

Plant functional traits have globally consistent effects on competition

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Phenotypic traits and their associated trade-offs have been shown to have globally consistent effects on individual plant physiological functions^{1–3}, but how these effects scale up to influence competition, a key driver of community assembly in terrestrial vegetation, has remained unclear⁴. Here we use growth data from more than 3 million trees in over 140,000 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 effect on neighbours, while high specific leaf area was correlated with a low competitive effect. Thus, traits generate trade-offs between performance with competition versus performance without competition, a fundamental ingredient in the classical hypothesis that the coexistence of plant species is enabled via differentiation in their successional strategies⁵. 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 or wood density, and only a weak benefit for maximum height. Our trait-based approach to modelling competition makes generalization possible across the forest ecosystems of the world and their highly diverse species composition.

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}. By contrast, we still have a 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 determined⁴. A long-standing hypothesis is that the intensity of competition decreases as two species diverge in trait values⁷ (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. By 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: first, competition is analysed at an unprecedented scale covering all the major forest biomes on Earth (Fig. 1a and Extended Data Fig. 1), and second, 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 by: (1) permitting faster maximum growth in the absence of competition¹⁵; (2) exerting a stronger competitive effect^{16,17}, meaning that competitor species possessing those

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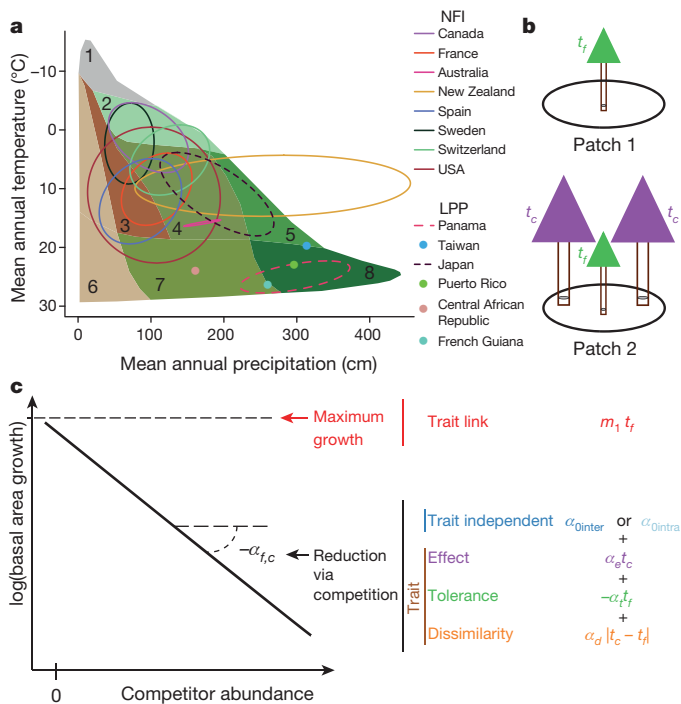


Figure 1 | Assessing competitive interactions at global scale.

a, Precipitation–temperature space occupied by each data set (LPP, large permanent plots data; NFI, national forest inventories 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; and 8, tropical rainforest (see Methods for details). **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 ($-\alpha_{f,c}$, 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_i), 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 , $\alpha_{0,intra}$, $\alpha_{0,inter}$, α_e , α_i and α_d are fitted from data using a maximum likelihood method.

traits suppress more strongly the growth of their neighbours; or (3) permitting a better tolerance of competition (described as a competitive 'response' in ref. 16), meaning that the 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 competition⁷. 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 the basal area growth (annual increase in the cross-section area of a tree trunk at 1.3 m height) of more than 3 million trees from over 2,500 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 base¹⁸ (see Methods). We analysed how the basal area growth of each individual tree was reduced by the abundance of competitors in its local neighbourhood¹⁹ (measured as the sum of basal areas of competitors in $\text{m}^2 \text{ha}^{-1}$), 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 earlier (Fig. 1c).

Across all biomes, the strongest driver of individual growth was the total abundance of neighbours, irrespective of their traits (parameters $\alpha_{0,intra}$ and $\alpha_{0,inter}$ in Fig. 2). Values were strongly positive, indicating that neighbours had competitive rather than facilitative effects. 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 influences on its maximum growth—that is, in the absence of competition—(parameter m_1 in Fig. 2 and Extended Data Table 1). The fastest growing species had low wood density and high SLA values, although the confidence interval on the trait effect intercepted zero in two out of five biomes for SLA (Fig. 2). This is in agreement with previous studies^{15,20} 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 and Extended Data Table 1). High wood density was correlated with better tolerance of competition from neighbours and with a stronger competitive effect on 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-tolerant¹⁵ and have deeper and wider crowns^{21,22}, hence potentially higher light interception (further detail in Supplementary Discussion). The shorter leaf lifespan associated with high SLA results in lower leaf mass fraction²³. The low competitive effect associated with high SLA species could thus result from a lower light interception, but few data are available on this link²³. 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-tolerant²¹. We found, however, no correlation between maximum height and competitive effect. The current height of an individual does have an influence on light interception, a key process in competition¹³. 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 growth²⁴.

After separating trait-independent differences between intraspecific versus interspecific competition, trait dissimilarity had little effect on competition between species (Fig. 2). Only dissimilarity in maximum height between focal and neighbouring 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^{25,26}. The average differences in strength of interspecific versus intraspecific competition between two species—a key indicator of processes that could stabilize coexistence—were thus only weakly related to trait dissimilarity (Extended Data Fig. 2). Trait dissimilarity effects are widely considered to be a key mechanism by which traits affect competition¹³, but our analysis shows at global scale that trait dissimilarity effects are weak or absent. It remains unclear why the trait-independent competitive effects are higher within species than between species. Higher loads of shared specialized pathogens²⁷ could plausibly contribute. Other traits or combinations of traits (see ref. 12) 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 the idea that competition for light is important in most forests, and this may explain why we find consistency across such diverse forest types (see Supplementary Discussion for further details).

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, in which fast-growing species are more abundant in early successional

