

Plant functional traits have globally consistent effects on competition

Georges Kunstler^{1,2,3}, Daniel Falster³, David A. Coomes⁴, Francis Hui⁵, Robert M. Kooyman^{3,6}, Daniel C. Laughlin⁷, Lourens Poorter⁸, Mark Vanderwel⁹, Ghislain Vieilledent¹⁰, S. Joseph Wright¹¹, Masahiro Aiba¹², Christopher Baraloto^{13,14}, John Caspersen¹⁵, J. Hans C. Cornelissen¹⁶, Sylvie Gourlet-Fleury¹⁰, Marc Hanewinkel^{17,18}, Bruno Herault¹⁹, Jens Kattge^{20,21}, Hiroko Kurokawa^{12,22}, Yusuke Onoda²³, Josep Peñuelas^{24,25}, Hendrik Poorter²⁶, Maria Uriarte²⁷, Sarah Richardson²⁸, Paloma Ruiz-Benito^{29,30}, I-Fang Sun³¹, Göran Ståhl³², Nathan G. Swenson³³, Jill Thompson^{34,35}, Bertil Westerlund³², Christian Wirth^{36,21}, Miguel A. Zavala³⁰, Hongcheng Zeng¹⁵, Jess K. Zimmerman³⁵, Niklaus E. Zimmermann³⁷, and Mark Westoby³

¹Irstea, UR EMGR, 2 rue de la Papeterie BP-76, F-38402, St-Martin-d'Hères, France ,
georges.kunstler@irstea.fr

²Univ. Grenoble Alpes, F-38402 Grenoble, France

³Department of Biological Sciences, Macquarie University NSW 2109, Australia

⁴Forest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK

⁵Mathematical Sciences Institute, Australian National University, Canberra, Australia

⁶National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, Sydney, NSW, Australia

⁷Environmental Research Institute, School of Science, University of Waikato, Hamilton, New Zealand

⁸Forest Ecology and Forest Management Group, Wageningen University, Wageningen, The Netherlands

⁹Department of Biology, University of Regina, 3737 Wascana Pkwy, Regina, SK, S4S 0A2, Canada

¹⁰Cirad, UPR BSEF, F-34398 Montpellier, France

¹¹Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama

¹²Graduate School of Life Sciences, Tohoku University, Sendai 980-8578, Japan

¹³INRA, UMR Ecologie des Forêts de Guyane, BP 709, 97387 Kourou Cedex, France

¹⁴International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL, USA

¹⁵Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, Ontario, M5S 3B3, Canada

- ¹⁶Systems Ecology, Department of Ecological Science, VU University, Amsterdam, 1081 HV,
The Netherlands
- ¹⁷Swiss Federal Research Inst. WSL, Forest Resources and Management Unit, CH-8903
Birmensdorf, Switzerland
- ¹⁸University of Freiburg, Chair of Forestry Economics and Planning, D-79106 Freiburg,
Germany
- ¹⁹Cirad, UMR Ecologie des Forêts de Guyane, Campus Agronomique, BP 701, 97387 Kourou,
France
- ²⁰Max Planck Institute for Biogeochemistry, Hans Knöll Str. 10, 07745 Jena, Germany
- ²¹German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher
Platz 5e 04103 Leipzig, Germany
- ²²Forestry and Forest Products Research Institute, Tsukuba, 305-8687 Japan (current address)
- ²³Graduate School of Agriculture, Kyoto University, Kyoto, Japan
- ²⁴CSIC, Global Ecology Unit CREAF-CSIC-UAB, Cerdanyola del Vallès 08193, Catalonia,
Spain
- ²⁵CREAF, Cerdanyola del Vallès, 08193 Barcelona, Catalonia, Spain
- ²⁶Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, D-52425 Jülich, Germany
- ²⁷Department of Ecology, Evolution and Environmental Biology, Columbia University, New
York, NY 10027, United States of America
- ²⁸Landcare Research, PO Box 40, Lincoln 7640, New Zealand
- ²⁹Biological and Environmental Sciences, School of Natural Sciences, University of Stirling,
FK9 4LA, Stirling, UK
- ³⁰Forest Ecology and Restoration Group, Department of Life Sciences, Science Building,
University of Alcalá, Campus Universitario, 28805 Alcalá de Henares (Madrid), Spain
- ³¹Department of Natural Resources and Environmental Studies, National Dong Hwa
University, Hualien 97401, Taiwan
- ³²Department of Forest Resource Management, Swedish University of Agricultural Sciences
(SLU), Skogsmarksgränd, Umeå, Sweden
- ³³Department of Biology, University of Maryland, College Park, Maryland, United States of
America
- ³⁴Centre for Ecology and Hydrology—Edinburgh, Bush Estate, Penicuik, Midlothian EH26
0QB United Kingdom
- ³⁵Department of Environmental Sciences, University of Puerto Rico, Río Piedras Campus P.O.
Box 70377 San Juan, Puerto Rico 00936-8377, USA
- ³⁶Institute for Systematic, Botany and Functional Biodiversity, University of Leipzig,
Johannisallee 21 04103 Leipzig, Germany
- ³⁷Swiss Federal Research Inst. WSL, Landscape Dynamics Unit, CH-8903 Birmensdorf,
Switzerland

