

Widespread slow growth of acquisitive tree species

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L. Augusto¹✉, R. Borelle¹, A. Boća², L. Bon¹, C. Orazio³, A. Arias-González⁴, M. R. Bakker¹, N. Gartzia-Bengoetxea⁴, H. Auge^{5,6}, F. Bernier⁷, A. Cantero⁸, J. Cavender-Bares⁹, A. H. Correia¹⁰, A. De Schrijver¹¹, J. J. Diez-Casero¹², N. Eisenhauer^{6,13}, M. N. Fotelli¹⁴, G. Gâteblé¹⁵, D. L. Godbold^{16,17}, M. Gomes-Caetano-Ferreira¹⁸, M. J. Gundale¹⁹, H. Jactel²⁰, J. Koricheva²¹, M. Larsson¹⁹, V. A. Laudicina²², A. Legout²³, J. Martín-García^{12,24}, W. L. Mason²⁵, C. Meredieu²⁰, S. Mereu²⁶, R. A. Montgomery⁹, B. Musch²⁷, B. Muys^{28,29}, E. Paillassa³⁰, A. Paquette³¹, J. D. Parker³², W. C. Parker³³, Q. Ponette³⁴, C. Reynolds³⁵, M. J. Rozados-Lorenzo³⁶, R. Ruiz-Peinado³⁷, X. Santesteban-Insausti³⁸, M. Scherer-Lorenzen³⁹, F. J. Silva-Pando³⁶, A. Smolander⁴⁰, G. Spyrouglou¹⁴, E. B. Teixeira-Barcelos⁴¹, E. I. Vanguelova³⁵, K. Verheyen⁴², L. Vesterdal⁴³ & M. Charru¹✉

Trees are an important carbon sink as they accumulate biomass through photosynthesis¹. Identifying tree species that grow fast is therefore commonly considered to be essential for effective climate change mitigation through forest planting. Although species characteristics are key information for plantation design and forest management, field studies often fail to detect clear relationships between species functional traits and tree growth². Here, by consolidating four independent datasets and classifying the acquisitive and conservative species based on their functional trait values, we show that acquisitive tree species, which are supposedly fast-growing species, generally grow slowly in field conditions. This discrepancy between the current paradigm and field observations is explained by the interactions with environmental conditions that influence growth. Acquisitive species require moist mild climates and fertile soils, conditions that are generally not met in the field. By contrast, conservative species, which are supposedly slow-growing species, show generally higher realized growth due to their ability to tolerate unfavourable environmental conditions. In general, conservative tree species grow more steadily than acquisitive tree species in non-tropical forests. We recommend planting acquisitive tree species in areas where they can realize their fast-growing potential. In other regions, where environmental stress is higher, conservative tree species have a larger potential to fix carbon in their biomass.

The potential to mitigate current rates of climate change depends on reducing greenhouse gas emissions and enhancing carbon (C) sinks³. Along with oceans, forests constitute one of the two main carbon sinks on Earth³, but the potential for enhancing forest carbon sinks differs among biomes⁴. Tropical forests are under high anthropogenic pressure with a continuous decline in surface area⁵. Therefore, maintaining their role in climate change mitigation first requires protection and restoration¹. Conversely, despite being threatened by global changes⁶, the forested area in temperate and boreal regions is expanding and remains important for climate change mitigation through biophysical effects (evapotranspiration and albedo), carbon storage in soils, standing biomass and wood products^{1,4,5,7}. In such a context, storing carbon in tree biomass and therefore promoting tree species that grow fast may strengthen one of the pathways to increased mitigation. This leads to a key question for managing forests in a global change context regarding which tree species enable an efficient and sustainable mitigation.

Research in plant ecophysiology has shown under controlled conditions that species that are able to efficiently acquire resources (sunlight, water, nutrients) generally grow fast^{8–10}. These acquisitive species are characterized by high values of functional traits involved in resource collection, such as specific leaf area (SLA; for sunlight) and specific root length (SRL; for water and nutrients). Acquisitive species also have high values of functional traits involved in transforming resources into biomass (maximum photosynthetic capacity (A_{max}), and leaf content of nitrogen (N)). Owing to their ability to efficiently acquire and transform resources, acquisitive species are commonly considered to be fast-growing species in most environments^{8,10}. Similarly, species that are more efficient at keeping their internal resources (that is, nutrients, water and energy) than collecting external resources are defined as conservative species and are commonly assumed to be slow-growing species, except in particularly unfavourable environments. Current knowledge therefore suggests that acquisitive tree species should be promoted for mitigating

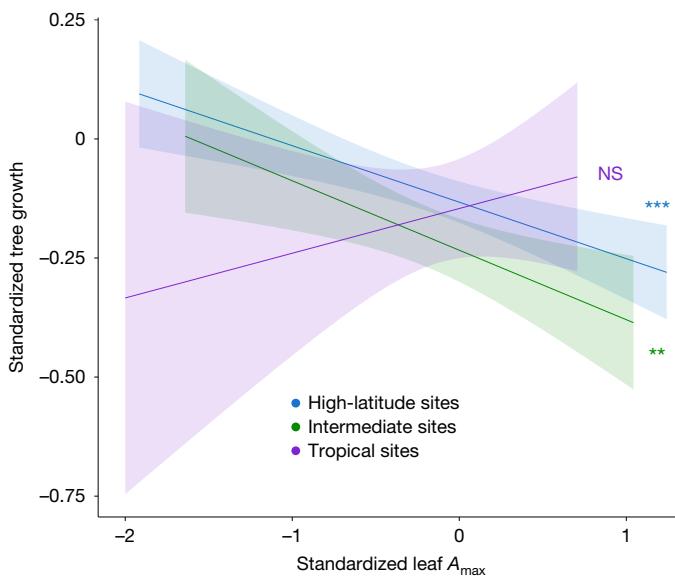


Fig. 1 | The negative relationship between the leaf A_{\max} of tree species and tree growth. Tree growth was quantified based on several metrics and values are standardized to enable comparisons among sites using the approach of the log growth ratio (positive values and negative values indicate values higher and lower than the site mean value, respectively; Methods). Results are presented by latitude class (high-latitude sites, $|\text{latitude}| \geq 45^\circ$; intermediate sites, $23^\circ < |\text{latitude}| < 45^\circ$; tropical sites, $|\text{latitude}| \leq 23^\circ$). A linear regression was fitted (level of confidence of the error band = 0.95) for each class (for high-latitude, intermediate and tropical sites, respectively: $P = 1.7 \times 10^{-4}$, $P = 0.005$ and $P = 0.379$; $t = -3.79, -2.83$ and 0.88 ; d.f. = 499, 434 and 135; $n = 501, 436$ and 137). *** $P < 0.001$; ** $P < 0.010$; NS, not significant, $P \geq 0.100$). For readability, data points are not presented together with regression lines and error bands (data points are presented class by class in Extended Data Fig. 3). Results are confirmed when presented by an independent dataset (Supplementary Methods 1).

