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Plant functional traits have globally consistent effects on competition

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Summary paragraph outline

Phenotypic traits and their associated trade-offs have been shown to have globally consistent effects on individual plant physiological functions[1–3], but it has remained unclear how these effects scale up to influence competition – a key driver of community assembly in terrestrial vegetation[4]. Here we use growth data, from more than 3 million trees in more than 140000 plots across the world, to show how three key functional traits – wood density, specific leaf area and maximum height – consistently influence competitive interactions. Fast maximum growth of a species was correlated negatively with its wood density in all biomes and positively with its specific leaf area in most biomes. Low wood density was also correlated with a low ability to tolerate competition and a low competitive impact on neighbours (competitive effect), while high specific leaf area was correlated with a low competitive effect. Thus, traits generate trade-offs between performance with *vs.* without competition, a fundamental ingredient in the classical hypothesis that coexistence of plant species is enabled via differentiation in their successional strategies[5]. Competition within species was stronger than between species, but an increase in trait dissimilarity between species had little influence in weakening competition. No benefit of dissimilarity was detected for specific leaf area and wood density and only a weak benefit for maximum height. Our trait-based approach to modelling competition makes generalisation possible across the forest ecosystems of the globe and their highly diverse species composition.

Main text

Phenotypic traits are considered fundamental drivers of community assembly and thus species diversity[1,6]. The effects of traits on individual plant physiologies and functions are increasingly understood, and have been shown to be underpinned by well-known and globally consistent trade-offs[1–3]. For instance, traits such as wood density and specific leaf area capture trade-offs between the construction cost and longevity or strength of wood and leaf tissues[2,3]. In contrast, we still have limited understanding of how such trait-based trade-offs translate into competitive interactions between species, particularly for long-lived organisms such as trees. Competition is a key filter through which ecological and evolutionary success is determined[4]. A long-standing hypothesis is that the intensity of competition decreases as two species diverge in trait values[7] (trait dissimilarity). The few studies[8–13] that have explored links between traits and competition have shown that linkages were more complex than this, as particular trait values may also confer competitive advantage independently from trait dissimilarity[9,13,14]. This distinction is fundamental for species coexistence and the local mixture of traits. If neighbourhood competition is driven mainly by trait dissimilarity, this will favour a wide spread of trait values at a local scale. In contrast, if neighbourhood interactions are mainly driven by the competitive advantage associated with particular trait values, those trait values should be strongly selected at the local scale, with coexistence operating at larger spatial or temporal scales[6,13]. Empirical investigations have been limited so far to a few particular locations, restricting our ability to find general mechanisms that link traits and competition in the main vegetation types of the world.

Here we quantify the links between traits and competition, measured as the influence of neighbouring trees on growth of a focal tree. Our framework is novel in two important ways: (i) competition is analysed at an unprecedented scale covering all the major forest biomes on Earth (Fig. 1a), and (ii) the influence of traits on competition is partitioned among four fundamental mechanisms (Fig. 1b,c) as follows. A competitive advantage for trees with some trait values compared to others can arise through: (1) permitting faster maximum growth in the absence of competition[15]; (2) exerting a stronger competitive effect[16,17], meaning that competitor species possessing those traits suppress more strongly the growth of their neighbours; or (3) permitting a better tolerance of competition (or competitive 'response' in Goldberg[16]), meaning that growth of species possessing those traits is less affected by competition from neighbours. Finally, (4) competition can promote trait diversification, if increasing trait dissimilarity between species reduces interspecific competition compared to intraspecific competition[7]. Here we show how these four mechanisms are connected to three key traits that describe plant strategies worldwide[1–3]. These traits are wood density (an indicator of a trade-off in stems between growth and strength), specific leaf area (SLA, an indicator of a trade-off in leaves between cheap construction cost and leaf longevity), and maximum height (an indicator of a trade-off between sustained access to light and early reproduction). We analyse basal area growth (annual increase in the area of the cross section of tree trunk at 1.3 m height) of more than 3 million trees from more than 2500 species, across all major forested biomes of the earth (Fig. 1). Species mean trait values were extracted from local data bases and the global TRY data base[18,19] (see Methods). We analysed how basal area growth of each individual tree was reduced by the abundance of competitors in its local neighbourhood[20] (measured as the sum of basal areas of competitors in m^2 ha^{-1}), accounting for traits of both the focal tree and its competitors. This analysis allowed effect sizes to be estimated for each of the four mechanisms outlined above (Fig. 1c).