Summary paragraph outline

Phenotypic traits and their associated trade-offs have been shown to have globally consistent effects on individual plant physiological functions¹⁻³, but it has remained unclear how these effects scale up to influence competition – a key driver of community assembly in terrestrial vegetation⁴. 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 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 and wood density and only a weak benefit for maximum height. Our trait-based approach to modelling competition makes generalisation possible across the forest ecosystems of the globe and their highly diverse species composition.

Main text

Phenotypic traits are considered fundamental drivers of community assembly and thus species diversity^{1,6}. The effects of traits on individual plant physiologies and functions are increasingly understood, and have been shown to be underpinned by well-known and globally consistent trade-offs¹⁻³. For instance, traits such as wood density and specific leaf area capture trade-offs between the construction cost and longevity or strength of wood and leaf tissues^{2,3}. In contrast, we still have limited understanding of how such trait-based trade-offs translate into competitive interactions between species, particularly for long-lived organisms such as trees. Competition is a key filter through which ecological and evolutionary success is determined⁴. A long-standing hypothesis is that the intensity of competition decreases as two species diverge in trait values⁷ (trait dissimilarity). The few studies⁸⁻¹³ that have explored links between traits and competition have shown that linkages were more complex than this, as particular trait values may also confer competitive advantage independently from trait dissimilarity^{9,13,14}. This distinction is fundamental for species coexistence and the local mixture of traits. If neighbourhood competition is driven mainly by trait dissimilarity, this will favour a wide spread of trait values at a local scale. In contrast, if neighbourhood interactions are mainly driven by the competitive advantage associated with particular trait values, those trait values should be strongly selected at the local scale, with coexistence operating at larger spatial or temporal scales^{6,13}. Empirical investigations have been limited so far to a few particular locations, restricting our ability

to find general mechanisms that link traits and competition in the main vegetation types of the world.

Here we quantify the links between traits and competition, measured as the influence of neighbouring trees on growth of a focal tree. Our framework is novel in two important ways: (i) competition is analysed at an unprecedented scale covering all the major forest biomes on Earth (Fig. 1a), and (ii) the influence of traits on competition is partitioned among four fundamental mechanisms (Fig. 1b,c) as follows. A competitive advantage for trees with some trait values compared to others can arise through: (1) permitting faster maximum growth in the absence of competition¹⁵; (2) exerting a stronger competitive effect^{16,17}, meaning that competitor species possessing those traits suppress more strongly the growth of their neighbours; or (3) permitting a better tolerance of competition (or competitive ‘response’ in Goldberg¹⁶), meaning that growth of species possessing those traits is less affected by competition from neighbours. Finally, (4) competition can promote trait diversification, if increasing trait dissimilarity between species reduces interspecific competition compared to intraspecific competition⁷. Here we show how these four mechanisms are connected to three key traits that describe plant strategies worldwide¹⁻³. These traits are wood density (an indicator of a trade-off in stems between growth and strength), specific leaf area (SLA, an indicator of a trade-off in leaves between cheap construction cost and leaf longevity), and maximum height (an indicator of a trade-off between sustained access to light and early reproduction). We analyse basal area growth (annual increase in the area of the cross section of tree trunk at 1.3 m height) of more than 3 million trees from more than 2500 species, across all major forested biomes of the earth (Fig. 1). Species mean trait values were extracted from local data bases and the global TRY data base^{18,19} (see Methods). We analysed how basal area growth of each individual tree was reduced by the abundance of competitors in its local neighbourhood²⁰ (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 above (Fig. 1c).