climate change through fast biomass growth, but this paradigm is only partly supported by the literature. We compiled data from 10 independent greenhouse experiments, involving a total of 212 tree species from all biomes, and confirmed the well-established result that seedlings of acquisitive species (that is, with high SLA values) grow faster than conservative species (low SLA values) under favourable conditions of temperature and resource availability (Extended Data Fig. 1). Conversely, while robust growth–trait relationships are observed for seedlings under controlled conditions, studies on adult trees in natural conditions displayed high variability. Even if local-to-regional-scale studies identified some growth–trait relationships^{11,12}, some others found only weak relationships at best^{13,14}, and studies that compared tree growth in contrasting regions did not find consistent patterns^{2,15}. This lack of a clear pattern has led some scientists to question whether trait-based studies are a good approach for predicting plant growth^{2,15,16}. The aim of this study was to evaluate whether acquisitive tree species do really grow fast in the field. The premises of our study are that (1) the observed growth–trait relationships are relevant only in environmental conditions that are favourable to biological activity (that is, moist warm climates and fertile soils)^{10,11,17}, but (2) these conditions are more and more uncommon due to widespread nutritive limitations and climatic stresses^{18–21}. On the basis of this, and because acquisitive species are resource demanding and also stress sensitive^{9,22–24}, we hypothesized that acquisitive species are often constrained by environmental limitations and, consequently, do not perform on average better than conservative species (Extended Data Fig. 2). To test this hypothesis, and therefore investigate the interactive effects

Table 1 | Interactive effects of functional traits values and site productivity on tree growth

Trait	Effects	Early growth (cm yr ⁻¹) (EAN+TDN+TED)	Late growth (tha ⁻¹ yr ⁻¹) (SBD)
Leaf A_{\max}	Trait	*** $P = 2.8 \times 10^{-4}$ ($n = 756$; $\chi^2 = 13.6$)	** $P = 0.006$ ($n = 257$; $\chi^2 = 7.8$)
	Trait \times Site _{prod}	** $P = 0.009$ ($n = 756$; $\chi^2 = 6.8$)	$P = 0.409$ ($n = 257$; $\chi^2 = 0.7$)
SLA	Trait	*** $P = 3.2 \times 10^{-7}$ ($n = 783$; $\chi^2 = 26.1$)	*** $P = 4.2 \times 10^{-6}$ ($n = 324$; $\chi^2 = 21.2$)
	Trait \times Site _{prod}	*** $P = 7.9 \times 10^{-5}$ ($n = 783$; $\chi^2 = 15.6$)	*** $P = 2.3 \times 10^{-4}$ ($n = 324$; $\chi^2 = 13.5$)
Leaf N	Trait	*	$P = 2.4 \times 10^{-4}$ ($n = 761$; $\chi^2 = 6.5$)
	Trait \times Site _{prod}	** $P = 0.010$ ($n = 761$; $\chi^2 = 6.6$)	$P = 0.108$ ($n = 325$; $\chi^2 = 2.6$)
Leaf P	Trait	*	$P = 0.012$ ($n = 755$; $\chi^2 = 6.3$)
	Trait \times Site _{prod}	*	$P = 0.022$ ($n = 755$; $\chi^2 = 5.2$)
Wood density	Trait	*** $P = 1.1 \times 10^{-4}$ ($n = 787$; $\chi^2 = 15.0$)	*
	Trait \times Site _{prod}	*	$P = 0.015$ ($n = 787$; $\chi^2 = 5.9$)
SRL	Trait	*** $P = 1.1 \times 10^{-4}$ ($n = 702$; $\chi^2 = 14.9$)	** $P = 0.002$ ($n = 231$; $\chi^2 = 9.7$)
	Trait \times Site _{prod}	*** $P = 3.5 \times 10^{-4}$ ($n = 702$; $\chi^2 = 12.8$)	(*) $P = 0.092$ ($n = 231$; $\chi^2 = 2.8$)

Values were standardized to enable comparisons among sites and removing the prominent effect of site productivity (Methods). Trait effects (and trait \times productivity interactions) were tested using linear mixed models with site identity and tree species identity as random factors, as follows: growth ~ trait + (trait \times site_{prod}) + (1|site_{ID}) + (1|species_{ID}). Site_{prod}, site productivity. *** $P < 0.001$; ** $P < 0.010$; * $P < 0.050$; (*) $P < 0.100$.

of functional traits, climate and soil on tree growth, we compiled data describing tree growth, functional traits and environmental conditions for 1,262 monospecific stands, distributed in 160 common gardens (hereafter, sites), and representing 223 distinct tree species. The consolidated database was composed of four independent datasets that enabled us to test the reliability of results in all forest biomes, all forested continents and at different tree ages (Methods): (1) the European Atlantic Network (EAN); (2) the Tree Diversity Network (TreeDivNet, hereafter TDN); (3) a global dataset of stand biomass (SBD); and (4) a dataset containing tropical extra data (TED).