Across all biomes the strongest driver of individual growth was the total abundance of neighbours, irrespective of their traits (parameters α_{0intra} and α_{0inter} in Fig. 2). Values were strongly positive, indicating neighbours had competitive rather than facilitative effect. The main effects of traits were that some trait values led to a competitive advantage compared to others through two main mechanisms. First, traits of the focal species had direct influences on its maximum growth – *i.e.* in the absence of competition – (parameter m_1 in Fig. 2 and Extended Data Table 3). The fastest growing species had low wood density and high SLA, though the confidence interval intercepted zero in two out of five biomes for SLA (Fig. 2). This is in agreement with previous studies[15,21] of adult trees reporting a strong link between maximum growth and wood density but a weaker link for SLA. Second, some trait values were associated with species having stronger competitive effects, or better tolerance of competition (Fig. 2; Extended Data Table 3). High wood density was correlated with better tolerance of competition from neighbours and with a stronger competitive effect upon neighbours, whereas low SLA was correlated only with a stronger competitive effect. This agrees with studies reporting that high wood density species are more shade-tolerant[15] and have deeper and wider crowns[22,23], hence potentially higher light interception (further detail in Supplementary Discussion). The shorter leaf lifespan associated with high SLA results in lower leaf mass fraction[24]. The low competitive effect associated with high SLA species could thus result from a lower light interception but few data are available on this link[24]. Maximum height was weakly negatively correlated with tolerance to competition in three out of five biomes, supporting the idea that sub-canopy trees are more shade-tolerant[22]. We found however no correlation between maximum height and competitive effect. Current height of an individual has of course an influence on light interception, a key process in competition[13]. But maximum height of a species reflects its long-term strategy and would possibly have stronger effects on long-term population level competition outcomes than it did on short-term basal area growth[25].

After separating trait-independent differences between intraspecific *vs.* interspecific competition, trait dissimilarity had little effect on competition between species (Fig. 2). Only dissimilarity in maximum height between focal and neighbour species led to a weak, but consistent, decrease in competitive suppression of tree growth (Fig. 2). Mechanisms explaining this effect are poorly understood, but could possibly result from complementary crown architectures[26,27]. The average differences in strength of interspecific *vs.* intraspecific competition between two species – a key indicator of processes that could stabilise coexistence – were thus only weakly related to trait dissimilarity (Extended Data Fig. 3). Trait dissimilarity effects are widely considered to be a key mechanism by which traits affect competition[13], but our analysis shows at global scale that trait dissimilarity effects are weak or absent. It remains unclear why the trait-independent competitive effects is higher within species than that between species. Higher loads of shared specialised pathogens[28] could plausibly contribute. Other traits may show stronger trait dissimilarity effects, but we currently lack the trait data to capture such effects.

Analyses allowing for different effects among biomes did not show any particular biome behaving consistently differently from the others (Fig. 2). This lack of context dependence in trait effects may seem surprising, but reinforces that competition for light is important in most forests, and this may explain why we find consistency across such diverse forest types (further details in Supplementary Discussion).

Our global study supports the hypothesis that trait values favouring high tolerance of competition or high competitive effects also render species slow growing in the absence of competition across all forested biomes (Fig. 3). This trait-based trade-off is a key ingredient in the classical model of successional coexistence in forests, where fast-growing species are more abundant in early successional stages where competitors are absent or rare, and are later replaced by slow-growing species in late successional stages where competitors become more abundant[5]. Human or natural disturbances are conspicuous in all the forests analysed, hence successional dynamics are likely to be present in all these sites (see Supplementary Methods). This trade-off was strongest for wood density, with high wood density associated with slow potential growth rate but high tolerance to competition and strong competitive effect (Fig. 3). A similar pattern was present, though less clear, for SLA. High SLA was correlated with low competitive effect but fast maximum growth (confidence intervals not spanning zero in three biomes, Fig. 2 and 3). Given that long-term outcomes of competition at the population level may be more influenced by tolerance of competition than by competitive effect[16], SLA might be less influential in succession.

Coordination between trait values conferring strong competitive effect and trait values conferring high tolerance of competition has been widely expected[9,16], but rarely documented[16,29]. Only wood density showed such coordination, as it was correlated with both competitive effect and tolerance of competition in the same direction (Fig. 2).

The globally consistent links that we report here between traits and competition have considerable promise for predicting species interactions governing forest communities across different forest biomes and continents of the globe. Our analysis demonstrates that trait dissimilarity is not the major determinant of local-scale competitive impacts on tree growth, at least for these three traits. In contrast, the trait-based trade-off in performance with *vs.* without competition, reported here, could promote coexistence of species with diverse traits, provided disturbances create a mosaic of successional stages. A challenge for the future is to move beyond growth to analyse all key demographic rates and life history stages, to analyse how traits influence competitive outcomes at the population level and control stable coexistence.

Supplementary Information is available in the online version of the paper.

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Author contributions GK and MW conceived the study and with DF led a workshop with the participation of DAC, FH, RMK, DCL, LP, MV, GV, and SJW. GK wrote the manuscript with key inputs from all workshop participants and help from all authors. GK, DF and FH wrote the computer code and processed the data. GK devised the main analytical approach and performed analyses with assistance from DF for the figures. GK, DAC, DF, FH, RMK, DCL, MV, GV, SJW, MA, CB, JC, JHCC, SGF, MH, BH, JK, HK, YO, JP, HP, MU, SR, PRB, IFS, GS, NS, JT, BW, CW, MAZ, HZ, JZ, NEZ collected and processed the raw data.