Across all biomes the strongest driver of individual growth was the total abundance of neighbours, irrespective of their traits (parameters α_{0intra} and α_{0inter} in Fig. 2). Values were strongly positive, indicating neighbours had competitive rather than facilitative effect. The main effects of traits were that some trait values led to a competitive advantage compared to others through two main mechanisms. First, traits of the focal species had direct influences on its maximum growth – *i.e.* in the absence of competition – (parameter m_1 in Fig. 2 and Extended Data Table 3). The fastest growing species had low wood density and high SLA, though the confidence interval intercepted zero in two out of five biomes for SLA (Fig. 2). This is in agreement with previous studies^{15,21} of adult trees reporting a strong link between maximum growth and wood density but a weaker link for SLA. Second, some trait values were associated with species having stronger competitive effects, or better tolerance of competition (Fig. 2; Extended Data Table 3). High wood density was correlated with better tolerance of competition from neighbours and with a stronger competitive effect upon neighbours, whereas low SLA was correlated only with a stronger competitive effect. This agrees with studies reporting that high wood density species are more shade-tolerant¹⁵ and have deeper and wider crowns^{22,23}, hence

potentially higher light interception (further detail in Supplementary Discussion). The shorter leaf lifespan associated with high SLA results in lower leaf mass fraction²⁴. The low competitive effect associated with high SLA species could thus result from a lower light interception but few data are available on this link²⁴. Maximum height was weakly negatively correlated with tolerance to competi-
 150 tion in three out of five biomes, supporting the idea that sub-canopy trees are more shade-tolerant²². 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 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 growth²⁵.

155 After separating trait-independent differences between intraspecific *vs.* interspecific competition, trait dissimilarity had little effect on competition between species (Fig. 2). Only dissimilarity in maximum height between focal and neighbour species led to a weak, but consistent, decrease in competitive suppression of tree growth (Fig. 2). Mechanisms explaining this effect are poorly understood, but could possibly result from complementary crown architectures^{26,27}. The average differences in strength
 160 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 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 is higher within species than that
 165 between species. Higher loads of shared specialised pathogens²⁸ 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
 170 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
 175 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 abundant⁵. Human or natural disturbances are conspicuous in all the forests analysed, hence successional dynamics are likely to be present in all
 180 these sites (see Supplementary Methods). This trade-off was strongest for wood density, with high wood density associated with slow potential growth rate but high tolerance to competition and strong competitive effect (Fig. 3). A similar pattern was present, though less clear, for SLA. High SLA was correlated with low competitive effect but fast maximum growth (confidence intervals not spanning

zero in three biomes, Fig. 2 and 3). Given that long-term outcomes of competition at the population level may be more influenced by tolerance of competition than by competitive effect¹⁶, SLA might be less influential in succession.

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

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

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

Acknowledgements We are especially grateful to the researchers whose long-term commitment to establish and maintain forest plots and their associated databases made this study possible, and to those who granted us data access: forest inventories and permanent plots of New Zealand, Spain (MAGRAMA), France, Switzerland, Sweden, US, Canada (for the provinces of Quebec, Ontario, Saskatchewan, Manitoba, New Brunswick, Newfoundland and Labrador), CTFS (BCI, Fushan and Luquillo), Cirad (Paracou), Cirad, MEFCP, and ICRA (M'Baïki) and Japan. GK was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Program (Demo-Traits project, no. 299340). The working group that initiated this synthesis was supported by Macquarie University and by Australian Research Council through a fellowship to MW.