First, we investigated growth–trait relationships without taking into account possible interactions with site conditions. We found that, in non-tropical forests, tree growth showed significant correlations with many functional traits (Extended Data Figs. 3 and 4) such as wood density (Extended Data Fig. 3c), a functional trait that is consistently and negatively associated with growth rate^{16,25,26}. Notably, we found that tree growth was negatively associated with several important traits that are typically linked to fast growth (such as SLA and leaf N and phosphorus (P) content; Extended Data Fig. 3a,e,f). This was particularly noticeable for the A_{\max} of tree species (Fig. 1 and Extended Data Fig. 5), which is a key trait in plant growth as it integrates the effects of other traits^{24,27}. In a second step, following our first premise and because there was large variability in growth–trait relationships (Fig. 1 and Extended Data Fig. 5), we investigated the extent to which local conditions influence growth–trait relationships. For this purpose, we analysed the growth–trait–site interactions using random-forest models, mixed linear models and linear modelling of growth–trait correlation values. The analysis of the EAN data showed that drivers of forest growth such as atmospheric N deposition²⁸, climate^{19,29} and soil properties³⁰ were all highly influential

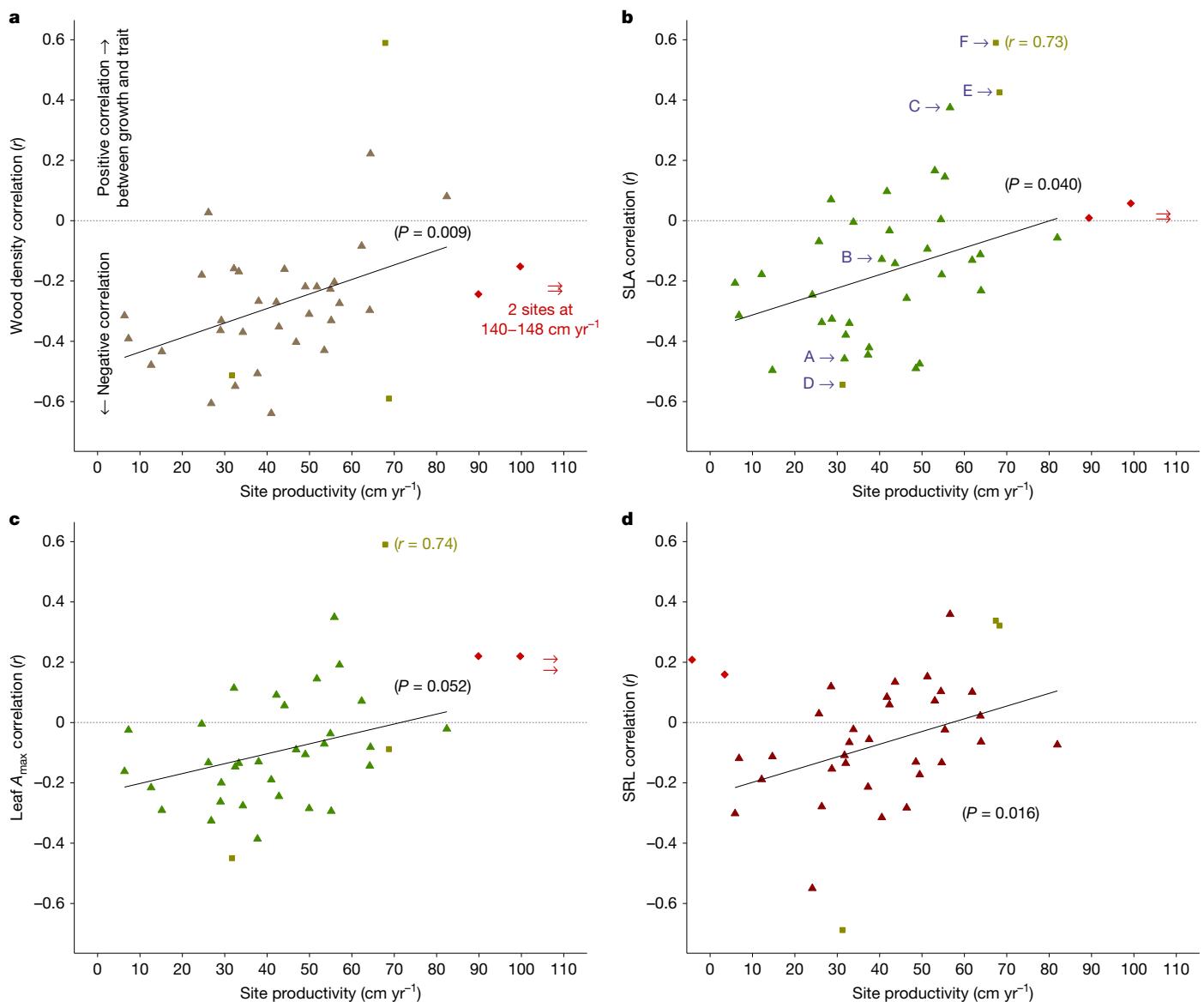


Fig. 2 | The influence of site productivity on growth-trait relationships. **a–d**, Site productivity (xaxis) is the mean growth value of all tree species of a given site (in cm per year of height growth). The correlation coefficient (yaxis) refers to the relationship at a given site between tree species growth and species trait value: positive y-axis values and negative y-axis values indicate a positive growth–trait correlation and a negative growth–trait correlation, respectively (Pearson method). The presented traits are as follows: wood density (a), SLA (b), leaf A_{\max} (c) and SRL (d). Data were selected from the sites that had at least ten different tree species, which comprised all EAN sites (triangles), three TDN sites (squares) and four TED sites (diamonds). The black line represents the linear regression between the productivity and correlation

r value (with the *P* value in parentheses). As the TDN and TED sites did not have the same number of tree species as the EAN sites, and because *r* values tend to increase with decreasing size of data (Methods), the TDN–TED sites were not used to fit the regressions. One TDN site had very high *r* values that were beyond the y-axis limit (b and c) and this was plotted in the upper part of the graph (with its *r* value in brackets). Two TED sites had very high site productivity and their correlation value was indicated with red arrows. Six examples of relationships between growth and trait values are presented in Extended Data Fig. 6, and these six sites are identified by the letters A–F (b). For a–d, the respective statistics were as follows: *t* = 2.80, 2.15, 2.02 and 2.56; *d.f.* = 30 and *n* = 32 in all cases; *r* = 0.45, 0.37, 0.35 and 0.42.

(random forest models; Extended Data Table 1). At these sites, three functional traits had consistent relationships with tree growth across sites and, consequently, along environmental gradients (Extended Data Table 2; negative effect, wood density; positive effect, leaf carbon and root phosphorus).

