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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<sup>1-3</sup>, but it has remained unclear how these effects scale up to influence competition – a key driver of community assembly in terrestrial vegetation<sup>4</sup>. 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<sup>5</sup>. 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<sup>1,6</sup>. 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<sup>1-3</sup>. 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<sup>2,3</sup>. 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<sup>4</sup>. A long-standing hypothesis is that the intensity of competition decreases as two species diverge in trait values<sup>7</sup> (trait dissimilarity). The few studies<sup>8-13</sup> 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<sup>9,13,14</sup>. 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<sup>6,13</sup>. 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  
 110 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<sup>15</sup>; (2) exerting  
 115 a stronger competitive effect<sup>16,17</sup>, 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<sup>16</sup>), 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 intraspe-  
 120 cific competition<sup>7</sup>. Here we show how these four mechanisms are connected to three key traits that  
 describe plant strategies worldwide<sup>1–3</sup>. 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  
 125 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<sup>18,19</sup> (see Methods).  
 We analysed how basal area growth of each individual tree was reduced by the abundance of competi-  
 tors in its local neighbourhood<sup>20</sup> (measured as the sum of basal areas of competitors in  $\text{m}^2 \text{ha}^{-1}$ ),  
 130 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  $\alpha_{0intra}$  and  $\alpha_{0inter}$  in Fig. 2). Values were strongly positive, in-  