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

Author information The authors declare no competing financial interests.

FIGURES

Accepted manuscript

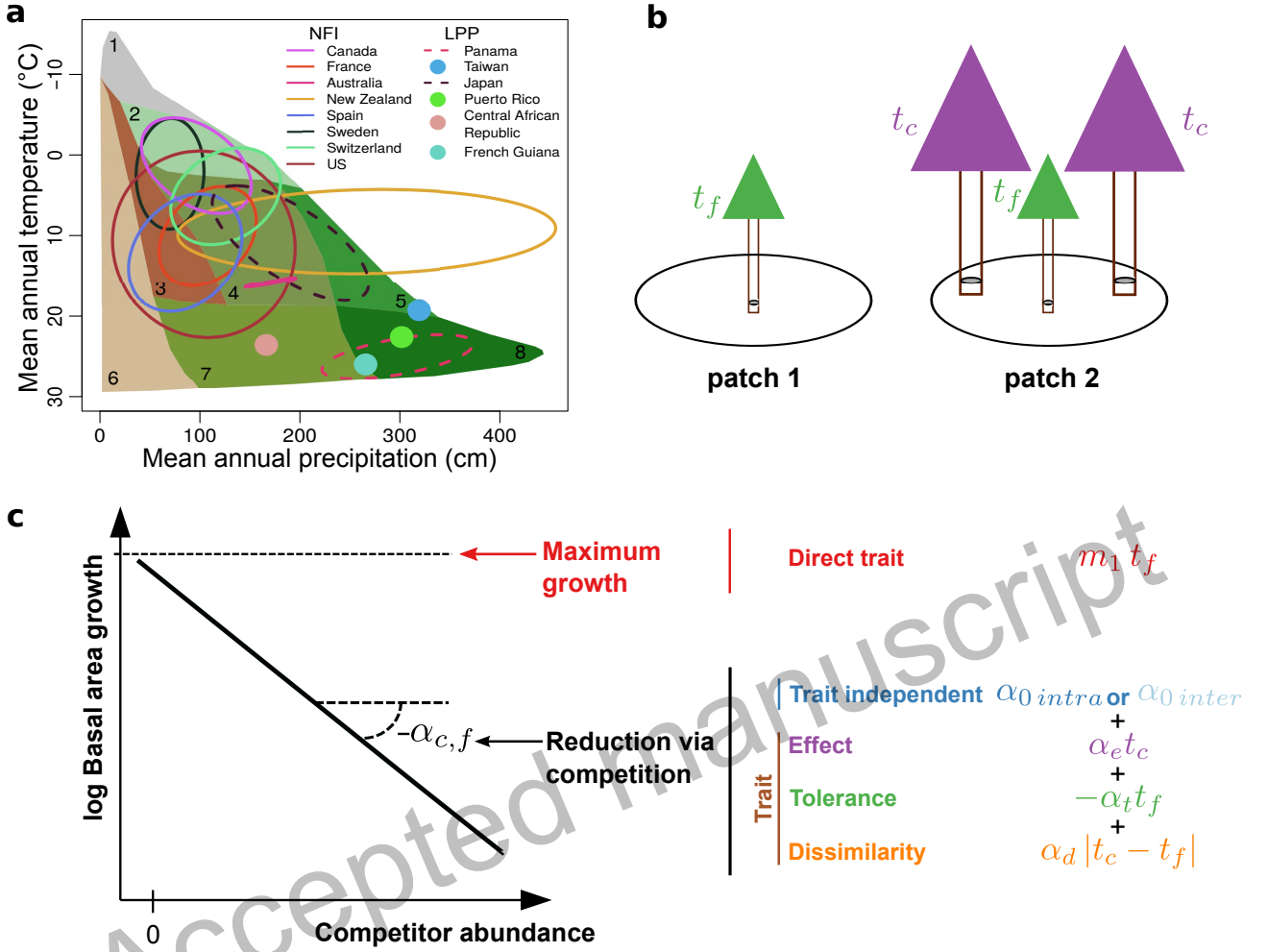


Figure 1: **Assessing competitive interactions at global scale.** **a**, Precipitation-temperature space occupied by each data set (NFI – national forest inventories data, LPP – large permanent plots data). For data with multiple plots, the range of climatic condition is represented by an ellipse covering 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 Ricklefs³⁰). **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 (α_e), the effect of the focal tree's traits (t_f) on its tolerance of competition (α_t), and the effect of trait dissimilarity between the focal tree and its competitors ($|t_c - t_f|$) on competition (α_d). The parameters $m_0, m_1, \alpha_0 \text{intra}, \alpha_0 \text{inter}, \alpha_e, \alpha_t$ and α_d are fitted from data using a maximum likelihood method.