By contrast, some traits (such as SLA, SRL, leaf N, leaf A_{\max}) had inconsistent relationships with tree growth (Extended Data Table 2). We considered that these inconsistent relationships may be due to growth–trait–site interactions, and investigated such interactions using mixed linear modelling. We found statistically significant growth–trait–site interactions for most functional traits, at the worldwide scale and at

different development stage of trees (Table 1). Finally, we explored these interactions by studying the extent to which the growth–trait relationships depended on local conditions (as approximated by the site productivity, which integrates all environmental constraints on plants). We found that, for these traits, both the strength and the direction of the growth–trait relationships depended on the local environment. Notably, if some traits such as wood density had a consistent effect across different environments, as the site productivity increased, the strength of the correlation between growth rate and trait value weakened (Fig. 2a). This dependency on site conditions was particularly clear for several functional traits, such as A_{\max} , SLA and SRL,

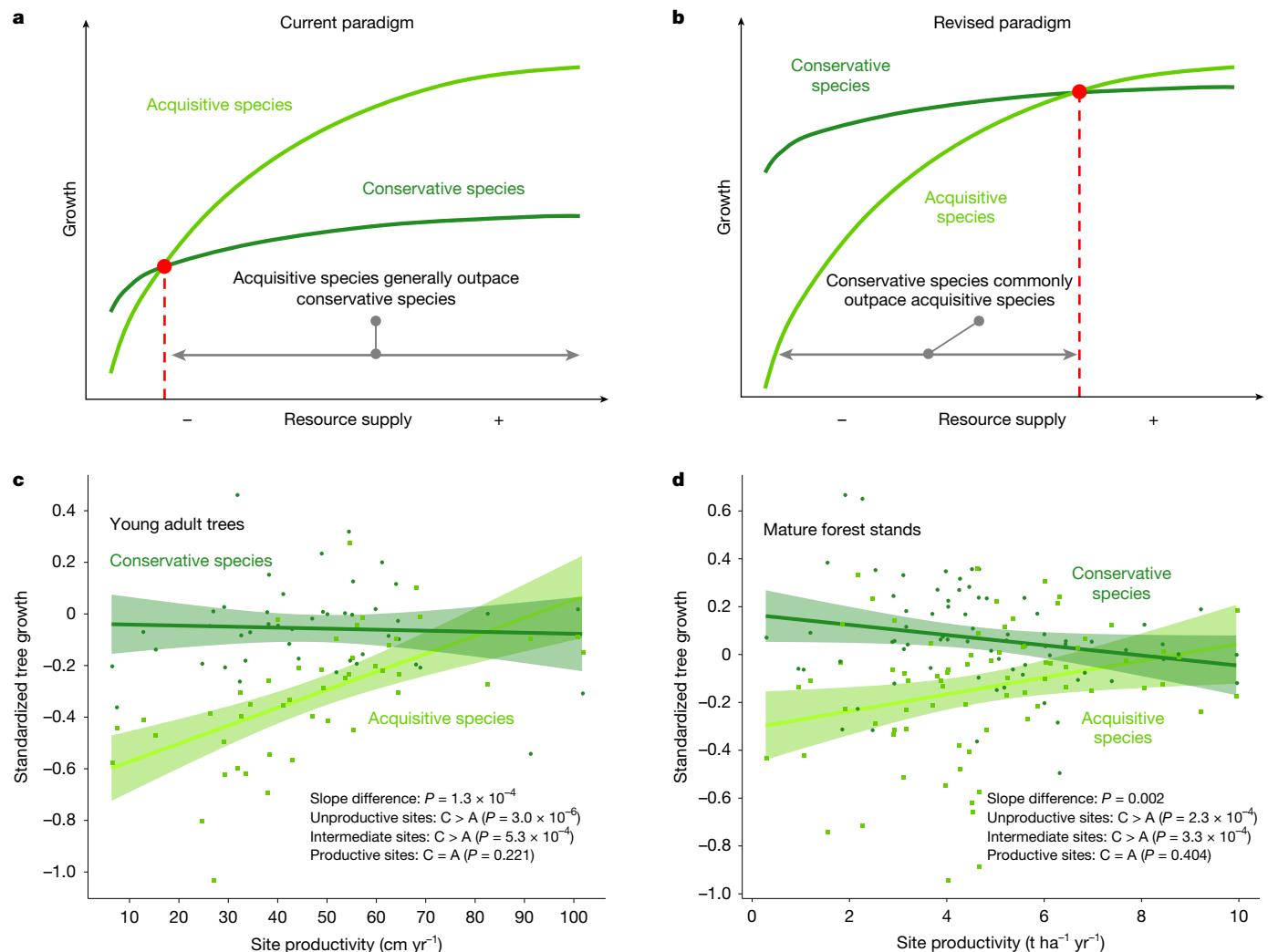


Fig. 3 | Growth rates according to species strategy and resource supply. **a,b**, The expected response of tree species to environmental conditions. The current paradigm, which is adapted from a previous study²³, with acquisitive species and conservative species representing high- and low-resource species, respectively (a), and a revised version of the paradigm (b). **c,d**, This revised version is supported by the results of this study of tree species growth along gradients of site productivity for young trees (c; the dataset, EAN + TDN + TED) and mature stands (d; dataset, SBD). Values were standardized to enable comparison of sites from all datasets (Methods). Growth strategies (that is, acquisitive versus conservative) were defined a priori, based on theory and trait values (leaf A_{max} , SLA and leaf N; Methods). Sites that included only acquisitive species, or only conservative species, were not taken into account in data analyses. Three classes of site productivity were defined based on percentiles

33% and 66%, before testing possible differences between acquisitive and conservative species (two-sided Kruskal–Wallis test). A linear regression was fitted (level of confidence of the error band = 0.95) for each growth strategy. The slope difference was tested using covariance analysis. As the number of species highly varied from site to site, values were averaged by site (that is, one acquisitive average value + one conservative average value per site) to give the same statistical weight to all sites. n was 776 and 288 for individual values, which were averaged into 92 and 150 final values for c and d. Test of slope difference: $F = 16.11$ and 9.48 for c and d (averaged values). The results remained unchanged if individual values were used. Similarly, the results remained statistically significant if the two outlier sites (identified in the 'Assessment of the datasets' section of the Methods) were included.

which previously showed inconsistent effects over sites (Extended Data Table 2). For these traits, which are key for acquiring and using resources, the correlation with growth rate progressively switched from negative to positive with increasing site productivity (Fig. 2b–d and Extended Data Fig. 6). We observed this pattern for most traits at the EAN sites (Extended Data Fig. 7) and it was confirmed in three common gardens of the TDN network and four tropical common gardens (Fig. 2 and Extended Data Fig. 6).