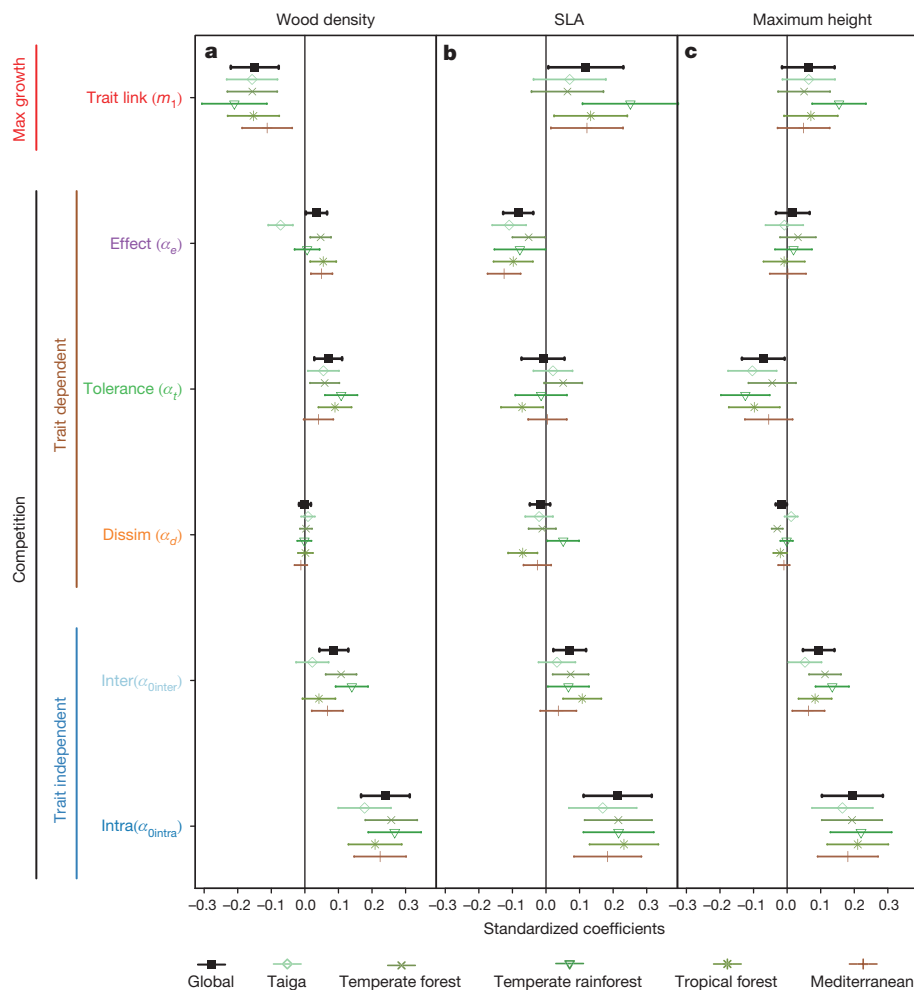


Figure 2 | Trait-dependent and trait-independent effects on maximum growth and competition across the globe, and their variation among biomes. a–c, Standardized regression coefficients for growth models, fitted separately for wood density (a), SLA (b) and maximum height (c) (points denote average estimates, lines denote 95% confidence intervals). Black points and lines represent global estimates, and coloured points and lines represent the biome level estimates. The parameter estimates represent: the 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 (α_{0intra}) and heterospecific (α_{0inter}) competitors. 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).

stages where competitors are absent or rare, and are later replaced by slow-growing species in late successional stages where competitors become more abundant⁵. Human or natural disturbances are conspicuous in all of the forests analysed, hence successional dynamics are

likely to be present in all these sites (see Supplementary Information). This trade-off was strongest for wood density, with high wood density associated with a slow potential growth rate but a high tolerance to competition and a strong competitive effect (Fig. 3). A similar pattern

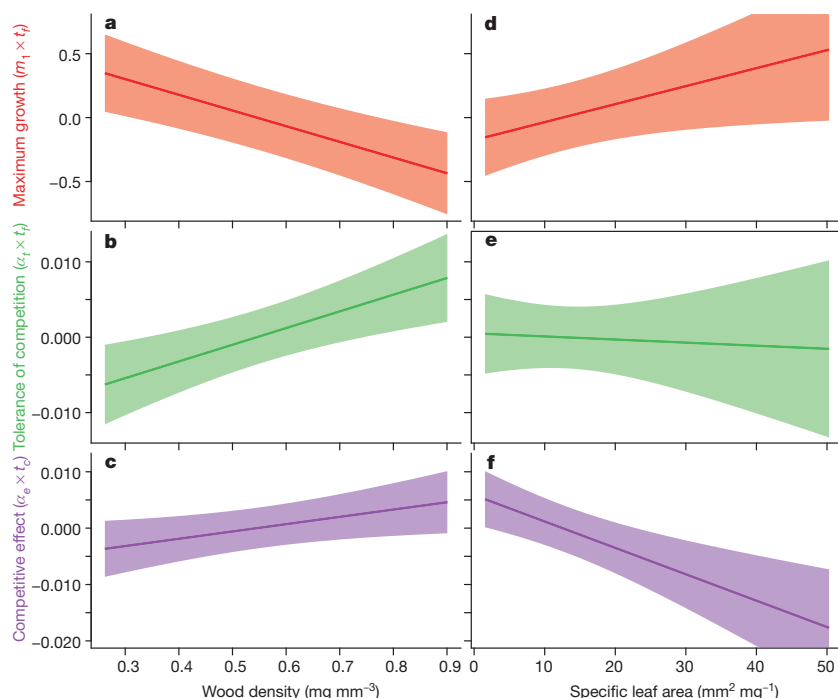


Figure 3 | Variation of maximum growth, competitive effects and competitive tolerance with wood density and SLA predicted by global traits models. a–f, Variation of maximum growth ($m_1 \times t_f$) (a, d), tolerance of competition ($\alpha_t \times t_f$) (b, e) and competitive effect ($\alpha_e \times t_e$) (c, f) parameters with wood density (a–c) and SLA (d–f). The shaded area represents the 95% confidence interval of the prediction (including uncertainty associated with α_0 or m_0).

was present, although less clear, for SLA. High SLA was correlated with a low competitive effect but fast maximum growth (confidence intervals not spanning zero in three biomes, Figs 2 and 3, see Extended Data Fig. 3 for maximum height). Given that the long-term outcomes of competition at the population level may be more influenced by tolerance of competition than by the competitive effect¹⁶, SLA might be less influential in succession.

Coordination between trait values conferring a strong competitive effect and trait values conferring a high tolerance of competition has been widely expected^{9,16}, but rarely documented^{16,28}. 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 effects on tree growth, at least for these three traits. By contrast, the trait-based trade-off in performance with competition versus without competition, reported here, could promote the 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, and analyse how traits influence competitive outcomes and stable coexistence at the population level.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. a. & Wright, I. J. Plant Ecological Strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* **33**, 125–159 (2002).
- Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).
- Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–366 (2009).
- Keddy, P. A. *Competition* (Springer Netherlands, 1989).
- Rees, M., Condit, R., Crawley, M., Pacala, S. W. & Tilman, D. Long-term studies of vegetation dynamics. *Science* **293**, 650–655 (2001).
- Adler, P. B., Fajardo, A., Kleinhesselink, A. R. & Kraft, N. J. B. Trait-based tests of coexistence mechanisms. *Ecol. Lett.* **16**, 1294–1306 (2013).
- MacArthur, R. & Levins, R. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385 (1967).
- Uriarte, M. *et al.* Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecol. Lett.* **13**, 1503–1514 (2010).
- Kunstler, G. *et al.* Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecol. Lett.* **15**, 831–840 (2012).
- HilleRisLambers, J., Adler, P., Harpole, W., Levine, J. & Mayfield, M. Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Syst.* **43**, 227–248 (2012).
- Lasky, J. R., Uriarte, M., Boukili, V. K. & Chazdon, R. L. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proc. Natl Acad. Sci. USA* **111**, 5616–5621 (2014).
- Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci. USA* **112**, 797–802 (2015).
- Mayfield, M. M. & Levine, J. M. Opposing effects of competitive exclusion on the phylogenetic structure of communities: phylogeny and coexistence. *Ecol. Lett.* **13**, 1085–1093 (2010).