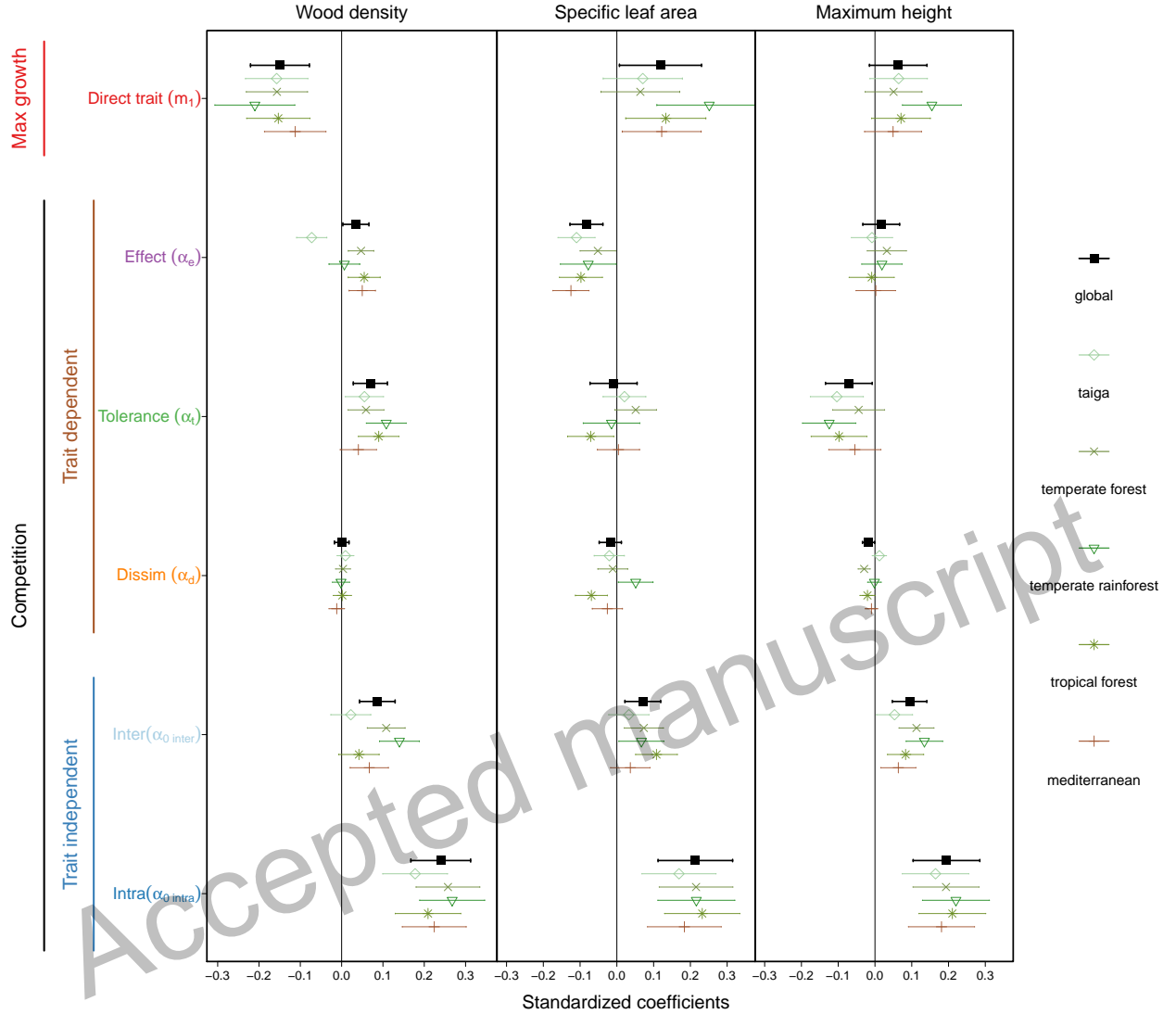


Figure 2: **Trait-dependent and trait-independent effects on maximum growth and competition across the globe and their variation among biomes.** Standardized regression coefficients for growth models, fitted separately for each trait (points: mean estimates and lines: 95% confidence intervals). Black points and lines represent global estimates and coloured points and lines represent the biome level estimates. The parameter estimates represent: effect of focal tree's trait value on maximum growth m_1 , the effect of competitor trait values on their competitive effect α_e (positive values indicate that higher trait values lead to a stronger reduction in growth of the focal tree), the effect of the focal tree's trait value on its tolerance of competition α_t (positive values indicate that greater trait values result in greater tolerance of competition), the effect on competition of trait dissimilarity between the focal tree and its competitors α_d (negative values indicate that higher trait dissimilarity leads to a lower reduction of the growth of the focal tree), and the trait-independent competitive effect of conspecific $\alpha_{0\text{intra}}$ 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).