Author information The authors declare no competing financial interests.

FIGURES

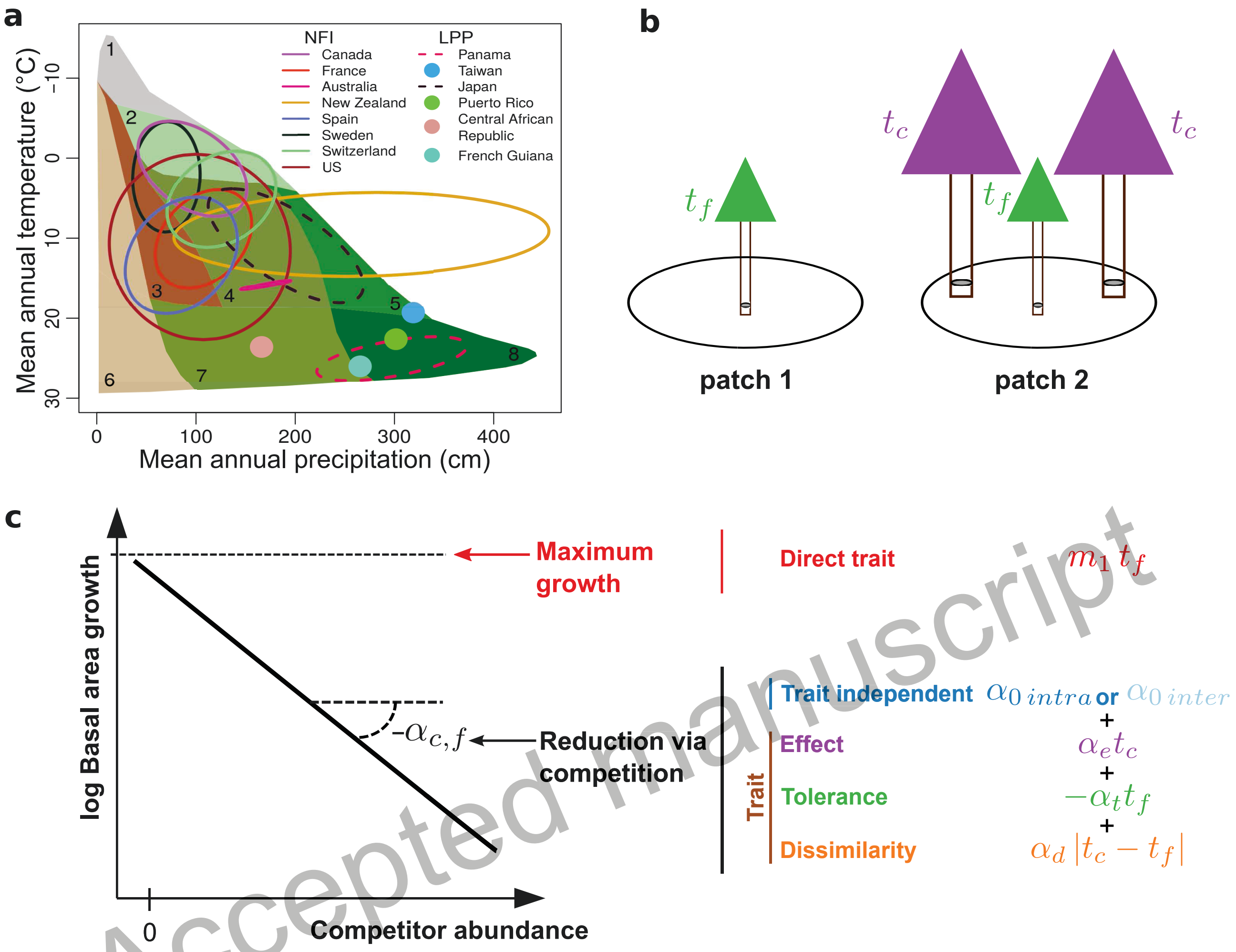

Figure 1: **Assessing competitive interactions at global scale. a,** Precipitation-temperature space occupied by each data set (NFI – national forest inventories data, LPP – large permanent plots data). For data with multiple plots, the range of climatic condition is represented by an ellipse covering 98% of the plots. Biomes are: 1 - tundra; 2 - taiga; 3 - mediterranean; 4 - temperate forest; 5 - temperate rainforest; 6 - desert; 7 - tropical seasonal forest; 8 - tropical rainforest (as defined by Ricklefs[30]). **b,** Sampled patches vary in the abundance of competitors from species c around individuals of focal species f. **c,** We modelled how trait values of the focal tree (t_f), and the abundance (measured as the sum of their basal areas) and traits values of competitor species (t_c) influenced basal area growth of the focal tree. Species maximum growth (red) was influenced by trait of the focal tree ($m_0 + m_1\, t_f$, with m_0 maximum growth independent of the trait). Reduction in growth per unit basal area of competitors ($-\alpha_{c,f}$, black) was modelled as the sum of growth reduction independent of the trait (blue) by conspecific ($\alpha_{0\,intra}$) and heterospecific ($\alpha_{0\,inter}$) competitors, the effect of competitor traits (t_c) on their competitive effect (α_e), the effect of the focal tree's traits (t_f) on its tolerance of competition (α_t), and the effect of trait dissimilarity between the focal tree and its competitors ($|t_c - t_f|$) on competition (α_d). The parameters $m_0, m_1, \alpha_{0\,intra}, \alpha_{0\,inter}, \alpha_e, \alpha_t$ and α_d are fitted from data using a maximum likelihood method.