- Kraft, N. J. B., Crutsinger, G. M., Forrester, E. J. & Emery, N. C. Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos* **123**, 1391–1399 (2014).
- Wright, S. J. *et al.* Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **91**, 3664–3674 (2010).
- Goldberg, D. E. Competitive ability: definitions, contingency and correlated traits. *Phil. Trans. R. Soc. Lond. B* **351**, 1377–1385 (1996).
- Gaudet, C. L. & Keddy, P. A. A comparative approach to predicting competitive ability from plant traits. *Nature* **334**, 242–243 (1988).
- Kattge, J. *et al.* TRY – a global database of plant traits. *Glob. Change Biol.* **17**, 2905–2935 (2011).
- Uriarte, M., Canham, C. D., Thompson, J. & Zimmerman, J. K. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.* **74**, 591–614 (2004).
- Poorter, L. *et al.* Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* **89**, 1908–1920 (2008).
- Poorter, L., Bongers, L. & Bongers, F. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology* **87**, 1289–1301 (2006).
- Aiba, M. & Nakashizuka, T. Architectural differences associated with adult stature and wood density in 30 temperate tree species. *Funct. Ecol.* **23**, 265–273 (2009).
- Niinemets, Ü. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecol. Res.* **25**, 693–714 (2010).
- Adams, T. P., Purves, D. W. & Pacala, S. W. Understanding height-structured competition in forests: is there an R* for light? *Proc. R. Soc. B* **274**, 3039–3047 (2007).
- Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* **95**, 2479–2492 (2014).
- Jucker, T., Bouriaud, O. & Coomes, D. A. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Funct. Ecol.* **29**, 1078–1086 (2015).
- Bagchi, R. *et al.* Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**, 85–88 (2014).
- Wang, P., Stieglitz, T., Zhou, D. W. & Cahill, J. F. Jr. Are competitive effect and response two sides of the same coin, or fundamentally different? *Funct. Ecol.* **24**, 196–207 (2010).

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Author Contributions G.K. and M.W. conceived the study, and with D.F. led a workshop with the participation of D.A.C., F.H., R.M.K., D.C.L., L.P., M.V., G.V. and S.J.W. G.K. wrote the manuscript with key inputs from all workshop participants and help from all authors. G.K., D.F. and F.H. wrote the computer code and processed the data. G.K. devised the main analytical approach and performed analyses with assistance from D.F. for the figures. G.K., D.A.C., D.F., F.H., R.M.K., D.C.L., M.V., G.V., S.J.W., M.A., C.B., J.C., J.H.C.C., S.G.-F., M.H., B.H., J.K., H.K., Y.O., J.P., H.P., M.U., S.R., P.R.-B., I.-F.S., G.S., N.G.S., J.T., B.W., C.W., M.A.Z., H.Z., J.K.Z. and N.E.Z. collected and processed the raw data.

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METHODS

Model and analysis. To examine the link between competition and traits, we used a neighbourhood modelling framework^{8,29} 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

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

in which $G_{i,f,p,s,t}$ and $D_{i,f,p,s,t}$ are the annual basal area growth (G) and diameter (D) at breast height of individual (i), from species (f), plot or quadrat (p) (see below), 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); that is, 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 ε_{γ_f} (as $\gamma_f = \gamma_0 + \varepsilon_{\gamma_f}$, in which $\varepsilon_{\gamma_f} \sim (0, \sigma_{\gamma})$)—a normal distribution of mean 0 and standard deviation σ_{γ}). $\alpha_{f,c}$ 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 neighbourhood 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 except the tree (i), and N_i is the number of competitor species in the local neighbourhood of focal tree (i). Values of $\alpha_{f,c} > 0$ indicate competition, whereas $\alpha_{f,c} < 0$ indicates facilitation.

A log-transformation of equation (1) leads to a linearized model of the form

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

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^{8,9,11}. 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:

$$\log(G_{\max,f,p,s}) = m_0 + m_1 t_f + m_2 \text{MAT} + m_3 \text{MAP} + \varepsilon_{G_{\max},f} + \varepsilon_{G_{\max},p} + \varepsilon_{G_{\max},s} \quad (3)$$

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 $\varepsilon_{G_{\max},f}$, $\varepsilon_{G_{\max},p}$ and $\varepsilon_{G_{\max},s}$ are normally distributed random effects for species (f), plot or quadrat (p) (see below), and data set (s) (in which $\varepsilon_{G_{\max},f} \sim \mathcal{N}(0, \sigma_{G_{\max},f})$, $\varepsilon_{G_{\max},p} \sim \mathcal{N}(0, \sigma_{G_{\max},p})$ and $\varepsilon_{G_{\max},s} \sim \mathcal{N}(0, \sigma_{G_{\max},s})$).

As shown in Fig. 1, competitive parameter (α) was modelled using an equation of the form:

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

in which $\alpha_{0\text{intra},f}$ and $\alpha_{0\text{inter},f}$ are (respectively) intraspecific and average interspecific trait independent competition for the focal species (f), modelled each with a normally distributed random effect of species (f) and normally distributed random effect of data set (s) (such as $\alpha_{0\text{intra},f} = \alpha_{0\text{intra}} + \varepsilon_{\alpha_{0\text{intra},f}}$ and $\varepsilon_{\alpha_{0\text{intra},f}} \sim \mathcal{N}(0, \sigma_{\alpha_{0\text{intra},f}})$ and $\varepsilon_{\alpha_{0\text{intra},s}} \sim \mathcal{N}(0, \sigma_{\alpha_{0\text{intra},s}})$, and replacing intra by inter gives the expressions for $\alpha_{0\text{inter},f}$). 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, that is, change in competition tolerance due to traits (t_f) of the focal tree with a normally distributed random effect of data set (s) included ($\varepsilon_{\alpha_t,s} \sim \mathcal{N}(0, \sigma_{\alpha_t,s})$). α_e is the competitive effect, that is, change in competition effect due to traits (t_c) of the competitor tree with a normally distributed random effect of data set (s) included ($\varepsilon_{\alpha_e,s} \sim \mathcal{N}(0, \sigma_{\alpha_e,s})$), and α_d is the effect of trait dissimilarity, that is, change in competition due to absolute distance between traits $|t_c - t_f|$ with a normally distributed random effect of data set (s) included ($\varepsilon_{\alpha_d,s} \sim \mathcal{N}(0, \sigma_{\alpha_d,s})$).

Our decomposition of the competition parameter (α) into trait-based processes builds on previous studies. In one of the first studies, Uriarte *et al.*⁸ modelled α as $\alpha = \alpha_0 + \alpha_d |t_f - t_c|$. Then, Kunstler *et al.*⁹ used two different models: $\alpha = \alpha_0 + \alpha_d |t_f - t_c|$ or $\alpha = \alpha_0 + \alpha_t |t_f - t_c|$. Finally, Lasky *et al.*¹¹ developed a single model including multiple processes as $\alpha = \alpha_0 + t_f + \alpha_h(t_f - t_c) + \alpha_d |t_f - t_c|$. Here we extended the approach of this most recent study¹¹ by splitting $\alpha_h(t_f - t_c)$ into $\alpha_t t_f + \alpha_e t_c$ (which is equivalent to the hierarchical distance if $\alpha_t = -\alpha_e$) and including two α_0 , one for intraspecific and one for interspecific competition.

To simplify the estimation, equation (4) was combined with the basal area of each competing species to relate the parameters directly to the community weighted means of the different trait variables as:

$$\sum_{c=1}^{N_i} \alpha_{c,f} B_{i,c,p,s} = \alpha_{0,f,\text{intra}} B_{i,f} + \alpha_{0,f,\text{inter}} B_{i,\text{het}} - \alpha_t t_f B_{i,\text{tot}} + \alpha_e B_{i,t_c} + \alpha_d B_{i,|t_c - t_f|} \quad (5)$$

Where $B_{i,\text{het}} = \sum_{c \neq f} B_{i,c}$ is the sum of basal area of heterospecific competitors (het), $B_{i,\text{tot}} = B_{i,f} + B_{i,\text{het}}$ is the sum of basal area of all competitors, $B_{i,t_c} = \sum_{c=1}^{N_i} t_c \times B_{i,c}$ and $B_{i,|t_c - t_f|} = \sum_{c=1}^{N_i} |t_c - t_f| \times B_{i,c}$. N_i is the number of species in the local neighbourhood of the tree (i) (note that the indices p and s for plot and data set are not shown here for sake of simplicity).