 dicating neighbours had competitive rather than facilitative effect. The main effects of traits were that  
 135 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<sup>15,21</sup> of adult trees reporting  
 140 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  
 145 high wood density species are more shade-tolerant<sup>15</sup> and have deeper and wider crowns<sup>22,23</sup>, hence

potentially higher light interception (further detail in Supplementary Discussion). The shorter leaf lifespan associated with high SLA results in lower leaf mass fraction<sup>24</sup>. 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<sup>24</sup>. 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<sup>22</sup>. 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<sup>13</sup>. 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<sup>25</sup>.

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<sup>26,27</sup>. 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<sup>13</sup>, 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<sup>28</sup> 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<sup>5</sup>. 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  
185 level may be more influenced by tolerance of competition than by competitive effect<sup>16</sup>, 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<sup>9,16</sup>, but rarely documented<sup>16,29</sup>. Only wood  
190 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  
195 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.

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

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210 **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  
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**FIGURES**

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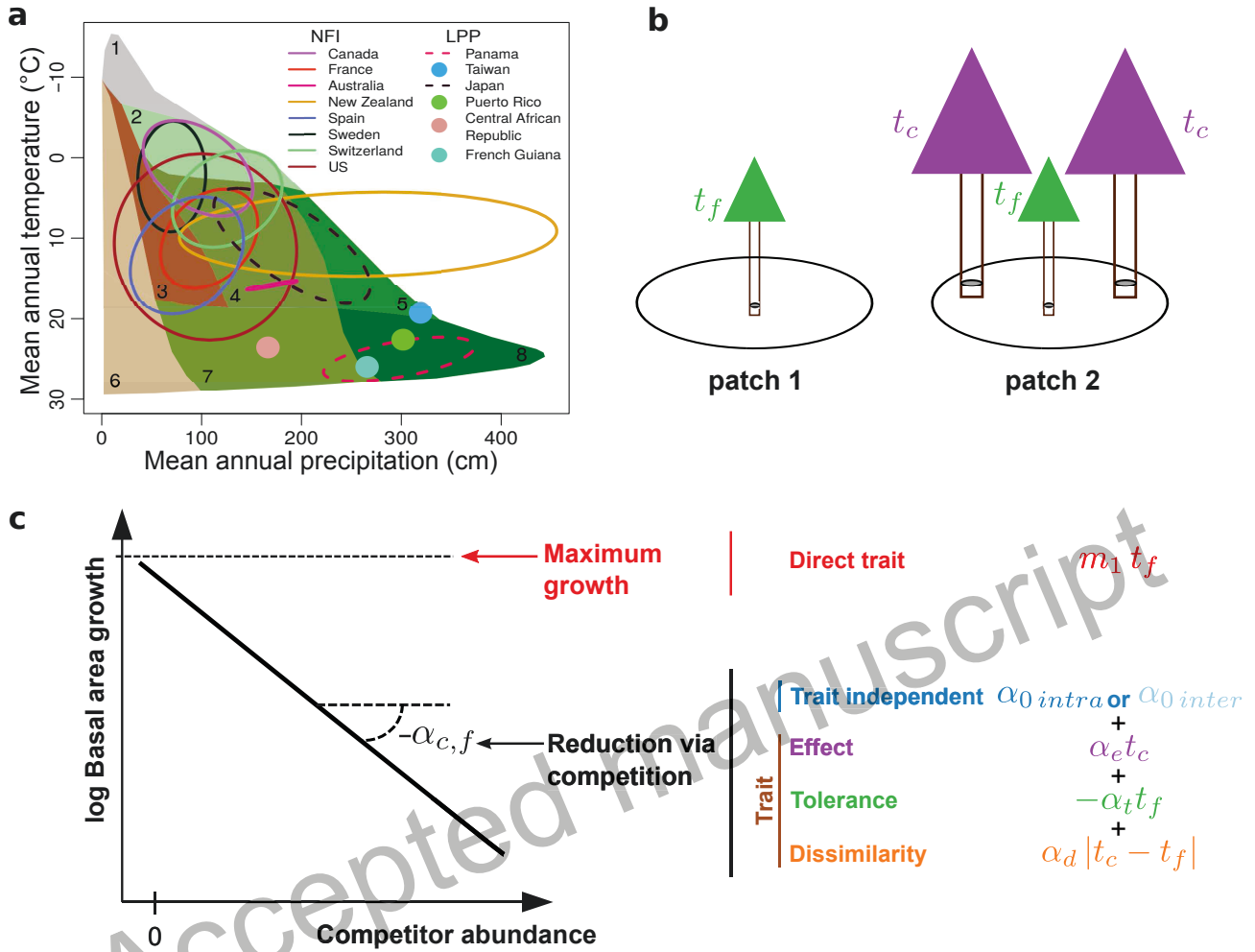