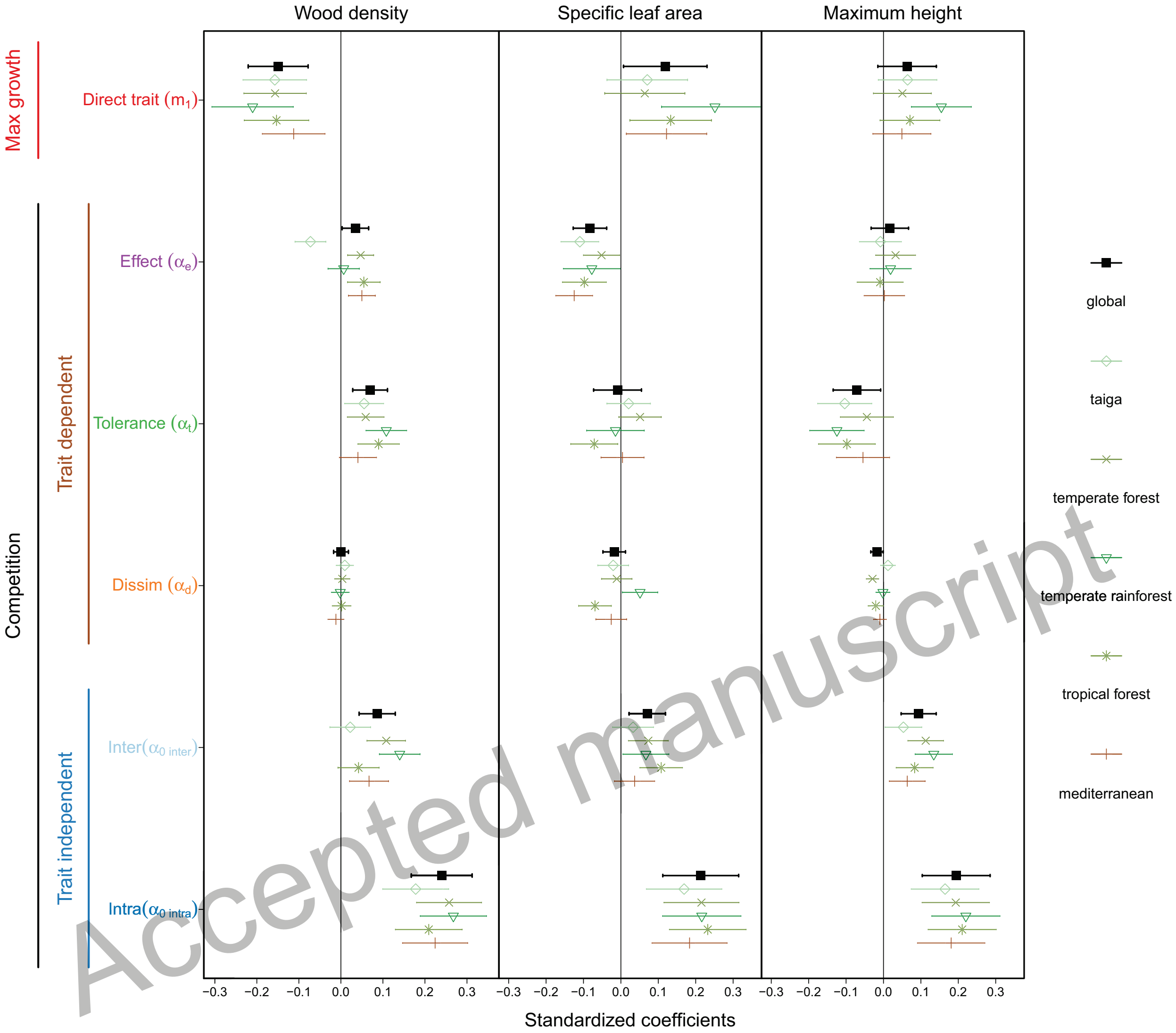

Figure 2: **Trait-dependent and trait-independent effects on maximum growth and competition across the globe and their variation among biomes.** Standardized regression coefficients for growth models, fitted separately for each trait (points: mean estimates and lines: 95% confidence intervals). Black points and lines represent global estimates and coloured points and lines represent the biome level estimates. The parameter estimates represent: effect of focal tree's trait value on maximum growth m_1, the effect of competitor trait values on their competitive effect α_e (positive values indicate that higher trait values lead to a stronger reduction in growth of the focal tree), the effect of the focal tree's trait value on its tolerance of competition α_t (positive values indicate that greater trait values result in greater tolerance of competition), the effect on competition of trait dissimilarity between the focal tree and its competitors α_d (negative values indicate that higher trait dissimilarity leads to a lower reduction of the growth of the focal tree), and the trait-independent competitive effect of conspecific $\alpha_{0\,intra}$ and heterospecific $\alpha_{0\,inter}$. Tropical rainforest and tropical seasonal forest were merged together as tropical forest, tundra was merged with taiga, and desert was not included as too few plots were available (see Fig 1a. for biomes definitions).