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 (that is, there was a single value for α_0), as previous studies have generally not made this distinction, using the following equation:

$$\alpha_{f,c} = \alpha_{0,f} - \alpha_t t_f + \alpha_e t_c + \alpha_d |t_c - t_f| \quad (6)$$

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 Extended Data Fig. 4.

Equations (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

$$G_{i,f,p,s,t} = 0.25\pi(D_{i,f,p,s,t+1}^2 - D_{i,f,p,s,t}^2)/(y_{t+1} - y_t) \quad (7)$$

To estimate standardised coefficients (one type of standardised effect size)³¹, response and explanatory variables were standardized (divided by their standard deviations) before analysis. Trait and diameter were also centred to facilitate convergence. The models were fitted using the *lmer* routine in the *lme4* package³² in the R statistical environment³³. We fitted two versions of each model. In the first version parameters m_0 , m_1 , α_0 , α_t , α_e , α_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 ecoregion³⁴ (see Supplementary Results).

Estimating the effect of traits on the average differences between intra and interspecific competition. Differences between inter and intraspecific competition have long been considered key to community assembly and species coexistence^{12,35–38}. Our estimated growth model allowed us to estimate the average inter and intraspecific competition from trait-independent and trait-dependent processes. For any combination of two trait values t_i and t_j , we can predict the interspecific (α_{t_i,t_j} and α_{t_j,t_i}) and intraspecific (α_{t_i,t_i} and α_{t_j,t_j}) competition parameters for a typical species by leaving out the random species effects in equation (4). We can then estimate the average differences between interspecific and intraspecific competition over all trait values combinations using the following expression:

$$\frac{(\alpha_{t_i,t_j} - \alpha_{t_i,t_i}) + (\alpha_{t_j,t_i} - \alpha_{t_j,t_j})}{2} \quad (8)$$

Substituting in from equation (4) (leaving out the species random effect) this simplifies as:

$$\alpha_{0\text{inter}} - \alpha_{0\text{intra}} + \alpha_d |t_j - t_i| \quad (9)$$

Thus, the average differences between inter and intraspecific competition are affected only by the difference between $\alpha_{0\text{intra}}$ and $\alpha_{0\text{inter}}$ and by trait dissimilarity via α_d (see Extended Data Fig. 2 for the results).

Growth data. Our main objective was to collate data sets spanning the dominant forest biomes of the world. Data sets were included if they allowed both growth of individual trees and the local abundance of competitors to be estimated, and if they 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^{39–48}); (2) large permanent plots (LPP) ranging in size from 0.5 to 50 ha, in which the x - y coordinates of all trees above a given diameter were recorded (references for LPP data used refs 49–56). LPP were mostly located in tropical regions.

The minimum diameter of recorded trees varied among sites from 1 to 12 cm. To allow comparison between data sets, we restricted our analysis to trees greater than 10 cm. 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 one-third of the data had repeated measurements). Because human and natural disturbances are present in all of these forests (see Supplementary Information), they probably all experience successional dynamics (as indicated by the forest age distribution available in some of these sites in Supplementary Information). See Supplementary Information and Extended Data Table 2 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 (1) with extreme positive or negative diameter growth measurements, following criteria developed at the BCI site³⁰ (see the R package CTFS R), (2) that were palms or tree ferns, or (3) 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 >10 cm diameter within a specified neighbourhood. For LPPs, we defined the neighbourhood as being a circle with a 15 m radius. This value was selected based on previous studies showing the maximum radius of interaction to lie in the range 10–20 m (refs 8, 19). To avoid edge effects, we also excluded trees less than 15 m from the edge of a plot. To account for variation of abiotic conditions within the LPPs, we divided plots into regularly spaced 20×20 m 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 7.35 m located within 20 m 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 to 25 m radius, with most plots from 10 to 15 m radius. We included variation in neighbourhood size in the constant w_i to compute competitor basal area in $\text{m}^2 \text{ha}^{-1}$.

We extracted MAT and MAP from the WorldClim data base⁵⁷ using the plot latitude and longitude (see Extended Data Fig. 1 for plot locations). MAT and MAP data were then used to classify plots into biomes, using the diagram provided by ref. 58 (modified from ref. 59).

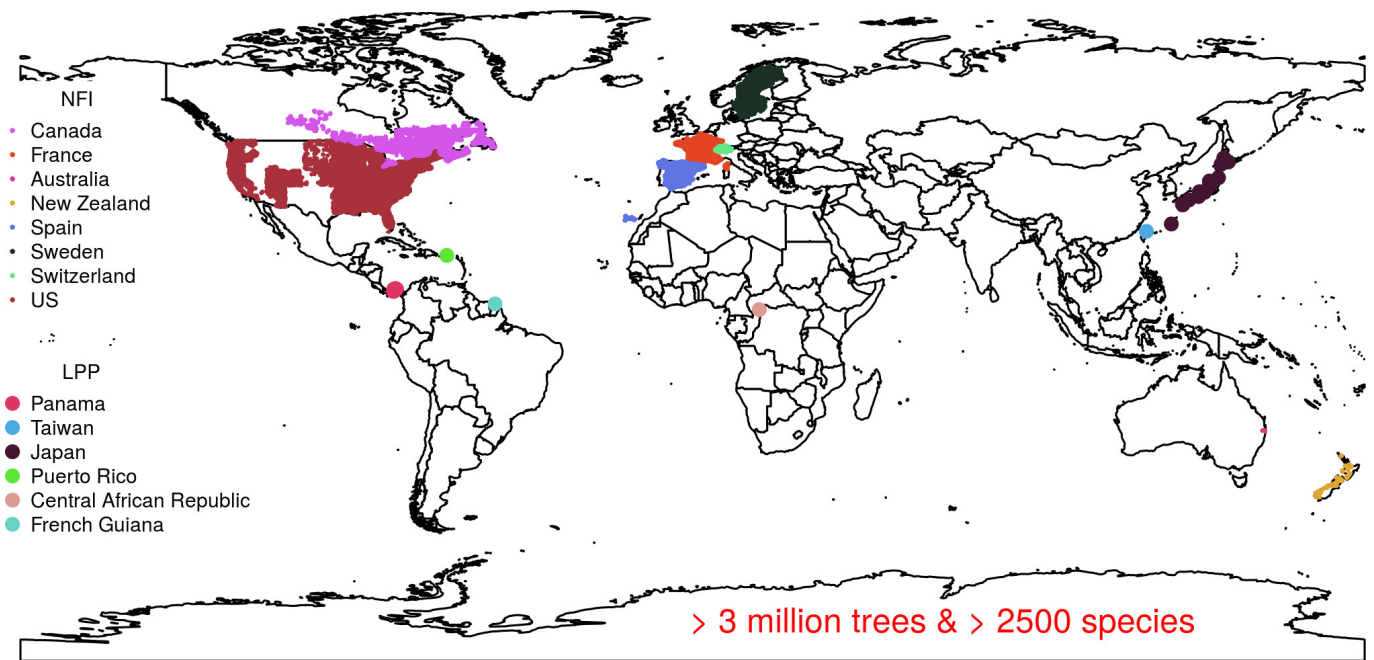
Traits. Data on species functional traits were extracted from existing sources. We focused on wood density, species SLA and maximum height, because these traits have previously been related to competitive interactions and are available for large numbers of species^{8,9,11,15,30} (see Extended Data Tables 3 and 4 for trait coverage and their correlations). Where available, we used data collected locally (references for the local trait data used in this analysis include refs 15, 51, 60–62); otherwise we sourced data from the TRY trait data base¹⁸ (references for the data extracted from the TRY database used in this analysis include refs 2, 3, 15, 63–130). Local data were available for most tropical sites and species (see Supplementary Information). 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, USA, Spain and Switzerland). For Sweden, we used the estimate from the French data set and for Canada we used the estimate from the USA 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 (1) the percentage of basal area contributed by trees with no species level trait data was less than 10%, and (2) the percentage of basal area of trees with neither species nor genus level trait data was less than 5%.