Together, our results supported our initial expectation that positive relationships between key functional traits and tree growth occur only in field conditions with favourable environments but are uncommon in stressful environments. The discrepancy between an abundant literature based on experiments under controlled conditions (Extended Data Fig. 1) and observations in the field can therefore be explained

by ontogenetic effects, functional ecology and changes in resource allocation. Indeed, for obvious technical constraints, experiments under controlled conditions (often greenhouse experiments) used seedlings as model plants, whereas *in situ* studies often focused on saplings or adult trees. Seedlings, saplings and adult trees respond differently to environmental constraints^{11,16}, which may explain why our results did not align with expectations derived from theory and greenhouse experiments. Moreover, greenhouse seedlings were generally grown under conditions with optimal temperature, light intensity, water and nutrient supplies, and with no herbivory pressure. In such non-limiting conditions, acquisitive species are by definition able to acquire resources fast (due to high SLA and SRL) and can in turn produce new biomass quickly (A_{max} , leaf N), defining the concept of fast-growing species. Conversely, under unfavourable conditions, plant growth is

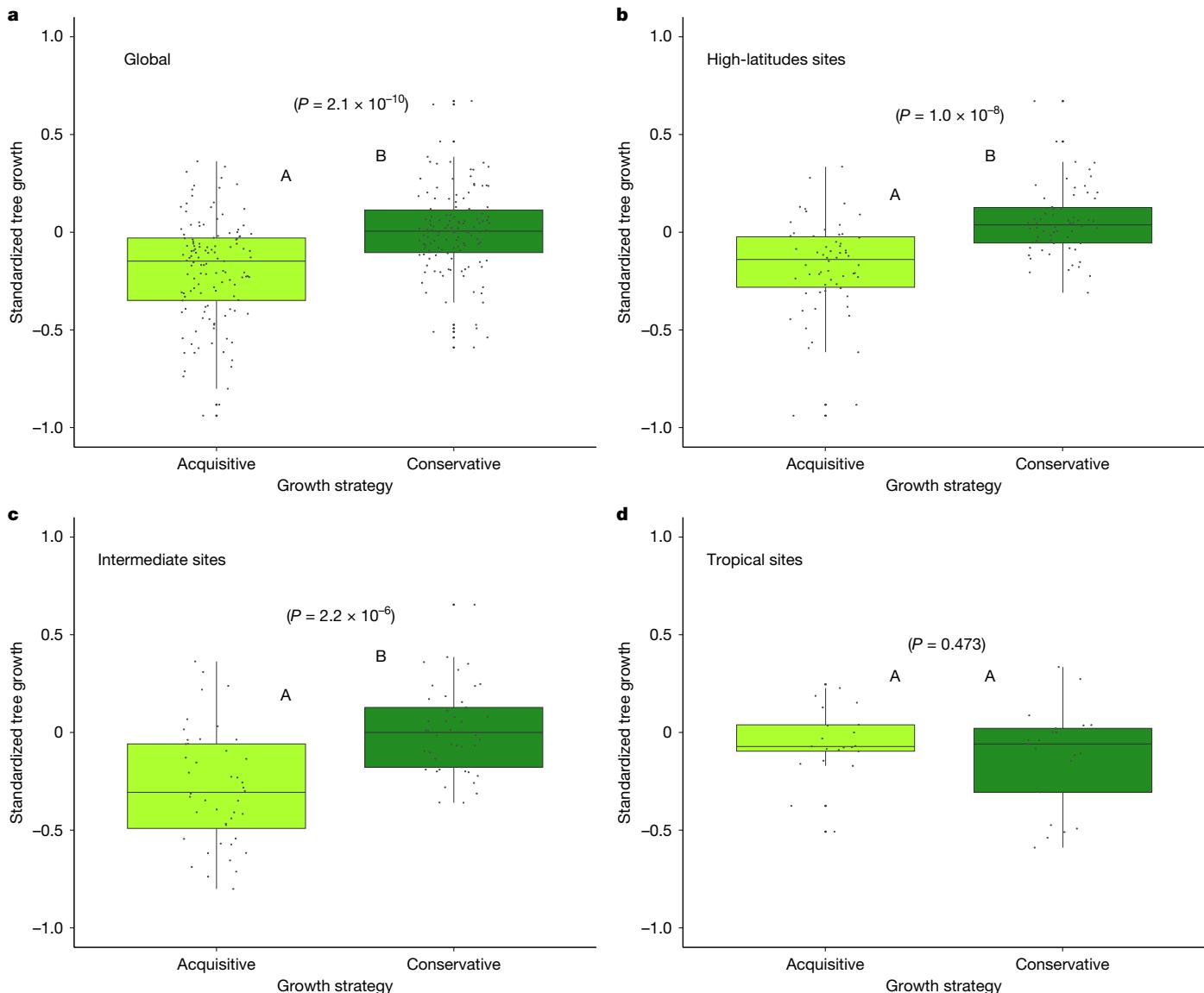


Fig. 4 | The effective ability of acquisitive tree species and conservative tree species to grow fast. **a–d**, Growth strategies (that is, acquisitive versus conservative) were defined *a priori* based on theory and trait values (leaf A_{\max} , SLA and leaf N; Methods). Growth values were standardized to enable comparison of sites from all datasets (Methods). Results are presented together (a) and by latitudinal classes (high (b), intermediate (c) and tropical (d)), with 23° and 45° as limit values. The results are confirmed when presented by dataset (Supplementary Methods 2). Sites that included only acquisitive species, or only conservative species, were not taken into account in data analyses. As the number of species highly varied from site to site, values were averaged by site

(that is, one acquisitive average value + one conservative average value per site) to give the same statistical weight to all sites. n was 1,159, 514, 427 and 218 for individual values, which were averaged into 256, 124, 90 and 42 final values for **a–d**. The box plots represent the median (centre line), the first and third quartiles (box limits) and $1.5 \times$ the interquartile range (whiskers). Different letters indicate a significant difference between the two growth strategies. Differences were tested using the two-sided Kruskal–Wallis non-parametric test. For **a–d**, $\chi^2 = 40.41, 32.83, 22.44$ and 0.51 ; $d.f. = 1$ in all cases. The results remained unchanged if individual values were used.

not limited by C assimilation (as it is under optimal conditions) but is constrained by the capacity to efficiently use nutrients and water from soils²⁷ and to endure stress, conditions under which tree species with high trait values (SLA and leaf N) tend to be less efficient^{10,23,24,31}. Furthermore, allocation of resources to processes and organs that promote stress tolerance (for example, for defence) and reproduction rather than growth changes the relationship between functional traits and growth³². Consequently, conservative species are generally stress tolerant^{10,23,33} and are, on average, able to maintain substantial effective growth under conditions of ambient environmental stress despite trait values (such as low SLA^{24,34}) that reduce maximum growth rate. In the field, along gradients of environmental conditions from favourable to stressful, functional traits involved in plant growth shift

progressively from beneficial to deleterious. This observed change explains the inconsistency in the literature between greenhouse experiments and field studies^{2,16,35}.

