were not necessarily consistent within and across species, echoing the fact that trait coordination along environmental gradients may change at different organizational levels (Anderegg et al., 2018; Fajardo & Siefert, 2018; Vilà-Cabrera et al., 2015). Of the 10 relationships that were significant for either BAI or GE, only two were significant at both levels (LMA and Hv effects on GE). Although in these two cases the

direction of the effect was consistent, slopes were always steeper across species. Overall, our results show that trait effects on growth rates were largely driven by differences across species means, likely reflecting a higher trait variability among species and their turnover along the water availability gradient (Figure 1e; cf. Poorter et al., 2018).

However, a few caveats are in order. First, the fact that we only sampled six species greatly contrasts with the large number of species employed in global assessments of interspecific trait variation (Díaz et al., 2016; Wright et al., 2004). Although the study species capture a substantial part of the functional variability in the study region (Vilà-Cabrera et al., 2015), this low sample size may limit our capacity to detect relationships across species. Second, although sample size was substantial (450 individuals in total, 75 per species) and covered a relatively wide environmental gradient, it did not cover the whole distribution ranges of the study species. In addition, we sampled a relatively low number of individuals per plot ($n = 5$), and selected healthy individuals with sun-exposed branches, which is likely to have resulted in an underestimation of total intraspecific trait variability. This may be particularly so for species showing high intra-plot variability, such as *Fagus sylvatica* (e.g. Aranda et al., 2017). In addition, our relatively long, sequential sampling aimed at minimizing phenological variation within species implies that some of the variability across species could correspond to temporal effects, particularly for relatively labile traits such as $\delta^{13}C$. Finally, we should consider that previous assessments of trait–growth relationships at the plot level found globally consistent patterns (Kunstler et al., 2016). Taken together, these results suggest that traits may be good proxies for growth and competitive interactions in the context of community assembly, but not necessarily along environmental gradients, where multiple, coordinated trait shifts occur as a result of ecotypic variation and species replacements (Rosas et al., 2019).

4.2 | Trait effects cannot be considered in isolation

One important implication of our results is that relationships between individual traits and growth cannot be understood without considering trait covariation (Figure 4), which makes it difficult to interpret individual trait effects and determine whether they are direct or indirect. It is possible, for instance, that resistance to xylem embolism allows species to maintain functionality for longer during extended periods of summer drought, which are common in the study area, or permits rapid recovery of gas exchange (and growth) after the first autumn rains (Skelton et al., 2017). These effects could indirectly explain the association between conservative leaves and high growth rates, given that resistance to embolism was associated with conservative leaf traits. Our results also highlight the importance of allocation when considering trait–growth relationships (Yang et al., 2018). In particular, we found a compensation between Hv and K_s (cf. Mencuccini et al., 2019), such that species showing higher GE rates had lower K_s but also higher Hv, resulting in a non-significant interspecific relationship with K_L.

Our results emphasize the need to account for ecological context and trait coordination when assessing trait–growth or trait–demography relationships. The composite trait metrics obtained here (Figure 4) are largely consistent with the main axes of functional variation reported for vascular plants globally, in which the first axis corresponds to plant size and wood density and the second to the leaf economics spectrum (Díaz et al., 2016). The fact that in our case the importance of these two axes is reversed is to be expected given the limited variability in plant size in our study, and agrees with previous regional assessments (Fyllas et al., 2020). Previous global studies, however, have not accounted for other potentially relevant functional dimensions, such as those described by root and hydraulic traits. Concerning the latter, a study of a reforestation trial in Costa Rica reported similar results as ours, with the leaf economics spectrum being roughly orthogonal to wood density and hydraulic conductivity, although in their case hydraulic conductivity (estimated from anatomy) was negatively related to wood density (Kleinschmidt et al., 2020). In another study in Bolivia, wood density strongly covaried with leaf economics traits and vulnerability to xylem embolism, whereas hydraulic conductance was largely orthogonal to that axis (Markesteijn et al., 2011. Although our results provide evidence for a tight coordination between stem hydraulics (at least P_{50}) and leaf-level traits (cf. Reich, 2014), further studies are needed to better understand this coordination and its implications for whole-plant performance at local, regional and global scales.