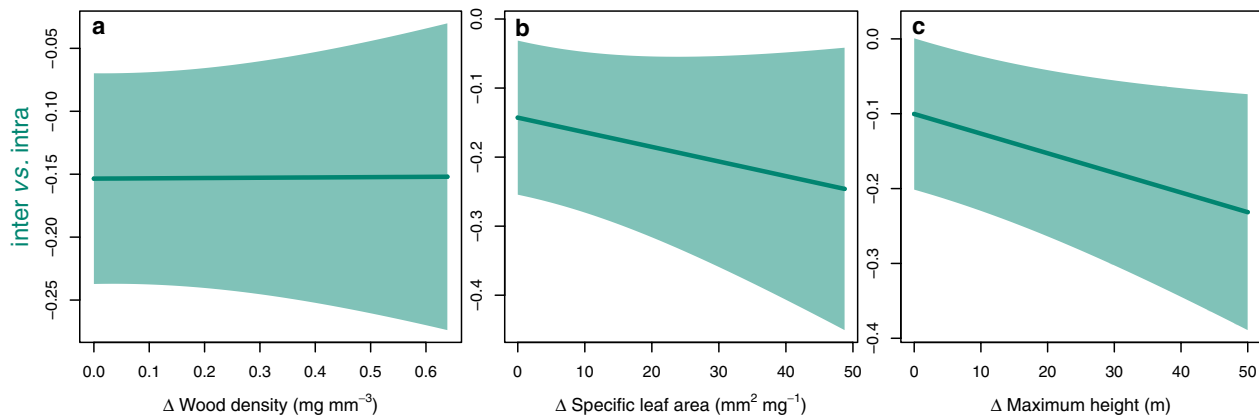
29. Canham, C. D. *et al.* Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecol. Appl.* **16**, 540–554 (2006).
30. Rüger, N., Wirth, C., Wright, S. J. & Condit, R. Functional traits explain light and size response of growth rates in tropical tree species. *Ecology* **93**, 2626–2636 (2012).
31. Schielzeth, H. Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113 (2010).

32. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* **67**, 1–48 (2014).
33. R Development Core Team. *R: A Language and Environment for Statistical Computing* <http://www.R-project.org/> (R Foundation for Statistical Computing, 2014).
34. Kriticos, D. J. *et al.* CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods Ecol. Evol.* **3**, 53–64 (2012).
35. Connell, J. H. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Am. Nat.* **122**, 661–696 (1983).
36. Chesson, P. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
37. Chesson, P. In *Ecological Systems* (ed. Leemans, R.) 223–256 (Springer, 2012).
38. Godoy, O. & Levine, J. M. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology* **95**, 726–736 (2014).
39. IGN Inventaire Forestier; <http://inventaire-forestier.ign.fr/spip/spip.php?rubrique153>.
40. Kooyman, R., Rossetto, M., Allen, C. & Cornwell, W. Australian tropical and subtropical rain forest community assembly: phylogeny, functional biogeography, and environmental gradients. *Biotropica* **44**, 668–679 (2012).
41. New Zealand National Vegetation Survey Databank; <https://nvs.landcareresearch.co.nz/>.
42. Wiser, S. K., Bellingham, P. J. & Burrows, L. E. Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *N. Z. J. Ecol.* **25**, 1–17 (2001).
43. Ministerio de Agricultura, Alimentación y Medio Ambiente. *Inventario Forestal Nacional*; <http://www.magrama.gob.es/es/desarrollo-rural/temas/politica-forestal/inventario-cartografia/inventario-forestal-nacional/default.aspx>.
44. Villaseca, R. & Diaz, R. *Segundo Inventario Forestal Nacional (1986–1996)* (Ministerio de Medio Ambiente, 1998).
45. Villanueva, J. *Tercer Inventario Forestal Nacional (1997–2007)* (Ministerio de Medio Ambiente, 2004).
46. Fridman, J. & Stahl, G. A three-step approach for modelling tree mortality in Swedish forests. *Scand. J. For. Res.* **16**, 455–466 (2001).
47. Swiss National Forest Inventory (NFI); <http://www.lfi.ch/index-en.php>.
48. USDA Forest Inventory and Analysis National Program; <http://www.fia.fs.fed.us/tools-data/>.
49. Condit, R., Engelbrecht, B. M. J., Pino, D., Perez, R. & Turner, B. L. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Natl Acad. Sci. USA* **110**, 5064–5068 (2013).
50. Condit, R., Hubbell, S. P. & Foster, R. B. Mortality and growth of a commercial hardwood 'el cativo', *Prioria copaifera*, in Panama. *For. Ecol. Manage.* **62**, 107–122 (1993).
51. Lasky, J. R., Sun, I., Su, S.-H., Chen, Z.-S. & Keitt, T. H. Trait-mediated effects of environmental filtering on tree community dynamics. *J. Ecol.* **101**, 722–733 (2013).
52. Ishihara, M. I. *et al.* Forest stand structure, composition, and dynamics in 34 sites over Japan. *Ecol. Res.* **26**, 1007–1008 (2011).
53. Thompson, J. *et al.* Land use history, environment, and tree composition in a tropical forest. *Ecol. Appl.* **12**, 1344–1363 (2002).
54. Ouedraogo, D.-Y., Mortier, F., Gourlet-Fleury, S., Frey, V. & Picard, N. Slow-growing species cope best with drought: evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa. *J. Ecol.* **101**, 1459–1470 (2013).
55. Hérault, B., Ouallet, J., Blanc, L., Wagner, F. & Baraloto, C. Growth responses of neotropical trees to logging gaps. *J. Appl. Ecol.* **47**, 821–831 (2010).
56. Hérault, B. *et al.* Functional traits shape ontogenetic growth trajectories of rain forest tree species. *J. Ecol.* **99**, 1431–1440 (2011).
57. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
58. Ricklefs, R. E. *The Economy of Nature* (WH Freeman, 2001).
59. Whittaker, R. H. *Communities and Ecosystems* (Macmillan, 1970).
60. Swenson, N. G. *et al.* Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology* **93**, 490–499 (2012).
61. Gourlet-Fleury, S. *et al.* Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. *J. Ecol.* **99**, 981–990 (2011).
62. Baraloto, C. *et al.* Decoupled leaf and stem economics in rain forest trees. *Ecol. Lett.* **13**, 1338–1347 (2010).
63. Ackerly, D. D. & Cornwell, W. K. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.* **10**, 135–145 (2007).
64. Castro-Diez, P., Puyravaud, J., Cornelissen, J. & Villar-Salvador, P. Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia* **116**, 57–66 (1998).
65. Cornelissen, J. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *J. Ecol.* **84**, 573–582 (1996).
66. Cornelissen, J., Diez, P. C. & Hunt, R. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *J. Ecol.* **84**, 755–765 (1996).
67. Cornelissen, J., Werger, M., Castro-Diez, P., Van Rheenen, J. & Rowland, A. Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. *Oecologia* **111**, 460–469 (1997).
68. Cornelissen, J. *et al.* Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Funct. Ecol.* **18**, 779–786 (2004).