On the basis of empirical observations, the current paradigm is that acquisitive species are fast-growing species because they generally outpace conservative species, except in particularly resource-deficient sites (Fig. 3a). However, based on common gardens worldwide, our data suggest that the optimal conditions required by acquisitive species are the exception rather than the rule (Fig. 3b–d). Indeed, if acquisitive species do perform well in particularly favourable environments^{36,37}, they are more sensitive to environmental harshness^{38,39}, whereas conservative, stress-tolerant tree species perform better in most environments, therefore supporting our initial hypothesis that environmental

conditions are generally disadvantageous to acquisitive species. In practice, acquisitive species grew on average more slowly in field conditions than conservative tree species (Fig. 4a–c), except in tropical regions (Fig. 4d). This difference was large in terms of height growth rate for young adult trees (Fig. 3c), and it remained significant in terms of biomass growth and accumulation in mature stands (Fig. 3d; final biomass: $P = 5.9 \times 10^{-7}$, $\chi^2 = 24.9$, $n = 288$). Such a persistent difference over time may be partly explained by a similar survival rate at young stages ($P = 0.775$, $\chi^2 = 0.1$, $n = 571$ EAN stands), and longer lifespan values of conservative species⁴⁰ (Extended Data Table 3). Despite this step forward, further research is still needed as several questions remain open (that is, growth–trait interactions with other important processes such as growth–survival–reproduction trade-offs, competition along gradients of productivity, intraspecific variability, interspecific effects in mixed forests or multistrata forests). This is particularly the case for tropical forests for which functional traits and ecological strategies have on average less importance than in non-tropical forests (Fig. 1 and Extended Data Fig. 3), confirming previous studies that found a non-significant or minor effect of functional traits—except wood density⁴¹—on the growth rate of tropical trees^{12,15,35,42}. This average weak effect is consistent with our main findings as tropical forests generally present favourable climatic conditions and high net primary production⁴³ (Methods). In wet tropical regions, a general positive growth–trait relationship might even have been expected, but tropical forests are often locally limited by water supply or nutrient availability^{18,19,43,44}, resulting in complex growth–trait–site interactions^{36,45}. As such, and based on our tropical data, we posit that local conditions are probably favourable from site to site for acquisitive species or conservative species^{36,38,46}.

Forests provide many ecosystem services⁴⁷ and not only wood production and carbon storage. Although our findings have implications for carbon storage, the other ecosystem services and sustainable silviculture encompass more than just selecting the fastest growing tree species. Our results do not question the general guidelines for sustainable forest management, including favouring a high level of biodiversity, which is important for conservation. Biodiversity is an even more important issue because mixing tree species in forests is an efficient lever for increasing carbon storage⁴⁸ and for improving forest resistance to disturbances and stressors⁴⁹. On the other hand, taking into account the complexity of forest management, this does not mean that favouring certain tree species is not important. Indeed, the change of view regarding the so-called fast-growing species has implications for climate change mitigation through tree growth^{7,50}. In tropical regions, where functional traits seem to have a limited influence on tree growth, we posit that protecting forests from degradation⁵ remains the priority. Conversely, in non-tropical regions, to enhance carbon storage in biomass, tree species should not be favoured based on their absolute potential, but by matching them with the local conditions, each tree species having its own ecological niche and specific requirements²⁹. In a context of promotion for programmes of massive tree planting, we stress that the choice of tree species should not rely on *a priori* expectations but on local forester knowledge. Furthermore, if low-risk strategies for mitigating climate change are a priority, then dedicated approaches should always consider choosing tree species with caution, regardless of the other silvicultural options used. As such, conservative tree species—which are stress-tolerant and long-lived—appear to be a better strategy for fixing carbon than the so-called ‘fast growing’ acquisitive tree species, which generally grow slowly.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions

and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-025-08692-x>.