4.3 | Climate effects on growth are mediated by changes in traits, stand structure and tree size

We did not find a direct effect of P/PET on growth metrics but only indirect effects through changes in traits, tree basal area and stand structure. As expected, plots with higher water availability (higher P/PET) were denser and contained larger trees. Wetter sites were also associated with more acquisitive leaf and hydraulic strategies (low LMA, less negative P_{50}), as seen in previous studies (e.g. Maherali et al., 2004; Wright et al., 2005). We also found a negative relationship between P/PET and hydraulic sufficiency (PCA axis 2), although significant climatic effects on K_S, K_L or WD (individually) were not detected in a previous study using the same traits (Rosas et al., 2019). Higher plot basal area, presumably associated with competition intensity, only showed a negative effect on BAI, probably because GE already captures compensatory changes in tree leaf area as a function of competitive environment (Waring, 1983). Not surprisingly, trees with higher basal area showed higher BAI, but the opposite was true when we normalized BAI by total tree leaf area (Mencuccini et al., 2005). Importantly, when environmental drivers and tree size were simultaneously considered, results were consistent with trait–growth associations obtained for individual traits: high hydraulic capacity and dense wood were associated with low BAI, while GE was enhanced by conservative leaf resource use and drought tolerance strategies

(Figure 5). Our finding that climate effects on growth were largely indirect, mediated by changes in stand structure, tree size and plant traits is consistent with earlier reports across species in temperate and Mediterranean systems (Martínez-Vilalta et al., 2010) and highlights the importance of the ecological context in interpreting climate-growth relationships (cf. Chu et al., 2016; Michaletz et al., 2014; Yang et al., 2018).

5 | CONCLUSIONS

Our results show that traits, including widely used 'functional traits' and even 'mechanistic', hydraulic traits (sensu Brodribb, 2017), may be poor predictors of tree growth variability along environmental gradients. Although trait–growth relationships were more predictable across than within species, their direction was frequently unexpected and contrary to the notion that the conservative–acquisitive continuum of traits at the organ level is an indicator of whole-plant performance (cf. Reich, 2014). These results have to be considered in the context of the study species, and specifically the contrasting functional properties of Pinaceae and Fagaceae (Vilà-Cabrera et al., 2015), but they also highlight the importance of accounting for ecological context and trait coordination when assessing and interpreting the relationships between traits and performance. It is not (only) that 'soft' traits are not necessarily good proxies for more 'hard' or 'mechanistic' traits, but also that different traits may reflect different functional dimensions that covary in ways we do not yet fully understand. A refined understanding of plant resource use strategies that explicitly addresses trait coordination at the whole-plant level is needed to improve our ability to predict tree performance (and fitness) from trait measurements under changing environmental conditions.

CONFLICT OF INTEREST
The authors have no known conflict of interest to declare.

AUTHORS' CONTRIBUTIONS
J.M.-V., M.M., T.R., F.S. and S.S.-M. conceived the ideas and designed methodology; T.R., C.B. and I.R. collected the data; T.R. analysed the data; T.R. and J.M.-V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.vt4b8gtqr (Martinez-Vilalta et al., 2020).

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REFERENCES

Anderegg, L. D. L., Berner, L. T., Badgley, G., Sethi, M. L., Law, B. E., & HilleRisLambers, J. (2018). Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters*, *21*(5), 734–744. https://doi.org/10.1111/ele.12945

Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., 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 of the United States of America*, *113*(18), 5024–5029. https://doi.org/10.1073/pnas.1525678113

Aranda, I., Bahamonde, H. A., & Sánchez-Gómez, D. (2017). Intra-population variability in the drought response of a beech (*Fagus sylvatica* L.) population in the southwest of Europe. *Tree Physiology*, *37*(7), 938–949. https://doi.org/10.1093/treephys/tpx058

Bartlett, M. K., 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*(5), 393–405. https://doi.org/10.1111/j.1461-0248.2012.01751.x

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Brodribb, T. J. (2017). Progressing from 'functional' to mechanistic traits. *New Phytologist*, *215*(1), 9–11. https://doi.org/10.1111/nph.14620