69. Cornelissen, J. *et al.* Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *J. Veg. Sci.* **14**, 311–322 (2003).
70. Cornwell, W. K. & Ackerly, D. D. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.* **79**, 109–126 (2009).
71. Cornwell, W. K., Schwiik, L. D. W. & Ackerly, D. D. A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**, 1465–1471 (2006).
72. Cornwell, W., Bhaskar, R., Sack, L. & Cordell, S. Adjustment of structure and function of Hawaiian *Metrosideros polymorpha* at high vs. low precipitation. *Funct. Ecol.* **21**, 1063–1071 (2007).
73. Cornwell, W. K. *et al.* Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* **11**, 1065–1071 (2008).
74. Diaz, S. *et al.* The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* **15**, 295–304 (2004).
75. Fonseca, C. R., Overton, J. M., Collins, B. & Westoby, M. Shifts in trait-combinations along rainfall and phosphorus gradients. *J. Ecol.* **88**, 964–977 (2000).
76. Fortunel, C. *et al.* Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* **90**, 598–611 (2009).
77. Freschet, G. T., Cornelissen, J. H., Van Logtestijn, R. S. & Aerts, R. Evidence of the 'plant economics spectrum' in a subarctic flora. *J. Ecol.* **98**, 362–373 (2010).
78. Freschet, G. T., Cornelissen, J. H., van Logtestijn, R. S. & Aerts, R. Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytol.* **186**, 879–889 (2010).
79. Garnier, E. *et al.* Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann. Bot. (Lond.)* **99**, 967–985 (2007).
80. Green, W. USDA PLANTS compilation, version 1, 09-02-02; <http://bricol.net/downloads/data/PLANTSdatabase/> (2009).
81. Han, W., Fang, J., Guo, D. & Zhang, Y. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytol.* **168**, 377–385 (2005).
82. He, J.-S. *et al.* A test of the generality of leaf trait relationships on the Tibetan Plateau. *New Phytol.* **170**, 835–848 (2006).
83. He, J.-S. *et al.* Leaf nitrogen: phosphorus stoichiometry across Chinese grassland biomes. *Oecologia* **155**, 301–310 (2008).
84. Hoof, J., Sack, L., Webb, D. T. & Nilsen, E. T. Contrasting structure and function of pubescent and glabrous varieties of Hawaiian *Metrosideros polymorpha* (Myrtaceae) at high elevation. *Biotropica* **40**, 113–118 (2008).
85. Kattge, J., Knorr, W., Raddatz, T. & Wirth, C. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Glob. Change Biol.* **15**, 976–991 (2009).
86. Kleyer, M. *et al.* The LEDA traitbase: a database of life-history traits of the Northwest European flora. *J. Ecol.* **96**, 1266–1274 (2008).
87. Kurokawa, H. & Nakashizuka, T. Leaf herbivory and decomposability in a Malaysian tropical rain forest. *Ecology* **89**, 2645–2656 (2008).
88. Laughlin, D. C., Leppert, J. J., Moore, M. M. & Sieg, C. H. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Funct. Ecol.* **24**, 493–501 (2010).
89. Martin, R. E., Asner, G. P. & Sack, L. Genetic variation in leaf pigment, optical and photosynthetic function among diverse phenotypes of *Metrosideros polymorpha* grown in a common garden. *Oecologia* **151**, 387–400 (2007).
90. McDonald, P., Fonseca, C., Overton, J. & Westoby, M. Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Funct. Ecol.* **17**, 50–57 (2003).
91. Medlyn, B. E. *et al.* Effects of elevated [CO₂] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant Cell Environ.* **22**, 1475–1495 (1999).
92. Medlyn, B. E. & Jarvis, P. G. Design and use of a database of model parameters from elevated [CO₂] experiments. *Ecol. Modell.* **124**, 69–83 (1999).
93. Medlyn, B. *et al.* Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *New Phytol.* **149**, 247–264 (2001).
94. Messier, J., McGill, B. J. & Lechowicz, M. J. How do traits vary across ecological scales? A case for trait-based ecology. *Ecol. Lett.* **13**, 838–848 (2010).
95. Moles, A. T. *et al.* Factors that shape seed mass evolution. *Proc. Natl Acad. Sci. USA* **102**, 10540–10544 (2005).
96. Moles, A. T. *et al.* A brief history of seed size. *Science* **307**, 576–580 (2005).
97. Moles, A. T., Falster, D. S., Leishman, M. R. & Westoby, M. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *J. Ecol.* **92**, 384–396 (2004).
98. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**, 453–469 (2001).
99. Niinemets, Ü. Research review: components of leaf dry mass per area—thickness and density—alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytol.* **144**, 35–47 (1999).
100. Ogaya, R. & Peñuelas, J. Experimental drought in a holm oak forest: different photosynthetic response of the two dominant species, *Quercus ilex* and *Phillyrea latifolia*. *Environ. Exp. Bot.* **50**, 137–148 (2003).
101. Ogaya, R. & Peñuelas, J. Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. *Biol. Plant.* **50**, 373–382 (2006).
102. Ogaya, R. & Peñuelas, J. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. *Plant Ecol.* **189**, 291–299 (2007).
103. Ogaya, R. & Peñuelas, J. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. *Plant Ecol.* **189**, 291–299 (2007).
104. Onoda, Y. *et al.* Global patterns of leaf mechanical properties. *Ecol. Lett.* **14**, 301–312 (2011).
105. Ordoñez, J. C. *et al.* Plant strategies in relation to resource supply in mesic to wet environments: does theory mirror nature? *Am. Nat.* **175**, 225–239 (2010).
106. Ordoñez, J. C. *et al.* Leaf habit and woodiness regulate different leaf economy traits at a given nutrient supply. *Ecology* **91**, 3218–3228 (2010).
107. Pakeman, R. J. *et al.* Impact of abundance weighting on the response of seed traits to climate and land use. *J. Ecol.* **96**, 355–366 (2008).
108. Pakeman, R. J., Lepš, J., Kleyer, M., Lavorel, S. & Garnier, E. Relative climatic, edaphic and management controls of plant functional trait signatures. *J. Veg. Sci.* **20**, 148–159 (2009).
109. Peñuelas, J. *et al.* Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native plant species. *Glob. Change Biol.* **16**, 2171–2185 (2010).
110. Peñuelas, J. *et al.* Higher allocation to low cost chemical defenses in invasive species of Hawaii. *J. Chem. Ecol.* **36**, 1255–1270 (2010).
111. Poorter, L. & Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**, 1733–1743 (2006).
112. Poorter, L. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytol.* **181**, 890–900 (2009).
113. Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J. & Villar, R. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol.* **182**, 565–588 (2009).
114. Preston, K. A., Cornwell, W. K. & DeNoyer, J. L. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytol.* **170**, 807–818 (2006).
115. Pyankov, V. I., Kondratchuk, A. V. & Shipley, B. Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tajikistan. *New Phytol.* **143**, 131–142 (1999).
116. Quested, H. M. *et al.* Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology* **84**, 3209–3221 (2003).
117. Reich, P. B. *et al.* Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecol. Lett.* **11**, 793–801 (2008).
118. Reich, P. B., Oleksyn, J. & Wright, I. J. Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. *Oecologia* **160**, 207–212 (2009).
119. Sack, L. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos* **107**, 110–127 (2004).
120. Sack, L., Tyree, M. T. & Holbrook, N. M. Leaf hydraulic architecture correlates with regeneration irradiance in tropical rainforest trees. *New Phytol.* **167**, 403–413 (2005).
121. Sack, L., Melcher, P. J., Liu, W. H., Middleton, E. & Pardee, T. How strong is intracanal leaf plasticity in temperate deciduous trees? *Am. J. Bot.* **93**, 829–839 (2006).
122. Sardans, J., Peñuelas, J. & Ogaya, R. Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest. *For. Sci.* **54**, 513–522 (2008).
123. Sardans, J., Peñuelas, J., Prieto, P. & Estiarte, M. Changes in Ca, Fe, Mg, Mo, Na, and S content in a Mediterranean shrubland under warming and drought. *J. Geophys. Res.* **113**, G03039 (2008).
124. Shipley, B. & Vu, T.-T. Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytol.* **153**, 359–364 (2002).
125. Soudzilovskaia, N. A. *et al.* Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proc. Natl Acad. Sci. USA* **110**, 18180–18184 (2013).
126. Willis, C. G. *et al.* Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography* **33**, 565–577 (2010).
127. Wilson, K. B., Baldocchi, D. D. & Hanson, P. J. Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiol.* **20**, 565–578 (2000).
128. Wright, I. J. *et al.* Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann. Bot. (Lond.)* **99**, 1003–1015 (2007).
129. Wright, I. J. *et al.* Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. *New Phytol.* **169**, 309–319 (2006).
130. Zanne, A. E. *et al.* Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am. J. Bot.* **97**, 207–215 (2010).
131. South, A. *rworldmap*, a new R package for mapping global data. *Rem. J.* **3**, 35–43 (2011).
132. Nakagawa, S. & Hanson, P. J. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142 (2013).
133. Johnson, P. C. D. Extension of Nakagawa and Schielzeth's R²GLMM to random slopes models. *Methods Ecol. Evol.* **5**, 944–946 (2014).
134. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach* (Springer-Verlag, 2002).