Figure 1: **Assessing competitive interactions at global scale.** **a**, Precipitation-temperature space occupied by each data set (NFI – national forest inventories data, LPP – large permanent plots data). For data with multiple plots, the range of climatic condition is represented by an ellipse covering 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<sup>30</sup>). **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 ( $\alpha_0 \text{intra}$ ) and heterospecific ( $\alpha_0 \text{inter}$ ) competitors, the effect of competitor traits ( $t_c$ ) on their competitive effect ( $\alpha_e$ ), the effect of the focal tree's traits ( $t_f$ ) on its tolerance of competition ( $\alpha_t$ ), and the effect of trait dissimilarity between the focal tree and its competitors ( $|t_c - t_f|$ ) on competition ( $\alpha_d$ ). The parameters  $m_0, m_1, \alpha_0 \text{intra}, \alpha_0 \text{inter}, \alpha_e, \alpha_t$  and  $\alpha_d$  are fitted from data using a maximum likelihood method.

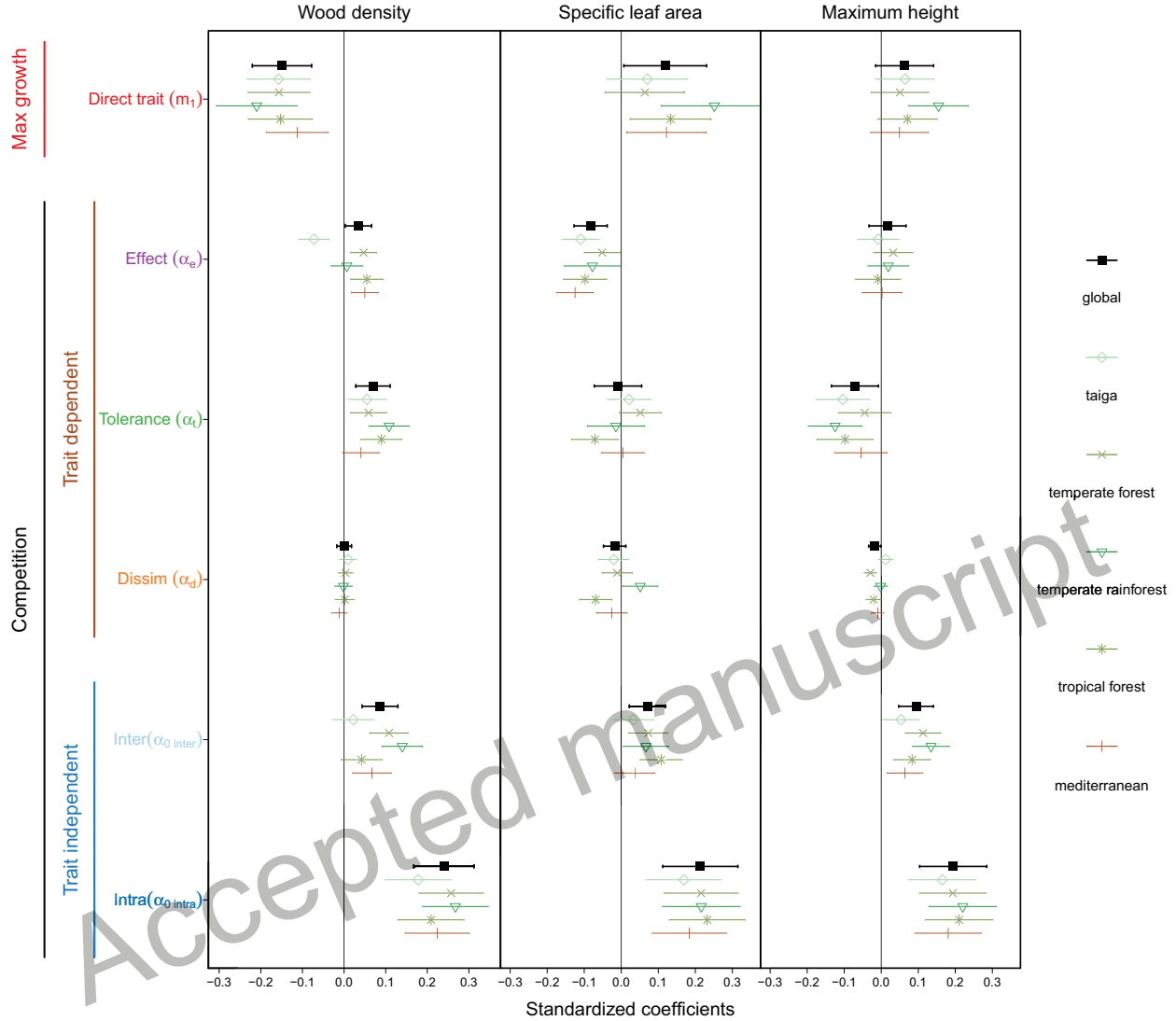


Figure 2: **Trait-dependent and trait-independent effects on maximum growth and competition across the globe and their variation among biomes.** Standardized regression coefficients for growth models, fitted separately for each trait (points: mean estimates and lines: 95% confidence intervals). Black 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  $\alpha_e$  (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  $\alpha_t$  (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  $\alpha_d$  (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  $\alpha_{0\text{intra}}$  and heterospecific  $\alpha_{0\text{inter}}$ . 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).