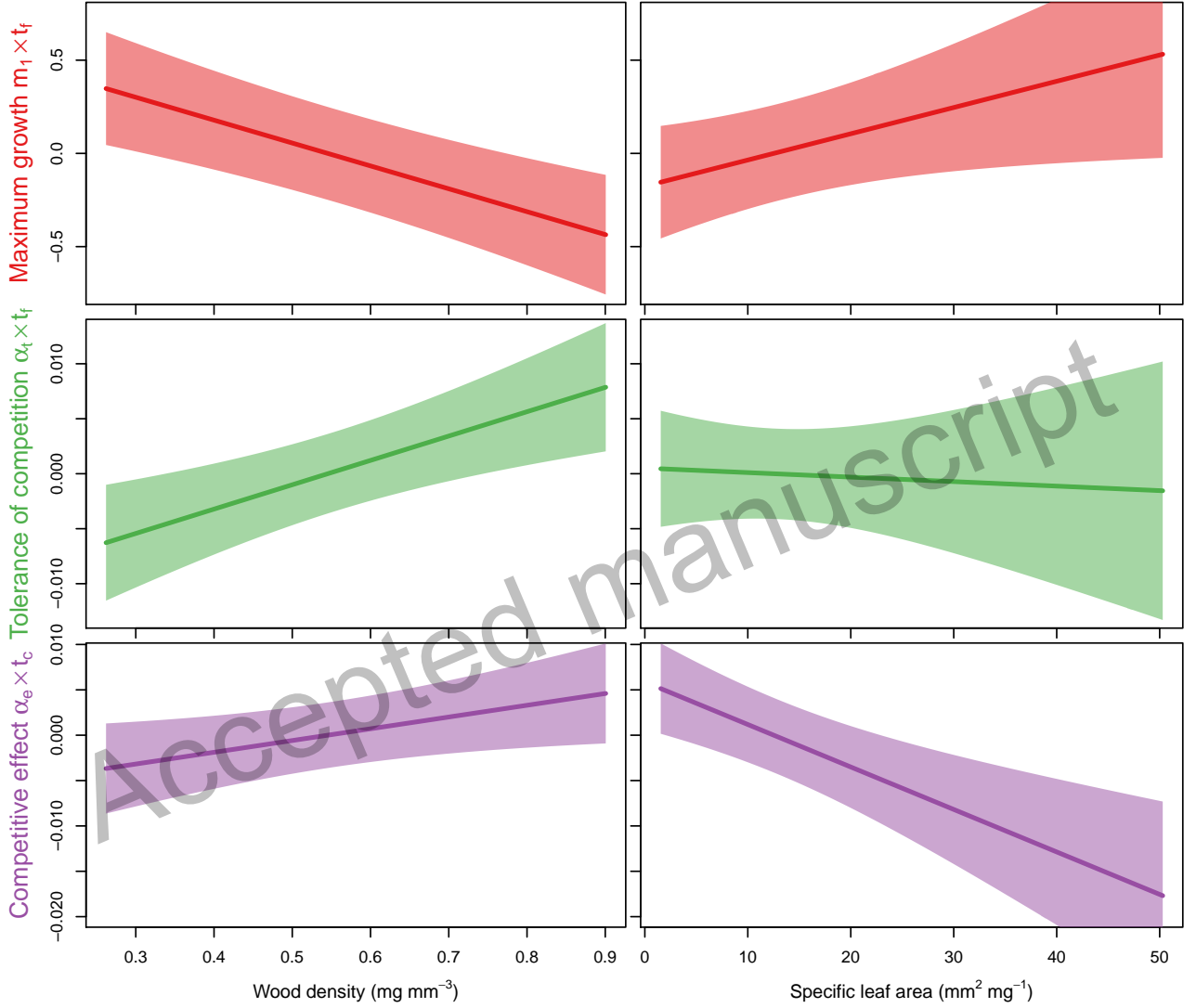


Figure 3: **Variation of maximum growth, competitive effects and competitive tolerance with wood density and specific leaf area predicted by global traits models.** Variation of maximum growth ($m_1 t_f$), tolerance of competition ($\alpha_t t_f$) and competitive effect ($\alpha_e t_c$) parameters with 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 α_0 or m_0).

References

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).
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).
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).
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).
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).
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).

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).

Accepted manuscript

Methods

Model and analysis

To examine the link between competition and traits we used a neighbourhood modelling framework¹⁻⁵ to model the growth of a focal tree of species f as a product of its maximum growth (determined by its traits and size) together with reductions due to competition from individuals growing in the local neighbourhood (see definition below). Specifically, we assumed a relationship of the form

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

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,