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¹INRAE, Bordeaux Sciences Agro, UMR 1391 ISPA, Villenave d'Ornon, France. ²Latvia University of Life Sciences and Technologies, Jelgava, Latvia. ³Institut Européen de la Forêt Cultivée (IEFC), Cestas, France. ⁴NEIKER, Basque Institute for Agricultural Research and Development, Department of Forest Sciences, Bizkaia, Spain. ⁵Helmholtz Centre for Environmental Research-UFZ, Halle, Germany. ⁶German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. ⁷INRAE, UEF, Cestas, France. ⁸Granja Modelo, HAZI, Arkaute, Spain. ⁹Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA. ¹⁰Forest Research Centre, School of Agriculture, University of Lisbon, Lisbon, Portugal. ¹¹Research Centre AgroFoodNature, HOGENT University of Applied Sciences and Arts, Ghent, Belgium. ¹²Sustainable Forest Management Research Institute (iuFOR), University of Valladolid, Palencia, Spain. ¹³Institute of Biology, Leipzig University, Leipzig, Germany. ¹⁴Forest Research Institute, Hellenic Agricultural Organization Dimitra, Thessaloniki, Greece. ¹⁵INRAE, UEVT, Antibes Juan-les-Pins, France. ¹⁶Department of Forest Protection and Wildlife Management, Mendel University in Brno, Brno, Czech Republic. ¹⁷Institute of Forest Ecology, Department of Ecosystem Management, Climate and Biodiversity, BOKU University, Vienna, Austria. ¹⁸SRAAC, Azores Regional Ministry for Environment and Climate Change, Angra do Heroísmo, Azores, Portugal. ¹⁹Swedish University of Agricultural Sciences, Umeå, Sweden. ²⁰INRAE, University of Bordeaux, BIOGECO, Cestas, France. ²¹Department of Biological Sciences, Royal Holloway University of London, Egham, UK. ²²Department of Agricultural, Food and Forest Sciences, University of Palermo, Palermo, Italy. ²³INRAE, BEF, Nancy, France. ²⁴Department of Plant Production and Forest Resources, University of Valladolid, Palencia, Spain. ²⁵Forest Research, Northern Research Station, Roslin, UK. ²⁶CNR-IBE, Consiglio Nazionale delle Ricerche, Istituto per la BioEconomia, Sassari, Italy. ²⁷ONF, UMR 0588 BioForA, Orléans, France. ²⁸Department of Earth & Environmental Sciences, KU Leuven, Leuven, Belgium. ²⁹Leuven Plant Institute, KU Leuven, Leuven, Belgium. ³⁰Institut pour le Développement Forestier (IDF), Paris, France. ³¹Centre for Forest Research, Université du Québec à Montréal, Montreal, Quebec, Canada. ³²Smithsonian Environmental Research Center, Edgewater, MD, USA. ³³Ontario Ministry of Natural Resources and Forestry, Sault Ste. Marie, Ontario, Canada. ³⁴Earth and Life Institute, UCLouvain–Université Catholique de Louvain, Louvain-la-Neuve, Belgium. ³⁵Forest Research, Alice Holt Lodge, Farnham, UK. ³⁶AGACAL-Centro de Investigación Forestal de Lourizán, Pontevedra, Spain. ³⁷Institute of Forest Science (ICIFOR-INIA), CSIC, Madrid, Spain. ³⁸GAN-NIK, Pamplona, Spain. ³⁹Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany. ⁴⁰Natural Resources Institute Finland (Luke), Helsinki, Finland. ⁴¹DROTRH, Ponta Delgada, Portugal. ⁴²Forest & Nature Lab, Department of Environment, Ghent University, Melle-Gontrode, Belgium. ⁴³Department of Geosciences and Natural Resource Management, University of Copenhagen, Frederiksberg, Denmark. ⁴⁴e-mail: laurent.augusto@inrae.fr; marie.charru@agro-bordeaux.fr

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Methods

Experimental networks and tree species

Our study was based on complementary sets of forest sites (EAN, TDN, SBD, TED), their common features being: (1) spread across large-scale geographical regions; and (2) composed of common gardens⁵¹ with at least two different tree species compared. In each common garden, characterized by homogeneous conditions, several monospecific stands were installed by planting only one tree species by stand. All stands within a given site were installed and managed identically. In total, tree growth was assessed in 1,262 monospecific stands distributed over 160 common gardens (hereafter referred to as sites) located mainly in Europe, but also in all other forested continents (Supplementary Methods 3). Together, these sites encompass large ranges of climatic conditions and soil properties (Supplementary Methods 4 and Supplementary Table 1). In total, our study comprised the growth data about 223 tree species representing 166 angiosperm species and 57 gymnosperm species, 114 genera and 42 families (mainly, in decreasing order of abundance: Pinaceae, Fabaceae, Fagaceae, Myrtaceae, Cupressaceae, Betulaceae, Malvaceae, Meliaceae and Sapindaceae). These tree species are representative of the main plant functional types (that is, broadleaf species: 59% deciduous and 41% evergreen; needleleaf species: 10% deciduous and 90% evergreen). The studied tree species are also representative of the main mycorrhizal symbioses (ectomycorrhizal, 20% and 75% in angiosperms and gymnosperms, respectively; arbuscular mycorrhizal, 65% and 25% in angiosperms and gymnosperms; mixed preference for mycorrhizae, 15% in angiosperms), and included tree species with N-fixing symbioses (20%).

EAN. The EAN, also known as the REINFORCE experimental network (<https://reinforce.iefc.net/en>)⁵², is composed of 38 common gardens found across the European Atlantic region. The EAN constitutes a gradient of latitude (38.7–56.5° N) and climatic conditions (Supplementary Table 1), from Portugal to Scotland. The common gardens were installed in 2011–2013 and monitored afterwards with common protocols. Each common garden had 2,000 trees and 37 common tree species (each having several geographical provenances) planted in an area (as flat and homogeneous as possible) of about 2 ha. All of the seedlings were produced in the same nursery at the same time, and their vigour and homogeneity were checked by the coordinators of the network before being sent to the different common gardens.

Among the tree species of the EAN, for our study we chose 23 tree species (*Acer pseudoplatanus*, *Betula pendula*, *Calocedrus decurrens*, *Castanea sativa*, *Cedrus atlantica*, *Cupressus sempervirens*, *Eucalyptus nitens*, *Fagus orientalis*, *Fagus sylvatica*, *Larix decidua*, *Liquidambar styraciflua*, *Pinus nigra*, *Pinus pinaster*, *Pinus sylvestris*, *Pinus taeda*, *Pseudotsuga menziesii*, *Quercus ilex*, *Quercus petraea*, *Quercus robur*, *Quercus rubra*, *Robinia pseudoacacia*, *Sequoia sempervirens*, *Thuja plicata*) based on several selection criteria, including: (1) species that have enough trait values reported in the literature (for example, leaf nutrient content and photosynthetic capacity); (2) having a diversity of plant functional types (that is, broadleaf species versus needleleaf species, deciduous versus evergreen, early- and late-successional species⁵³, N-fixing species or not and different mycorrhizal symbioses) and taxonomic families; and (3) species with a good survival rate in the network, implying that species that were planted outside their ecological niche were not retained (for example, *Ceratonia siliqua* and *Pinus caribaea*; Supplementary Note 2). We selected only one provenance per species based on several criteria (for example, survival rate, data availability and so on; Supplementary Note 3), one criterion being that we chose preferably a provenance that was within or close to the European Atlantic region or (for non-European species) having a climate similar to those of the European Atlantic region. A provenance of a given tree species was not replicated, except for four species (*B. pendula*, *C. atlantica*, *P. pinaster* and *Q. robur*) that were replicated three

times in each common garden. We used these replicates to exclude the common gardens that showed spatial heterogeneity, as quantified by the coefficient of variation of tree growth among replicates of a given provenance (in the retained sites, $CV = 26.6 \pm 2.7\%$). We also excluded a few common gardens where catastrophic events (disease problems, exceptional drought just after tree planting or destruction of most seedlings by dense populations of herbivores), caused very low survival and made it difficult to obtain reliable growth data. Finally, data from three common gardens were merged and considered as one single common garden because these sites were located next to each other (distance < 1 km). All in all, we retained 32 sites. The dataset comprised 139,049 values of total tree height from 18,576 different trees.