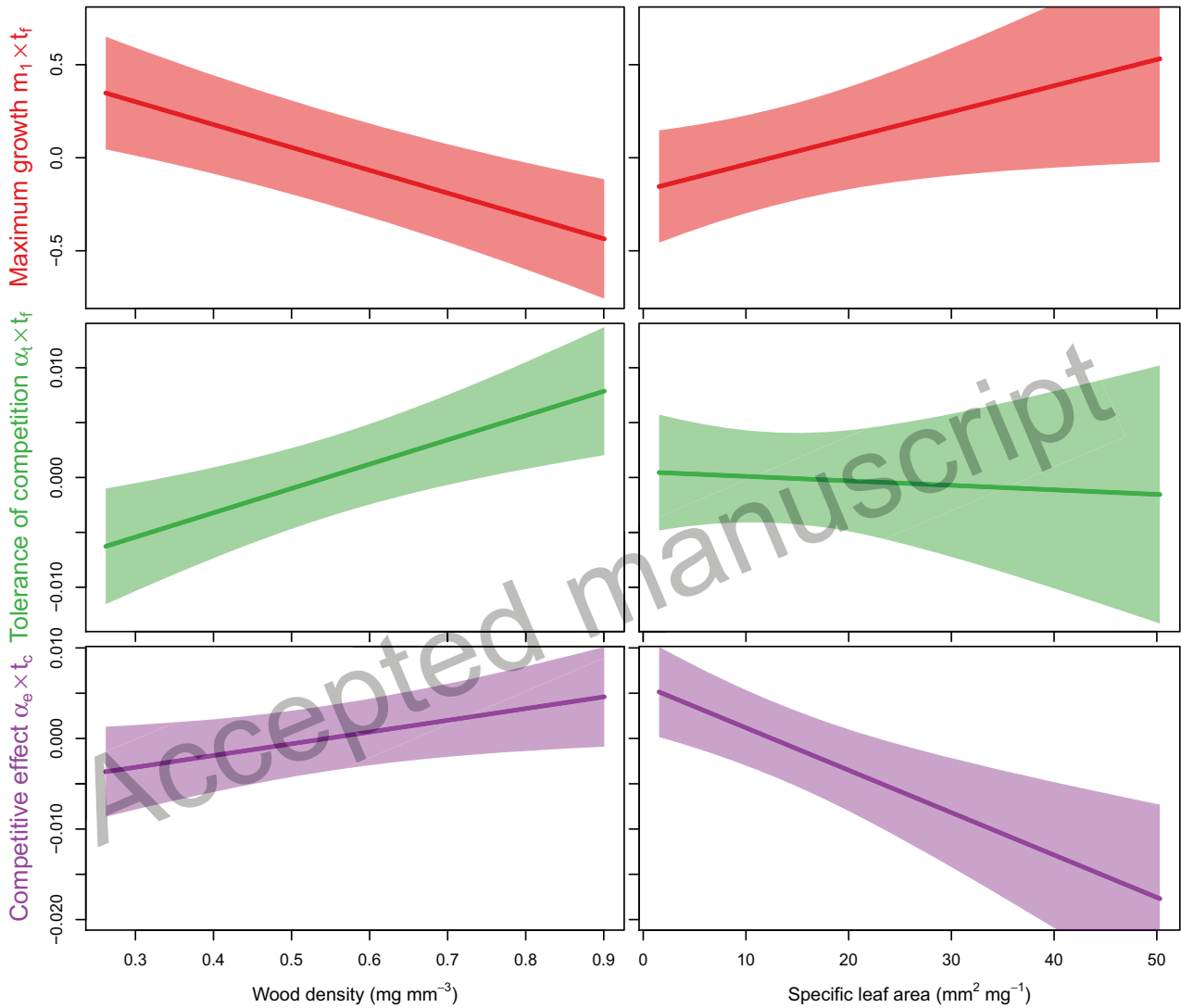


Figure 3: **Variation of maximum growth, competitive effects and competitive tolerance with wood density and specific leaf area predicted by global traits models.** Variation of maximum growth ( $m_1 t_f$ ), tolerance of competition ( $\alpha_t t_f$ ) and competitive effect ( $\alpha_e t_c$ ) parameters 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  $\alpha_0$  or  $m_0$ ).

## References

- 220 1. 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. Evol. Syst.* **33**, 125–159 (2002).
2. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–7 (2004).
3. Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–66 (2009).
- 225 4. Keddy, P. A. *Competition* (Springer Netherlands, 1989).
5. Rees, M., Condit, R., Crawley, M., Pacala, S. W. & Tilman, D. Long-term studies of vegetation dynamics. *Science* **293**, 650–655 (2001).
6. Adler, P. B., Fajardo, A., Kleinhesselink, A. R. & Kraft, N. J. B. Trait-based tests of coexistence mechanisms. *Ecol. Lett.* **16**, 1294–1306 (2013).
- 230 7. MacArthur, R. & Levins, R. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385 (1967).
8. 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).
- 235 9. 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**, 831–40 (2012).
10. HilleRisLambers, J., Adler, P., Harpole, W., Levine, J. & Mayfield, M. Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* **43**, 227–248 (2012).
- 240 11. 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. U.S.A.* **111**, 5616–5621 (2014).
12. Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 797–802 (2015).
- 245 13. 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).
14. Kraft, N. J. B., Crutsinger, G. M., Forrestel, 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).
- 250