- γ_f determines the rate at which growth changes with size for species f , modelled with a normally distributed random effect of species $\varepsilon_{\gamma,f}$ [as $\gamma_f = \gamma_0 + \varepsilon_{\gamma,f}$ where $\varepsilon_{\gamma,f} \sim \mathcal{N}(0, \sigma_\gamma)$ – a normal distribution of mean 0 and standard deviation σ_γ]
- $\alpha_{c,f}$ is the per unit basal area effect of individuals from species c on growth of an individual in species f ,
- $B_{i,c,p,s} = 0.25 \pi \sum_{j \neq i} w_j D_{j,c,p,s,t}^2$ is the sum of basal area of all individuals competitor trees j of the species c within the local neighbourhood of the tree i in plot p , data set s and census t , where w_j is a constant based on 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^{2,4,5}. We modelled the effect of traits, one trait at a time. The effect of a focal species' trait value, t_f , on its maximum growth was included as:

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

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 processes¹, and here we extended the approach of the most recent study⁵. As presented in Fig. 1, competitive interactions were modelled using an equation of the form²:

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

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),
- α_t is the **tolerance of competition** by the focal species, i.e. change in competition tolerance due to traits t_f of the focal tree with a normally distributed random effect of data set s included [45 $\varepsilon_{\alpha_t,s} \sim \mathcal{N}(0, \sigma_{\alpha_t})$],