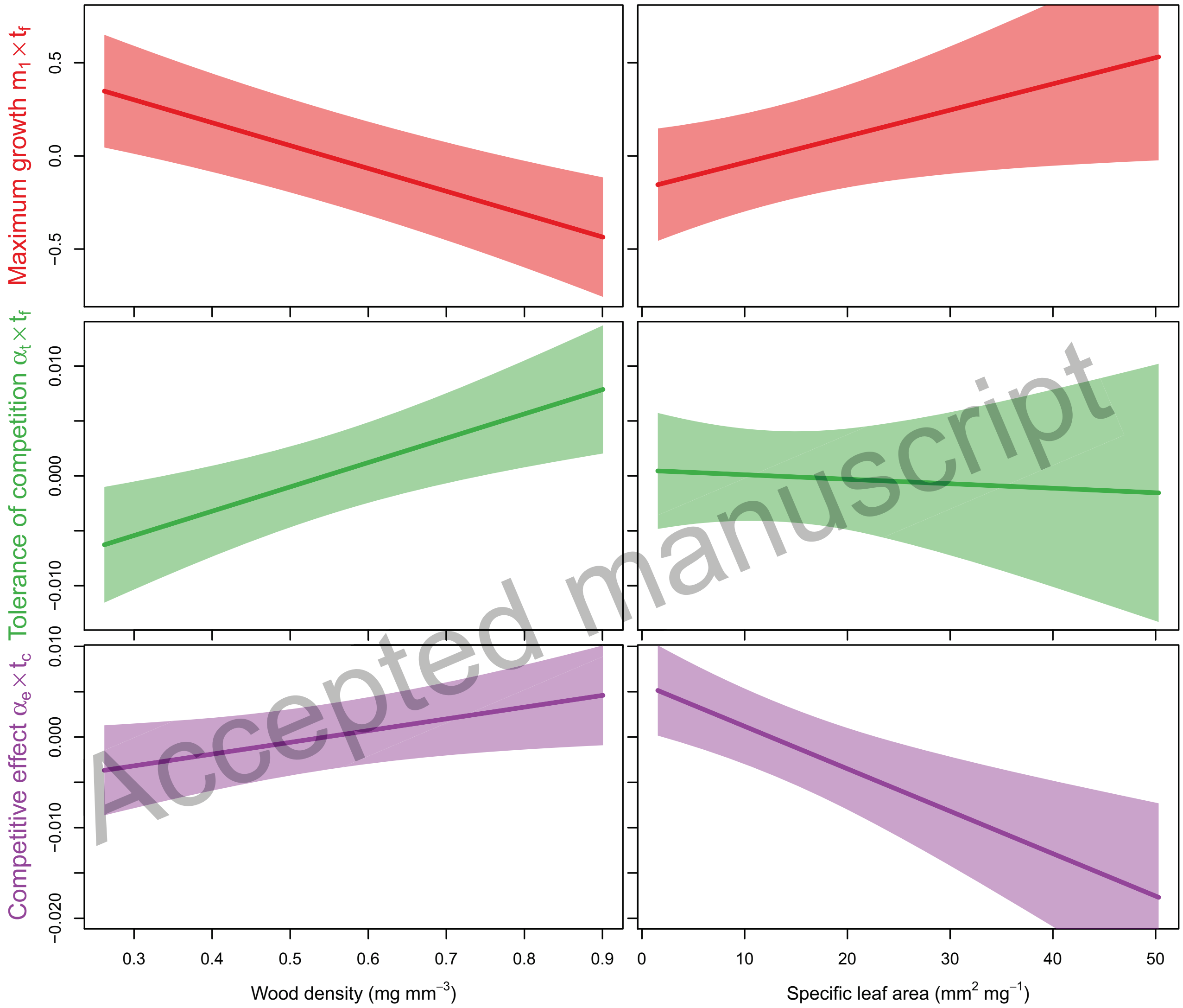

Figure 3: **Variation of maximum growth, competitive effects and competitive tolerance with wood density and specific leaf area predicted by global traits models.** Variation of maximum growth ($m_1\, t_f$), tolerance of competition ($\alpha_t\, t_f$) and competitive effect ($\alpha_e\, t_c$) parameters with wood density (first column) and specific leaf area (second column). The shaded area represents the 95% confidence interval of the prediction (including uncertainty associated with α_0 or m_0).