15. Wright, S. J. *et al.* Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **91**, 3664–3674 (2010).
16. Goldberg, D. E. Competitive ability: definitions, contingency and correlated traits. *Philos. T. Roy. Soc. B.* **351**, 1377–1385 (1996).
- 255 17. Gaudet, C. L. & Keddy, P. A. A comparative approach to predicting competitive ability from plant traits. *Nature* **334**, 242–243 (1988).
18. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Chang. Biol.* **17**, 2905–2935 (2011).
19. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**, 453–469 (2001).
- 260 20. 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).
21. Poorter, L. *et al.* Are functional traits good predictors of demographic rates? evidence from five neotropical forests. *Ecology* **89**, 1908–1920 (2008).
- 265 22. Poorter, L., Bongers, L. & Bongers, F. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology* **87**, 1289–1301 (2006).
23. Aiba, M. & Nakashizuka, T. Architectural differences associated with adult stature and wood density in 30 temperate tree species. *Funct. Ecol.* **23**, 265–273 (2009).
- 270 24. 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).
25. Adams, T. P., Purves, D. W. & Pacala, S. W. Understanding height-structured competition in forests: is there an  $R^*$  for light? *Proceedings of the Royal Society B-Biological Sciences* **274**, 3039–47 (2007).
- 275 26. 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).
27. Jucker, T., Bouriaud, O. & Coomes, D. A. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Functional Ecology* **29**, 1078–1086 (2015).
- 280 28. Bagchi, R. *et al.* Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**, 85–88 (2014).

29. Wang, P., Stieglitz, T., Zhou, D. W. & Cahill Jr, J. F. Are competitive effect and response two sides of the same coin, or fundamentally different? *Funct. Ecol.* **24**, 196–207 (2010).
30. Ricklefs, R. E. *The economy of nature* (WH Freeman New York, 2001).

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# Methods

## Model and analysis

To examine the link between competition and traits we used a neighbourhood modelling framework<sup>1-5</sup> 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

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

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,
- $\gamma_f$  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  $\sigma_\gamma$ ]
- $\alpha_{c,f}$  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 neighborhood 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.

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

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

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<sup>2,4,5</sup>. 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:

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

30 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  $\varepsilon_{G_{\max,s}} \sim \mathcal{N}(0, \sigma_{G_{\max,s}})$ ].

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

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

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),
- $\alpha_t$  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 [  $\varepsilon_{\alpha_t,s} \sim \mathcal{N}(0, \sigma_{\alpha_t})$  ],

<sup>1</sup>Different approaches have been proposed to model  $\alpha$  from traits. In one of the first studies Uriarte et al.<sup>2</sup> modelled  $\alpha$  as  $\alpha = \alpha_0 + \alpha_d |t_f - t_c|$ . Then Kunstler et al.<sup>4</sup> 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.<sup>5</sup> 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  $\alpha_h$  and  $\alpha_t$ ). We also included two  $\alpha_0$ , one for intra and one for interspecific competition.

<sup>2</sup>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.



- $\alpha_e$  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
- $\alpha_d$  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  $\alpha_0$  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  $\alpha_0$ ), as most previous studies have generally not made this distinction, using the following equation:

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

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

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

To estimate standardised coefficients (one type of standardised effect size)<sup>6</sup>, 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<sup>7</sup> in the R statistical environment<sup>8</sup>. 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<sup>9</sup> (see Supplementary Results).

## 75 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<sup>10,11</sup>. Our estimated growth model allowed us to predict inter and intraspecific competition from trait-independent and trait-dependent  
80 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  $\alpha_{ij}$  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:

$$\sqrt{\frac{e^{\alpha_{ij}} e^{\alpha_{ji}}}{e^{\alpha_{jj}} e^{\alpha_{ii}}}} \quad (7)$$

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

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

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  $\alpha_d$  (see Figure 3. in Extended Data for the results). This approach shares similarities with a method developed by Chesson<sup>12</sup>, and recently applied with population growth models in annual plants communities<sup>13,14</sup> – estimating  $\rho$  as a similar  
90 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

95 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  
100 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<sup>15-24</sup>); (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<sup>25–32</sup> ). 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<sup>26</sup> (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  $> 10$ cm 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<sup>2,33</sup>. 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<sup>34</sup>, using the plot latitude and longitude. MAT and MAP data were then used to classify plots into biomes, using the diagram provided by Ricklefs<sup>35</sup> (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<sup>2–5,36</sup> (see Extended Data

Table 2 for trait coverage). Where available we used data collected locally (references for the local  
140 trait data used in this analysis<sup>27,36–39</sup>); otherwise we sourced data from the TRY trait data base<sup>40</sup>  
(references for the data extracted from the TRY database used in this analysis<sup>36,41–110</sup>). 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  
145 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  
150 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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155 **References**