Brodribb, T. J., Holbrook, N. M., Edwards, E. J., & Gutiérrez, M. V. (2003). Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell and Environment*, *26*(3), 443–450. https://doi.org/10.1046/j.1365-3040.2003.00975.x

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531–539. https://doi.org/10.1038/s41586-018-0240-x

Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., & Sack, L. (2016). Does climate directly influence NPP globally? *Global Change Biology*, *22*(1), 12–24. https://doi.org/10.1111/gcb.13079

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., & Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Eller, C. B., de Barros, F. V., Bittencourt, P. R. L., Rowland, L., Mencuccini, M., & Oliveira, R. S. (2018). Xylem hydraulic safety and construction costs determine tropical tree growth. *Plant Cell and Environment*, *41*(3), 548–562. https://doi.org/10.1111/pce.13106

Fajardo, A. (2016). Wood density is a poor predictor of competitive ability among individuals of the same species. *Forest Ecology and Management*, *372*(15), 217–225. https://doi.org/10.1016/j.foreco.2016.04.022

Fajardo, A., & Siefert, A. (2018). Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology*, *99*(5), 1024–1030. https://doi.org/10.1002/ecy.2194

Farquhar, G. D., Hubick, K. T., Condon, A. G., & Richards, R. A. (1989). Carbon isotope fractionation and plant water-use efficiency. In P. Rundel, J. R. Ehleringer, & K. A. Nagy (Eds.), *Stable isotopes in ecological research* (Vol. 68, pp. 21–40). https://doi.org/10.1007/978-1-4612-3498-2_2

Fyllas, N. M., Michelaki, C., Galanidis, A., Evangelou, E., Zaragoza-Castells, J., Dimitrakopoulos, P. G., Tsadilas, C., Arianoutsou, M., & Lloyd, J. (2020). Functional trait variation among and within species and plant functional types in mountainous mediterranean forests. *Frontiers in Plant Science*, *11*, 212. https://doi.org/10.3389/fpls.2020.00212

Gersonde, R. F., & O'Hara, K. L. (2005). Comparative tree growth efficiency in Sierra Nevada mixed-conifer forests. *Forest Ecology and Management*, *219*(1), 95–108. https://doi.org/10.1016/j.foreco.2005.09.002

Gibert, A., Gray, E. F., Westoby, M., Wright, I. J., & Falster, D. S. (2016). On the link between functional traits and growth rate: Meta-analysis shows effects change with plant size, as predicted. *Journal of Ecology*, *104*(5), 1488–1503. https://doi.org/10.1111/1365-2745.12594

Gleason, S. M., Stephens, A. E. A., Tozer, W. C., Blackman, C. J., Butler, D. W., Chang, Y., Cook, A. M., Cooke, J., Laws, C. A., Rosell, J. A., Stuart, S. A., & Westoby, M. (2018). Shoot growth of woody trees and shrubs is predicted by maximum plant height and associated traits. *Functional Ecology*, *32*(2), 247–259. https://doi.org/10.1111/1365-2435.12972

Gracia, C., Burriel, J. A., Ibàñez, J. J., Mata, T., & Vayreda, J. (2004). *Inventari ecològic i forestal de Catalunya*. CREAF.

Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C. E. T., Wagner, F., & Baraloto, C. (2011). Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology*, *99*(6), 1431–1440. https://doi.org/10.1111/j.1365-2745.2011.01883.x

Iida, Y., Poorter, L., Sterck, F., Kassim, A. R., Potts, M. D., Kubo, T., & Kohyama, T. S. (2014). Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. *Ecology*, *95*(2), 353–363. https://doi.org/10.1890/11-2173.1

Johnson, J. D. (1984). A rapid technique for estimating total surface area of pine needles. *Forest Science*, *30*(4), 913–921. https://doi.org/10.1093/forestscience/30.4.913

Kleinschmidt, S., Wanek, W., Kreinecker, F., Hackl, D., Jenking, D., Weissenhofer, A., & Hietz, P. (2020). Successional habitat filtering of rainforest trees is explained by potential growth more than by functional traits. *Functional Ecology*, *34*(7), 1438–1447. https://doi.org/10.1111/1365-2435.13571