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Methods

Model and analysis

To examine the link between competition and traits we used a neighbourhood modelling framework[1–5] to model the growth of a focal tree of species f as a product of its maximum growth (determined by its traits and size) together with reductions due to competition from individuals growing in the local neighbourhood (see definition below). Specifically, we assumed a relationship of the form

$$G_{i,f,p,s,t} = G_{\max f,p,s}\, D_{i,f,p,s,t}^{\gamma_f} \exp\left(\sum_{c=1}^{N_i} -\alpha_{c,f} B_{i,c,p,s}\right), \tag{1}$$

where:

- $G_{i,f,p,s,t}$ and $D_{i,f,p,s,t}$ are the annual basal area growth and diameter at breast height of individual i from species f, plot or quadrat (see below) p, data set s, and census t,
- $G_{\max f,p,s}$ is the maximum basal area growth for species f on plot or quadrat p in data set s, i.e. in absence of competition,
- γ_f determines the rate at which growth changes with size for species f, modelled with a normally distributed random effect of species $\varepsilon_{\gamma,f}$ [as $\gamma_f = \gamma_0 + \varepsilon_{\gamma,f}$ where $\varepsilon_{\gamma,f} \sim \mathcal{N}(0, \sigma_\gamma)$ – a normal distribution of mean 0 and standard deviation σ_γ]
- $\alpha_{c,f}$ is the per unit basal area effect of individuals from species c on growth of an individual in species f,
- $B_{i,c,p,s} = 0.25\,\pi \sum_{j \neq i} w_j\, D_{j,c,p,s,t}^2$ is the sum of basal area of all individuals competitor trees j of the species c within the local neighbourhood of the tree i in plot p, data set s and census t, where w_j is a constant based on neighboorhood size for tree j depending on the data set (see below). Note that $B_{i,c,p,s}$ include all trees of species c in the local neighbourhood excepted the tree i, and
- N_i is the number of competitor species in the local neighbourhood of focal tree i.

Values of $\alpha_{c,f} > 0$ indicate competition, whereas $\alpha_{c,f} < 0$ indicates facilitation.

Log-transformation of equ. 1 leads to a linearised model of the form

$$\log G_{i,f,p,s,t} = \log G_{\max f,p,s} + \gamma_f \, \log D_{i,f,p,s,t} + \sum_{c=1}^{N_i} -\alpha_{c,f} B_{i,c,p,s}. \tag{2}$$

To include the effects of traits on the parameters of the growth model we build on previous studies that explored the role of traits for tree performances and tree competition[2,4,5]. We modelled the effect of traits, one trait at a time. The effect of a focal species' trait value, t_f, on its maximum growth was included as:

$$\log G_{\max f,p,s} = m_0 + m_1 \, t_f + m_2 \, MAT + m_3 \, MAP + \varepsilon_{G_{\max},f} + \varepsilon_{G_{\max},p} + \varepsilon_{G_{\max},s}. \tag{3}$$

Here m_0 is the average maximum growth, m_1 gives the effect of the focal species trait, m_2 and m_3 the effects of mean annual temperature MAT and sum of annual precipitation MAP respectively, and $\varepsilon_{G_{\max},f}$, $\varepsilon_{G_{\max},p}$, $\varepsilon_{G_{\max},s}$ are normally distributed random effects for species f, plot or quadrat p (see below), and data set s [where $\varepsilon_{G_{\max},f} \sim \mathcal{N}(0, \sigma_{G_{\max},f})$; $\varepsilon_{G_{\max},p} \sim \mathcal{N}(0, \sigma_{G_{\max},p})$ and $\varepsilon_{G_{\max},s} \sim \mathcal{N}(0, \sigma_{G_{\max},s})$].

Previous studies have proposed various decompositions of the competition parameter into key trait-based processes[1], and here we extended the approach of the most recent study[5]. As presented in Fig. 1, competitive interactions were modelled using an equation of the form[2]:

$$\alpha_{c,f} = \alpha_{0,f,intra} \, C + \alpha_{0,f,inter} \, (1 - C) - \alpha_t \, t_f + \alpha_e \, t_c + \alpha_d \, |t_c - t_f| \tag{4}$$

where:

- $\alpha_{0,f,intra}$ and $\alpha_{0,f,inter}$ are respectively **intra and interspecific trait independent competition** for the focal species f, modelled with a normally distributed random effect of species f and each with normally distributed random effect of data set s [as $\alpha_{0,f} = \alpha_0 + \varepsilon_{\alpha_0,f} + \varepsilon_{\alpha_0,s}$, where $\varepsilon_{\alpha_0,f} \sim \mathcal{N}(0, \sigma_{\alpha_0,f})$ and $\varepsilon_{\alpha_0,s} \sim \mathcal{N}(0, \sigma_{\alpha_0,s})$]. C is a binary variable taking the value one for $f = c$ (conspecific) and zero for $f \neq c$ (heterospecific),
- α_t is the **tolerance of competition** by the focal species, i.e. change in competition tolerance due to traits t_f of the focal tree with a normally distributed random effect of data set s included [$\varepsilon_{\alpha_t,s} \sim \mathcal{N}(0, \sigma_{\alpha_t})$],