1. Canham, C. D. *et al.* Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecol. Appl.* **16**, 540–54 (2006).
2. 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).  
160
3. 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).
4. 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**, 831–40 (2012).  
165
5. 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. U.S.A.* **111**, 5616–5621 (2014).
6. Schielzeth, H. Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. *Methods in Ecology and Evolution* **1**, 103–113 (2010).  
170
7. Bates, D., Maechler, M. & Bolker, B. *lme4*: Linear mixed-effects models using S4 classes (2014). URL <http://CRAN.R-project.org/package=lme4>.
8. Team, R. C. R: A language and environment for statistical computing. r foundation for statistical computing, vienna, austria, 2012 (2014).
9. Kriticos, D. J. *et al.* CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution* **3**, 53–64 (2012).  
175
10. Connell, J. H. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist* **122**, 661–696 (1983).
11. Chesson, P. Mechanisms of maintenance of species diversity. *Annual Review of Ecology, Evolution, and Systematics* **31**, 343–366 (2000).  
180
12. Chesson, P. Species competition and predation. In *Ecological Systems*, 223–256 (Springer, 2012).
13. Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 797–802 (2015).
14. Godoy, O. & Levine, J. M. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology* **95**, 726–736 (2014).  
185

15. Téléchargement des données brutes - INVENTAIRE FORESTIER. <http://inventaire-forestier.ign.fr/spip/spip.php?rubrique153>.
16. 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).
17. New Zealand - National Vegetation Survey. <https://nvs.landcareresearch.co.nz/>.
18. Wisser, 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).
19. Inventario Forestal Nacional - Inventario y Cartografía - Política forestal - Desarrollo Rural - magrama.es. <http://www.magrama.gob.es/es/desarrollo-rural/temas/politica-forestal/inventario-cartografia/inventario-forestal-nacional/default.aspx>.
20. Villaescusa, R. & Diaz, R. *Segundo Inventario Forestal Nacional (1986-1996)* (Ministerio de Medio Ambiente, ICONA, Madrid, 1998).
21. Villanueva, J. *Tercer Inventario Forestal Nacional (1997-2007)* (Comunidad de Madrid. Ministerio de Medio Ambiente, Madrid, 2004).
22. Fridman, J. & Stahl, G. A three-step approach for modelling tree mortality in swedish forests. *Scand. J. For. Res.* **16**, 455–466 (2001).
23. Swiss National Forest Inventory (NFI) - all you need to know about swiss forests. <http://www.lfi.ch/index-en.php>.
24. Forest Inventory and Analysis National Program – Tools and Data. <http://www.fia.fs.fed.us/tools-data/>.
25. 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. U.S.A.* **110**, 5064–5068 (2013).
26. 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).
27. 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).
28. Ishihara, M. I. *et al.* Forest stand structure, composition, and dynamics in 34 sites over japan. *Ecol. Res.* **26**, 1007–1008 (2011).

29. Thompson, J. *et al.* Land use history, environment, and tree composition in a tropical forest. *Ecol. Appl.* **12**, 1344–1363 (2002).
- 220 30. Ouédraogo, D.-Y., Mortier, F., Gourlet-Fleury, S., Freycon, 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).
31. Herault, B., Ouallet, J., Blanc, L., Wagner, F. & Baraloto, C. Growth responses of neotropical trees to logging gaps. *J. Appl. Ecol.* **47**, 821–831 (2010).
- 225 32. Herault, B. *et al.* Functional traits shape ontogenetic growth trajectories of rain forest tree species. *J. Ecol.* **99**, 1431–1440 (2011).
33. 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).
- 230 34. 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).
35. Ricklefs, R. E. *The economy of nature* (WH Freeman New York, 2001).
36. Wright, S. J. *et al.* Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **91**, 3664–3674 (2010).
- 235 37. Swenson, N. G. *et al.* Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology* **93**, 490–499 (2012).
38. 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).
39. Baraloto, C. *et al.* Decoupled leaf and stem economics in rain forest trees. *Ecol. Lett.* **13**, 1338–1347 (2010).
- 240 40. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Chang. Biol.* **17**, 2905–2935 (2011).
41. 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**, 135–45 (2007).
- 245 42. 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).
43. Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–66 (2009).

- 250 44. 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).
45. 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).
- 255 46. 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).
47. 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).
- 260 48. 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).
49. 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).
50. Cornwell, W. K., Schwilk, L. D. W. & Ackerly, D. D. A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**, 1465–71 (2006).
- 265 51. 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).
52. 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).
- 270 53. Diaz, S. *et al.* The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* **15**, 295–304 (2004).
54. 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).
- 275 55. 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).
56. 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).
- 280 57. 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).