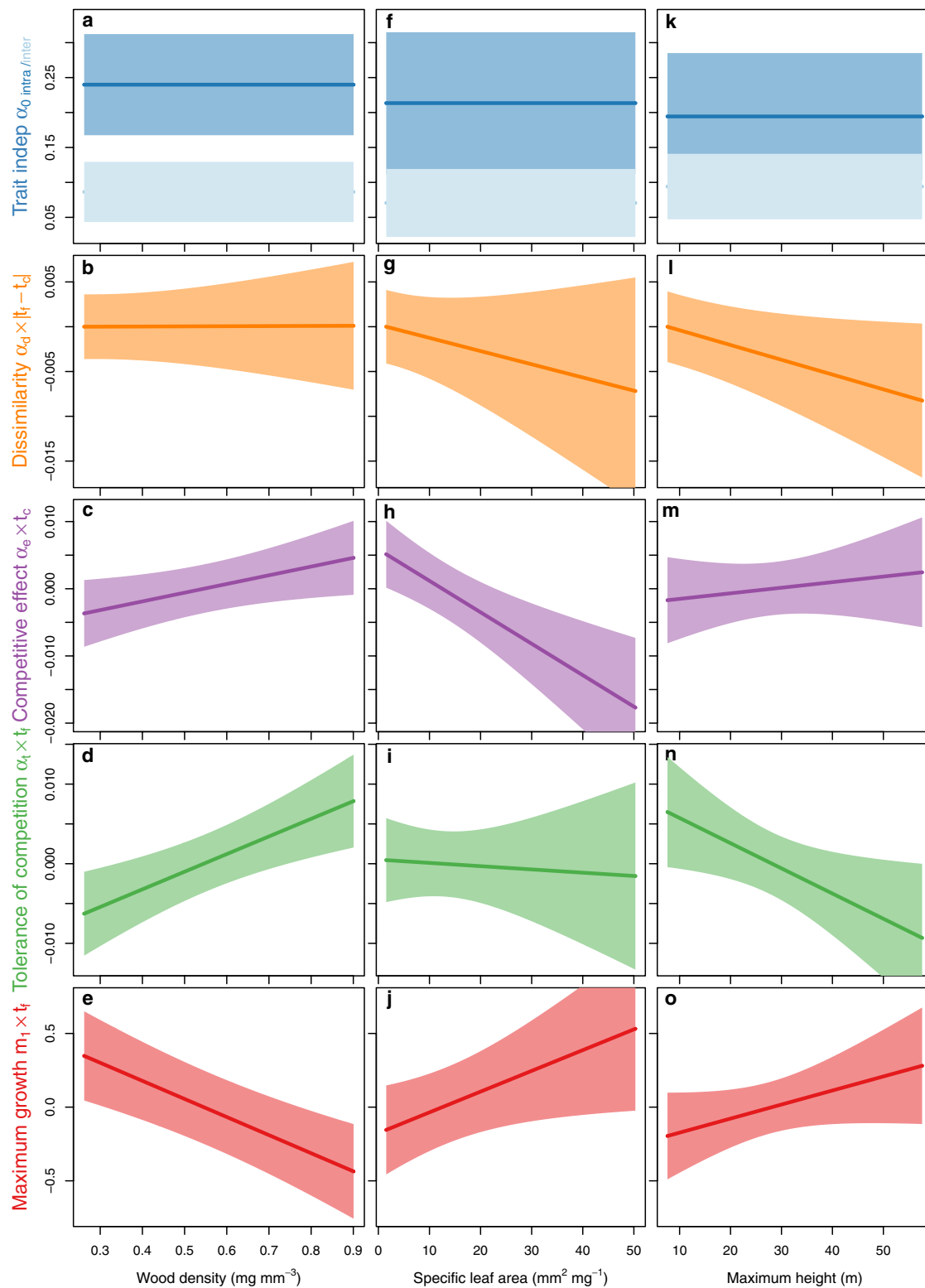


Extended Data Figure 1 | Map of the plot locations of all data sets analysed. LPP plots are represented with a large points and NFI plots with small points (the Panama data set comprises both a 50 ha plot and a network of 1 ha plots). The world map is from the R package *rworldmap*¹³¹ using Natural Earth data.