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[1] Different approaches have been proposed to model α from traits. In one of the first studies Uriarte et al.[2] modelled α as $\alpha = \alpha_0 + \alpha_d |t_f - t_c|$. Then Kunstler et al.[4] used two different models: $\alpha = \alpha_0 + \alpha_d |t_f - t_c|$ or $\alpha = \alpha_0 + \alpha_h (t_f - t_c)$. Finally, Lasky et al.[5] developed a single model including multiple processes as $\alpha = \alpha_0 + \alpha_t t_f + \alpha_h (t_f - t_c) + \alpha_d |t_f - t_c|$. In our study, we extended this last model. We considered that it was clearer to split $\alpha_h (t_f - t_c)$ into $\alpha_t t_f + \alpha_e t_c$, which is equivalent to the hierarchical distance if $\alpha_t = -\alpha_e$ (thus avoiding replication of t_f effect through both α_h and α_t). We also included two α_0, one for intra and one for interspecific competition.

[2] For fitting the model the equation of $\alpha_{c,f}$ was developed with species basal area in term of community weighted mean of the trait, see Supplementary Methods for more details.

- α_e is the **competitive effect**, i.e. change in competition effect due to traits t_c of the competitor tree with a normally distributed random effect of data set s included $[\varepsilon_{\alpha_i,s} \sim \mathcal{N}(0, \sigma_{\alpha_i})]$, and
- α_d is the effect of **trait dissimilarity**, i.e. change in competition due to absolute distance between traits $|t_c - t_f|$ with a normally distributed random effect of data set s included $[\varepsilon_{\alpha_d,s} \sim \mathcal{N}(0, \sigma_{\alpha_d})]$.

Estimating separate α_0 for intra and interspecific competition allowed us to account for trait-independent differences in interactions with conspecifics and heterospecifics. We also explored a simpler version of the model where trait-independent competitive effects were pooled (i.e. there was a single value for α_0), as most previous studies have generally not made this distinction, using the following equation:

$$\alpha_{c,f} = \alpha_{0,f} - \alpha_t \, t_f + \alpha_e \, t_c + \alpha_d \, |t_c - t_f| \tag{5}$$

In this alternative model any differences between intra and interspecific competition do enter into trait dissimilarity effects, with a trait dissimilarity of zero attached to them. This may lead to an overestimation of the trait dissimilarity effect. Results for this model are presented in Supplementary Results.

Eqs. 2-4 were then fitted to empirical estimates of growth based on change in diameter between census t and $t+1$ (respectively at year y_t and y_{t+1}), given by

$$G_{i,f,p,s,t} = 0.25\pi \left(D^2_{i,f,p,s,t+1} - D^2_{i,f,p,s,t} \right) / (y_{t+1} - y_t). \tag{6}$$

To estimate standardised coefficients (one type of standardised effect size)[6], response and explanatory variables were standardized (divided by their standard deviations) prior to analysis. Trait and diameter were also centred to facilitate convergence. The models were fitted using the *lmer* routine in the lme4 package[7] in the R statistical environment[8]. We fitted two versions of each model. In the first version parameters $m_0, m_1, \alpha_0, \alpha_t, \alpha_i, \alpha_d$ were estimated as constant across all biomes. In the second version, we allowed different fixed estimates of these parameters for each biome. This enabled us to explore variation among biomes. Because some biomes had few observations, we merged those with biomes with similar climates. Tundra was merged with taiga, tropical rainforest and tropical seasonal forest were merged into tropical forest, and deserts were not included in this final analysis as too few plots were available. To evaluate whether our results were robust to the random effect structure we also explored a model with a random effect attached to parameters both for the data set and for a local ecoregion using the Köppen-Geiger ecoregion[9] (see Supplementary Results).

Estimating the effect of traits on the differences between intra and interspecific competition

The differences between inter and intraspecific competition has long been considered crucial to community assembly as it is key in controlling species coexistence[10,11]. Our estimated growth model allowed us to predict inter and intraspecific competition from trait-independent and trait-dependent processes. The competitive effect of species j on species i can be defined in the tree basal area growth model (see equ. 2) as the reduction of growth of species i by one unit of basal area of competitors of the species j, and is given by $\frac{1}{e^{-\alpha_{ij}}}$ – with α_{ij} defined by equ. 4. High competitive effects translate into strong growth reduction. Then we can compare the strength of inter *vs.* intraspecific competition between two species i and j using the following expression:

$$\sqrt{\frac{e^{\alpha_{ij}} e^{\alpha_{ji}}}{e^{\alpha_{jj}} e^{\alpha_{ii}}}} \tag{7}$$

Which can be expressed in function the estimated parameters of eqn. 4 as:

$$\sqrt{\frac{e^{\alpha_{ij}} e^{\alpha_{ji}}}{e^{\alpha_{jj}} e^{\alpha_{ii}}}} = e^{(\alpha_{0,inter} - \alpha_{0,intra} + \alpha_d |t_j - t_i|)} \tag{8}$$

In summary, the strength of inter *vs.* intraspecific competition is only influenced by the difference between $\alpha_{0,intra}$ *vs.* $\alpha_{0,inter}$ and by trait dissimilarity via α_d (see Figure 3. in Extended Data for the results). This approach shares similarities with a method developed by Chesson[12], and recently applied with population growth models in annual plants communities[13,14] – estimating ρ as a similar ratio. It is however important to note that in the population growth model the ratio of inter *vs.* intraspecific competition is directly related to stabilising processes controlling species coexistence, whereas the tree basal growth model presented here cannot be used in itself to estimate coexistence.