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

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

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

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

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

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)⁶, response and explanatory variables were standardized (divided by their standard deviations) prior to analysis. Trait and diameter were also centred to facilitate convergence. The models were fitted using the *lmer* routine in the lme4 package⁷ in the R statistical environment⁸. 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 ecoregion⁹ (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^{10,11}. 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 α_{ij} defined by equ. 4. High competitive effects translate into strong growth reduction. Then we can compare the strength of inter *vs.* intraspecific competition between two species i and j using the following expression:

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

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 α_d (see Figure 3. in Extended Data for the results). This approach shares similarities with a method developed by Chesson¹², and recently applied with population growth models in annual plants communities^{13,14} – estimating ρ 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^{15–24}); (2) large permanent plots (LPP) ranging in size from 0.5-50ha, in which the x-y coordinates of all trees above a given diameter were recorded

(references for LPP data used^{25–32}). LPP were mostly located in tropical regions. The minimum diameter of recorded trees varied among sites from 1–12cm. To allow comparison between data sets, we restricted our analysis to trees greater than 10cm. Moreover, we excluded from the analysis any plots with harvesting during the growth measurement period, that were identified as plantations, or that overlapped a forest edge. Finally, we randomly selected only two consecutive census dates per plot or quadrat to avoid having to account for repeated measurements (less than a third of the data had repeated measurements). Because human and natural disturbances are present in all these forests (see Supplementary Methods), they probably all experience successional dynamics (as indicated by the forest age distribution available in some of these sites in Supplementary Methods). See Supplementary Methods and Extended Data Table 1 for more details on individual data sets.

Basal area growth was estimated from diameter measurements recorded between the two censuses. For the French NFI, these data were obtained from short tree cores. For all other data sets, diameter at breast height (D) of each individual was recorded at multiple census dates. We excluded trees (i) with extreme positive or negative diameter growth measurements, following criteria developed at the BCI site²⁶ (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^{2,33}. To avoid edge effects, we also excluded trees less than 15m from the edge of a plot. To account for variation of abiotic conditions within the LPPs, we divided plots into regularly spaced 20x20m quadrats and included a random quadrat effect in the model (see above).

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

We extracted mean annual temperature (MAT) and mean annual sum of precipitation (MAP) from the [worldclim](#) data base³⁴, using the plot latitude and longitude. MAT and MAP data were then used to classify plots into biomes, using the diagram provided by Ricklefs³⁵ (after Whittaker).

Traits

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

Table 2 for trait coverage). Where available we used data collected locally (references for the local
140 trait data used in this analysis^{27,36–39}); otherwise we sourced data from the TRY trait data base⁴⁰
(references for the data extracted from the TRY database used in this analysis^{36,41–110}). Local data
were available for most tropical sites and species (see Supplementary Methods). Several of the NFI
data sets also provided tree height measurements, from which we computed a species’ maximum
height as the 99% quantile of observed values (for France, US, Spain, Switzerland). For Sweden we
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%.

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).
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).
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).
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).
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).
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).

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. 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).
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).

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).
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).
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., Schilke, L. D. W. & Ackerly, D. D. A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**, 1465–71 (2006).
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).
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).
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).
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/>.
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).
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).
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).
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).
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).
70. Medlyn, B. *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).

71. Medlyn, B. E. & Jarvis, P. G. Design and use of a database of model parameters from elevated [CO₂] experiments. *Ecol. Model.* **124**, 69–83 (1999).
- 315 72. 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).
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).
- 320 74. Moles, A. T. *et al.* Factors that shape seed mass evolution. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 10540–10544 (2005).
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. Ordóñez, 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).

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).
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).
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).
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, Tadzhikistan. *New Phytol.* **143**, 131–142 (1999).
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).
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).

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 con-
tent in a Mediterranean shrubland under warming and drought. *J. Geophys. Res.: Biogeosci.*
113 (2008).
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).
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 photosyn-
thetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiol.*
20, 565–578 (2000).
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).
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).