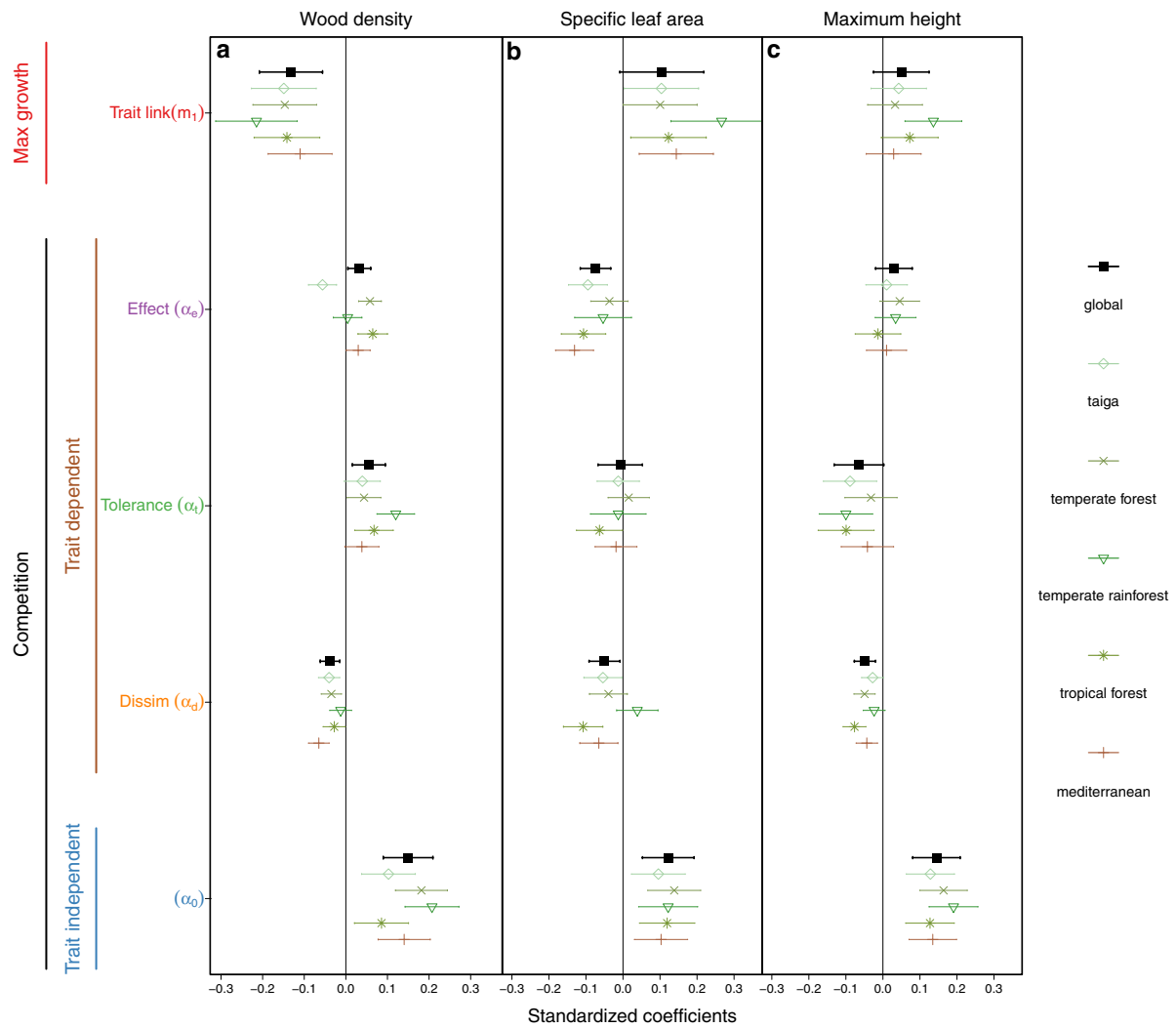
Extended Data Figure 2 | Average difference between interspecific and intraspecific competition predicted with estimates of trait-independent and trait-dependent processes influencing competition for models fitted for each trait. a–c, Models were fitted for wood density (a), SLA

(b) or maximum height (c). The average differences between interspecific and intraspecific competition are influenced by $\alpha_{0\text{intra}}$, $\alpha_{0\text{inter}}$ and α_d coefficients (see Methods for details). Negative values indicate that intraspecific competition is stronger than interspecific competition.



Extended Data Figure 3 | Variation of trait-independent inter and intraspecific competition, trait dissimilarity ($|t_f - t_c| \times \alpha_d$), competitive effect ($t_c \times \alpha_c$), tolerance to competition ($t_f \times \alpha_t$) and maximum growth ($t_f \times m_1$) with wood density, SLA and maximum height. a–o, Wood density (a–e), SLA (f–j) and maximum height (k–o).

Trait varied from their quantile at 5% to their quantile at 95%. The shaded area represents the 95% confidence interval of the prediction (including uncertainty associated with α_0 or m_0). $\alpha_{0\text{intra}}$ and $\alpha_{0\text{inter}}$ which do not vary with traits, are represented with their associated confidence intervals.



Extended Data Figure 4 | Trait-dependent and trait-independent effects on maximum growth and competition across the globe and their variation among biomes for models without separation of α_0 between intra and interspecific competition for wood density, SLA

and maximum height. a, Wood density. b, SLA. c, Maximum height. See Fig. 2 in the main text for parameters description, and see Fig. 1a in the main text for biome definition.

Extended Data Table 1 | Standardized coefficient estimates from models fitted for each trait

	Wood density	SLA	Maximum height
m_0	0.016 (0.127)	-0.087 (0.132)	0.084 (0.089)
γ	0.418 (0.011)	0.401 (0.012)	0.42 (0.01)
m_1	-0.149 (0.036)	0.119 (0.057)	0.063 (0.04)
m_2	0.111 (0.003)	0.093 (0.003)	0.081 (0.002)
m_3	0.053 (0.002)	0.056 (0.003)	0.048 (0.002)
$\alpha_{0 \text{ intra}}$	0.24 (0.037)	0.213 (0.052)	0.194 (0.046)
$\alpha_{0 \text{ inter}}$	0.086 (0.022)	0.071 (0.025)	0.094 (0.024)
α_e	0.034 (0.016)	-0.083 (0.023)	0.017 (0.026)
α_t	0.069 (0.021)	-0.009 (0.033)	-0.071 (0.032)
α_d	0 (0.009)	-0.018 (0.015)	-0.017 (0.008)
R_m^2 *	0.1393	0.1637	0.1429
R_c^2 *	0.7297	0.7593	0.7166
ΔAIC	0	0	0
$\Delta \text{AIC no trait}$	2469	1651	2748

Estimates and their standard error (in brackets) estimated for each trait, R^2 of models and ΔAIC of the model and of a model with no trait effect. See Methods for explanation of parameters

*We report the conditional and marginal R^2 of the models using the methods of ref. 132, modified by ref. 133. ΔAIC is the difference in the Akaike's information criterion (AIC; as defined by ref. 134) between the model and the best model (lowest AIC). The best-fitting model was identified as the one with a ΔAIC of 0. ΔAIC greater than 10 shows strong support for the best model¹³⁴.

Extended Data Table 2 | Trees data description

set	# of trees	# of species	# of plots/quadrats	% of angiosperm	% of evergreen
Sweden	202480	26	22552	27.0	73.0
New Zealand	53775	117	1415	94.0	99.1
US	1370541	492	59840	63.3	37.2
Canada	495008	75	14983	34.4	64.8
Australia	906	101	63	99.9	92.4
France	184316	127	17611	74.1	28.5
Switzerland	28286	60	2597	36.4	55.2
Spain	418805	122	36462	34.7	81.6
Panama	27089	237	2033	99.8	77.7
French Guiana	46360	712	2157	100.0	83.5
Japan	4658	139	318	72.8	70.0
Taiwan	14701	72	623	92.0	75.3
Puerto Rico	14011	82	399	100.0	99.0
Central African Republic	17638	204	989	99.5	72.4

For each site, the number of individual trees, species and plots in NFI data and quadrats in LPP data, and the percentage of angiosperm and evergreen species are shown.

Extended Data Table 3 | Traits data description

set	% cover SLA	% cover Wood density	% cover Max height
Sweden	99.7	99.6	97.9
New Zealand	99.8	99.5	99.9
US	91.3	94.4	100.0
Canada	99.4	99.4	99.9
Australia	0.0	99.2	100.0
France	99.2	98.9	99.9
Switzerland	96.7	95.1	99.7
Spain	97.3	98.9	100.0
Panama	93.0	93.1	95.4
French Guiana	73.3	73.5	63.5
Japan	99.7	99.7	100.0
Taiwan	99.9	99.3	95.8
Puerto Rico	99.3	99.3	99.3
Central African Republic	40.3	47.1	0.0

The coverage in each site is given with the percentage of species with species level trait data.

Extended Data Table 4 | Species traits pairwise correlations

	Wood density	SLA	Max height
Wood density	1	0.18	-0.04
SLA		1	0.24
Max height			1.00

Pearson's *R* correlations for the three traits.