Data

Growth data

Our main objective was to collate data sets spanning the dominant forest biomes of the world. Data sets were included if they (i) allowed both growth of individual trees and the local abundance of competitors to be estimated, and (ii) had good (>40%) coverage for at least one of the traits of interest (SLA, wood density, and maximum height).

The data sets collated fell into two broad categories: (1) national forest inventories (NFI), in which trees above a given diameter were sampled in a network of small plots (often on a regular grid) covering the country (references for NFI data used[15–24]); (2) large permanent plots (LPP) ranging in size from 0.5-50ha, in which the x-y coordinates of all trees above a given diameter were recorded (references for LPP data used[25–32]). LPP were mostly located in tropical regions. The minimum diameter of recorded trees varied among sites from 1-12cm. To allow comparison between data sets, we restricted our analysis to trees greater than 10cm. Moreover, we excluded from the analysis any plots with harvesting during the growth measurement period, that were identified as plantations, or that overlapped a forest edge. Finally, we randomly selected only two consecutive census dates per plot or quadrat to avoid having to account for repeated measurements (less than a third of the data had repeated measurements). Because human and natural disturbances are present in all these forests (see Supplementary Methods), they probably all experience successional dynamics (as indicated by the forest age distribution available in some of these sites in Supplementary Methods). See Supplementary Methods and Extended Data Table 1 for more details on individual data sets.

Basal area growth was estimated from diameter measurements recorded between the two censuses. For the French NFI, these data were obtained from short tree cores. For all other data sets, diameter at breast height (D) of each individual was recorded at multiple census dates. We excluded trees (i) with extreme positive or negative diameter growth measurements, following criteria developed at the BCI site[26] (see the R package CTFS R), (ii) that were palms or tree ferns, or (iii) that were measured at different heights in two consecutive censuses.

For each individual tree, we estimated the local abundance of competitor species as the sum of basal area for all individuals > 10cm diameter within a specified neighbourhood. For LPPs, we defined the neighbourhood as being a circle with 15m radius. This value was selected based on previous studies showing the maximum radius of interaction to lie in the range 10-20m[2,33]. To avoid edge effects, we also excluded trees less than 15m from the edge of a plot. To account for variation of abiotic conditions within the LPPs, we divided plots into regularly spaced 20x20m quadrats and included a random quadrat effect in the model (see above).

For NFI data coordinates of individual trees within plots were generally not available, thus neighbourhoods were defined based on plot size. In the NFI from the United States, four sub-plots of 7.35m located within 20m of one another were measured. We grouped these sub-plots to give a single estimate of the local competitor abundance. Thus, the neighbourhoods used in the competition analysis ranged in size from 10-25 m radius, with most plots 10-15 m radius. We included variation in neighbourhood size in the constant w_j to compute competitor basal area in m^2/ha.

We extracted mean annual temperature (MAT) and mean annual sum of precipitation (MAP) from the worldclim data base[34], using the plot latitude and longitude. MAT and MAP data were then used to classify plots into biomes, using the diagram provided by Ricklefs[35] (after Whittaker).

Traits

Data on species functional traits were extracted from existing sources. We focused on wood density, species specific leaf area (SLA) and maximum height, because these traits have previously been related to competitive interactions and are available for large numbers of species[2–5,36] (see Extended Data

Table 2 for trait coverage). Where available we used data collected locally (references for the local trait data used in this analysis[27,36–39]); otherwise we sourced data from the TRY trait data base[40] (references for the data extracted from the TRY database used in this analysis[36,41–110]). Local data were available for most tropical sites and species (see Supplementary Methods). Several of the NFI data sets also provided tree height measurements, from which we computed a species' maximum height as the 99% quantile of observed values (for France, US, Spain, Switzerland). For Sweden we used the estimate from the French data set and for Canada we used the estimate from the US data set. Otherwise, we extracted height measurements from the TRY database. We were not able to account for trait variability within species.

For each focal tree, our approach required us to also account for the traits of all competitors present in the neighbourhood. Most of our plots had good coverage of competitors, but inevitably there were some trees where trait data were lacking. In these cases we estimated trait data as follows. If possible, we used the genus mean, and if no genus data was available, we used the mean of the species present in the country. However, we restricted our analysis to plots where (i) the percentage of basal area contributed by trees with no species level trait data was less than 10%, and (ii) the percentage of basal area of trees with neither species nor genus level trait data was less than 5%.

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