Klooster, S.-H.-J.-T., Thomas, E. J. P., & Sterck, F. J. (2007). Explaining interspecific differences in sapling growth and shade tolerance in temperate forests. *Journal of Ecology*, *95*(6), 1250–1260. https://doi.org/10.1111/j.1365-2745.2007.01299.x

Kraft, N. J. B., Metz, M. R., Condit, R. S., & Chave, J. (2010). The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist*, *188*(4), 1124–1136. https://doi.org/10.1111/j.1469-8137.2010.03444.x

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., … Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, *529*, 204–207. https://doi.org/10.1038/nature16476

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. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and

systematics. *Methods in Ecology and Evolution*, 7, 573–579. https://doi.org/10.1111/2041-210X.12512

Liu, X., Swenson, N. G., Lin, D., Mi, X., Umaña, M. N., Schmid, B., & Ma, K. (2016). Linking individual-level functional traits to tree growth in a subtropical forest. *Ecology*, 97(9), 2396–2405. https://doi.org/10.1002/ecy.1445

Maherali, H., Pockman, W. T., & Jackson, R. B. (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, 85(8), 2184–2199. https://doi.org/10.1890/02-0538

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(2), 480–495. https://doi.org/10.1111/j.1469-8137.2011.03708.x

Martinez-Vilalta, J., Rosas, T., Mencuccini, M., Batlles, C., Regalado, Í., Saura-Mas, S., & Sterck, F.. (2020). Data from: Are leaf, stem and hydraulic traits good predictors of individual tree growth? (FUN2FUN project). *Dryad Digital Repository*. https://doi.org/10.5061/dryad.vt4b8gtqr

Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J. F. J., Llorens, P., Nikinmaa, E., Nolè, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U., & Zweifel, R. (2009). Hydraulic adjustment of Scots pine across Europe. *New Phytologist*, 184, 353–364. https://doi.org/10.1111/j.1469-8137.2009.02954.x

Martínez-Vilalta, J., Mencuccini, M., Vayreda, J., & Retana, J. (2010). Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *Journal of Ecology*, 98(6), 1462–1475. https://doi.org/10.1111/j.1365-2745.2010.01718.x

Martin-StPaul, N., Delzon, S., & Cochard, H. (2017). Plant resistance to drought depends on timely stomatal closure. *Ecology Letters*, 20(11), 1437–1447. https://doi.org/10.1111/ele.12851

Medeiros, C. D., Scoffoni, C., John, G. P., Bartlett, M. K., Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C., & Sack, L. (2019). An extensive suite of functional traits distinguishes Hawaiian wet and dry forests and enables prediction of species vital rates. *Functional Ecology*, 33(4), 712–734. https://doi.org/10.1111/1365-2435.13229

Mencuccini M., & Grace J. (1995). Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology*, 15(1), 1–10. https://doi.org/10.1093/treephys/15.1.1

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H. A., Korakaki, E., Lee, S., & Michiels, B. (2005). Size-mediated ageing reduces vigour in trees. *Ecology Letters*, 8(11), 1183–1190. https://doi.org/10.1111/j.1461-0248.2005.00819.x

Mencuccini, M., Rosas, T., Rowland, L., Choat, B., Cornelissen, H., Jansen, S., Kramer, K., Lapenis, A., Manzoni, S., Niinemets, Ü., Reich, P. B., Schrodt, F., Soudzilovskaia, N., Wright, I. J., & Martínez-Vilalta, J. (2019). Leaf economics and plant hydraulics drive leaf:wood area ratios. *New Phytologist*, 224(4), 1544–1556. https://doi.org/10.1111/nph.15998

Michaletz, S. T., Cheng, D., Kerkhoff, A. J., & Enquist, B. J. (2014). Convergence of terrestrial plant production across global climate gradients. *Nature*, 512, 39–43. https://doi.org/10.1038/nature13470

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Paine, C. E. T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., de Gouvenain, R. C., Doucet, J.-L., Doust, S., Fine, P. V. A., Fortunel, C., Haase, J., Holl, K. D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., … Hector, A. (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology*, 103(4), 978–989. https://doi.org/10.1111/1365-2745.12401