58. 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.* **99**, 967–985 (2007).
59. Green, W. USDA PLANTS compilation, version 1, 09-02-02. (2009). <http://bricol.net/downloads/data/PLANTSdatabase/>.
- 285
60. 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).
61. He, J.-S. *et al.* A test of the generality of leaf trait relationships on the Tibetan Plateau. *New Phytol.* **170**, 835–848 (2006).
- 290
62. He, J.-S. *et al.* Leaf nitrogen: phosphorus stoichiometry across Chinese grassland biomes. *Oecologia* **155**, 301–310 (2008).
63. 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).
- 295
64. 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. Chang. Biol.* **15**, 976–991 (2009).
65. Kleyer, M. *et al.* The LEDA traitbase: a database of life-history traits of the Northwest European flora. *J. Ecol.* **96**, 1266–1274 (2008).
- 300
66. Kurokawa, H. & Nakashizuka, T. Leaf herbivory and decomposability in a malaysian tropical rain forest. *Ecology* **89**, 2645–2656 (2008).
67. 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).
- 305
68. 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).
69. 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).
- 310
70. Medlyn, B. *et al.* Effects of elevated [CO<sub>2</sub>] on photosynthesis in european forest species: a meta-analysis of model parameters. *Plant Cell Environ.* **22**, 1475–1495 (1999).

71. Medlyn, B. E. & Jarvis, P. G. Design and use of a database of model parameters from elevated [CO<sub>2</sub>] experiments. *Ecol. Model.* **124**, 69–83 (1999).
- 315 72. Medlyn, B. *et al.* Stomatal conductance of forest species after long-term exposure to elevated CO<sub>2</sub> concentration: A synthesis. *New Phytol.* **149**, 247–264 (2001).
73. 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).
74. Moles, A. T. *et al.* Factors that shape seed mass evolution. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 10540–10544 (2005).
- 320 75. Moles, A. T. *et al.* A brief history of seed size. *Science* **307**, 576–580 (2005).
76. 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).
- 325 77. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**, 453–469 (2001).
78. 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).
- 330 79. 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).
80. Ogaya, R. & Penuelas, J. Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. *Biol. Plant.* **50**, 373–382 (2006).
- 335 81. 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).
82. 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).
- 340 83. Onoda, Y. *et al.* Global patterns of leaf mechanical properties. *Ecol. Lett.* **14**, 301–312 (2011).
84. Ordonez, 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).

- 345 85. Ordoñez, J. C. *et al.* Leaf habit and woodiness regulate different leaf economy traits at a given nutrient supply. *Ecology* **91**, 3218–3228 (2010).
86. 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).
87. 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).
- 350 88. Peñuelas, J. *et al.* Faster returns on ‘leaf economics’ and different biogeochemical niche in invasive compared with native plant species. *Glob. Chang. Biol.* **16**, 2171–2185 (2010).
89. Peñuelas, J. *et al.* Higher allocation to low cost chemical defenses in invasive species of Hawaii. *J. Chem. Ecol.* **36**, 1255–1270 (2010).
- 355 90. Poorter, L. & Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**, 1733–1743 (2006).
91. Poorter, L. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytol.* **181**, 890–900 (2009).
92. 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).
- 360 93. 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).
94. Pyankov, V. I., Kondratchuk, A. V. & Shipley, B. Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. *New Phytol.* **143**, 131–142 (1999).
- 365 95. Quested, H. M. *et al.* Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology* **84**, 3209–3221 (2003).
96. 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).
- 370 97. 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).
98. Sack, L. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos* **107**, 110–127 (2004).
99. 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).

- 375 100. Sack, L., Melcher, P. J., Liu, W. H., Middleton, E. & Pardee, T. How strong is intracanalopy leaf plasticity in temperate deciduous trees? *Am. J. Bot.* **93**, 829–839 (2006).
101. 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).
102. 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.: Biogeosci.* **113** (2008).
- 380 103. 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).
104. Soudzilovskaia, N. A. *et al.* Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 18180–18184 (2013).
- 385 105. 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).
106. 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).
- 390 107. Wright, I. J. *et al.* Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann. Bot.* **99**, 1003–1015 (2007).
108. 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).
- 395 109. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–7 (2004).
110. 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).