Pérez-Harguindeguy, N., Díaz, S., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., … Cornelissen, J. H. C. (2013). New Handbook for standardized measurment of plant functional traits worldwide. *Australian Journal of Botany*, 23(34), 167–234. https://doi.org/10.1071/BT12225

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., Villar, R., & Niinemets, U. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, 182(3), 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter, L., Castilho, C. V., Schietti, J., Oliveira, R. S., & Costa, F. R. C. (2018). Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. *New Phytologist*, 219(1), 109–121. https://doi.org/10.1111/nph.15206

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.-C., Peña-Claros, M., Sterck, F., Villegas, Z., & Sass-Klaassen, U. (2010). The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, 185, 481–492. https://doi.org/10.1111/j.1469-8137.2009.03092.x

Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., Harms, K. E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Peña-Claros, M., Webb, C. O., & Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, 89(7), 1908–1920. https://doi.org/10.1890/07-0207.1

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Rosas, T., Mencuccini, M., Barba, J., Cochard, H., Saura-Mas, S., & Martínez-Vilalta, J. (2019). Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. *New Phytologist*, 223(2), 632–646. https://doi.org/10.1111/nph.15684

Russo, S. E., Jenkins, K. L., Wiser, S. K., Uriarte, M., Duncan, R. P., & Coomes, D. A. (2010). Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. *Functional Ecology*, 24, 253–262. https://doi.org/10.1111/j.1365-2435.2009.01670.x

Shipley, B. (2013). The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology*, 94(3), 560–564. https://doi.org/10.1890/12-0976.1

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., Dantas, V. L., Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18(12), 1406–1419. https://doi.org/10.1111/ele.12508

Skelton, R. P., Brodribb, T. J., McAdam, S. A. M., & Mitchell, P. J. (2017). Gas exchange recovery following natural drought is rapid unless limited by loss of leaf hydraulic conductance: Evidence from an evergreen woodland. *New Phytologist*, 215(4), 1399–1412. https://doi.org/10.1111/nph.14652

Sperry, J. S., Hacke, U. G., & Pittermann, J. (2006). Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany*, 93(10), 1490–1500. https://doi.org/10.3732/ajb.93.10.1490

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., & Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, 17(11), 1351–1364. https://doi.org/10.1111/ele.12348

van der Sande, M. T., Arets, E. J. M. M., Peña-Claros, M., Hoosbeek, M. R., Cáceres-Siani, Y., van der Hout, P., & Poorter, L. (2018). Soil fertility

and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. *Functional Ecology*, *32*(2), 461–474. https://doi.org/10.1111/1365-2435.12968

van der Sande, M. T., Zuidema, P. A., & Sterck, F. (2015). Explaining biomass growth of tropical canopy trees: The importance of sapwood. *Oecologia*, *177*(4), 1145–1155. https://doi.org/10.1007/s00442-015-3220-y

Vilà-Cabrera, A., Martínez-Vilalta, J., & Retana, J. (2015). Functional trait variation along environmental gradients in temperate and Mediterranean trees. *Global Ecology and Biogeography*, *24*(12), 1377–1389. https://doi.org/10.1111/geb.12379

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*, 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Waring, R. (1983). Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Reserach*, *13*, 327–349.

Weemstra, M., Mommer, L., Visser, E. J. W., van Ruijven, J., Kuyper, T. W., Mohren, G. M. J., & Sterck, F. J. (2016). Towards a multidimensional root trait framework: A tree root review. *New Phytologist*, *211*(4), 1159–1169. https://doi.org/10.1111/nph.14003

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I., & Westoby, M. (2005). Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, *14*, 411–421. https://doi.org/10.1111/j.1466-822x.2005.00172.x

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D. D., Baruch, Z., Bongers, F., & Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth – Mortality trade-off in tropical trees. *Ecology*, *91*(12), 3664–3674. https://doi.org/10.1890/09-2335.1

Yang, J., Cao, M., & Swenson, N. G. (2018). Why functional traits do not predict tree demographic rates. *Trends in Ecology & Evolution*, *33*(5), 1–11. https://doi.org/10.1016/j.tree.2018.03.003

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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