TDN. The TDN is a global network of forest diversity experiments (<https://treedivnet.ugent.be>)^{54,55}. We selected sites from this network with the following criteria: (1) a limited number of sites that were located in the same areas as the EAN to avoid giving a high statistical weight to the European Atlantic region; (2) the tree species included in the experimental design are species for which trait data are available in the literature; and (3) stands were planted before 2010 to have growth data on young adult trees¹⁶. On the basis of these criteria and the response we received from their principal investigators, we retained 14 sites in Europe and Northern America (Supplementary Table 1 and Supplementary Methods 3). It is noticeable that the TDN sites are often (that is, 10 sites out of 14) located on land that was previously dedicated to agriculture (that is, fertilized croplands or grasslands). In each site, there were 3–12 different tree species, growing in monospecific stands, resulting in 88 site-species combinations. The choice of the planted tree species was made by each site principal investigator, based on knowledge of the ecological niche of tree species, and their suitability to local environmental conditions. Tree species were replicated at least twice in each site (except in one site where there was no replication). The dataset comprised 81,932 tree height measurements from 19,778 different trees.

SBD. The SBD originated from a study⁵⁶ that investigated the influence of tree functional traits on soil organic carbon, but which also used stand biomass values when available, as an explanatory variable. After assessing the data suitability, we extracted data from this publication that contained biomass information for 76 sites. We complemented this dataset with biomass values from 28 sites, provided by some authors of the present study or found in recent publications (Supplementary Note 4), giving 104 sites worldwide (Supplementary Methods 3). In each site, there were 2–14 different tree species growing in monospecific stands (mean value: 3.5 ± 0.2 tree species per site), generally following a common garden design⁵⁶. Stands that were described as unhealthy or containing important canopy gaps were not retained. In total, the SBD represented 359 site-species combinations. In contrast to EAN and TDN data that were successive surveys of identified trees, the SBD contained only one survey of aboveground tree biomass at the stand scale. For the SBD, the growth rate was estimated as the stand biomass divided by the stand age, and was consequently the mean rate of net biomass accumulation (see below).

TED. Because the EAN–TDN–SBD data were more representative of Mediterranean forests, temperate forests and boreal forests than of tropical forests, we complemented our study with data about this latter biome through an investigation of the literature. As field experiments with a common garden design with mature monospecific stands are rare in tropical studies, we used inclusion/exclusion criteria that were more flexible than for our other datasets (that is, growth metric, tree age). We retained 6 publications (Supplementary Note 4) that contained usable growth data about 10 sites (Supplementary Methods 3). After having checked that functional trait values existed in the literature (see below), we retained 71 distinct tree species and 196 site-species combinations

(Supplementary Table 1). In each TED site, there were 4–37 different tree species (19.6 ± 4.8 species per site) growing in monospecific stands.

Data about tree growth

Tree growth data in the EAN and TDN were based on surveys of young adult trees, enabling the quantification of growth rate in post-sapling stages. On the other hand, the SBD compiled information about above-ground net biomass accumulation during adult tree ageing. Finally, the TED were informative of growth dynamics of tropical tree species at different tree development stages (from saplings to adult trees). Thus, these independent datasets were complementary to each other, as it is well-established that the ontogenetic stage is an important factor driving trait-growth relationships^{57,58}.

Tree growth values were calculated based on the difference between two surveys at the tree scale for EAN and TDN data, on one survey at the stand scale for SBD data (by dividing the stand biomass value by the stand age) and on the available metric for TED.

Tree height growth (EAN, TDN). The quantification of tree growth rate was based on tree height, a variable that was monitored in all common gardens (contrary to other metrics such as biomass, volume or stem diameter). Growth rate values (cm yr^{-1}) were calculated as the difference in tree height between two surveys (each carried out during the dormant season for vegetation), taking into account the number of growing seasons between the two surveys. This method was compared with a method that estimates tree growth simply as the height:age ratio and found good consistency ($r = 0.97$). Nevertheless, we preferred to quantify tree growth based on two surveys because it enables excluding the period after plantation (that is, 1–2 years), which is often problematic for seedlings (transplant shock). We chose the final survey based on available data for each site, trying to find a trade-off between the quantity of available data and the duration of growth (that is, the time difference between the two surveys). The measurement period was generally between 3 and 9 years (41 sites) but was shortened to 1–2 years when necessary (5 sites). Taking into account the start of monitoring, growth data were mainly representative of young adult individuals (37 sites where age > 5 years; ontogenetic stage defined previously¹⁶), with a small proportion of saplings (9 sites; 1 year < age ≤ 5 years), but no seedlings (0 site; age ≤ 1 year).

Before analysis, data were curated with several quality controls. Notably a few negative values of tree growth were observed so we removed these trees, which apparently 'shrank' probably due to dieback of their top (~4% of trees). In the case of multistemmed trees (around 2% of trees), we selected the height value of the tallest stem as the tree height value. We also removed a few site-species combinations for which not enough surviving trees remained (that is, $n < 5$). In the EAN dataset, we observed that some trees (around 12%) died after the second survey retained in our study. For each site, we tested the extent to which these nearly dying trees might have biased our results, for example, due to a depressed growth rate before death. Comparing growth rate values with or without these nearly dying trees showed that there was a significant difference (Dunnett test on ratio values, and linear regression analysis testing for both zero intercept and unit slope) for only one common garden when growth rate was assessed in original values (that is, cm yr^{-1}), and that there was no difference at all when standardized values were used (see the 'Data analyses' section). On the basis of these tests, we decided to not remove trees that died after the second survey, except for the common garden mentioned above. After all of these quality checks, the growth rate was estimated for each site–species combination as the arithmetic mean height growth value of all trees.

SBD. The SBD contained data of standing aboveground biomass (in $\text{t}_{\text{dry weight}} \text{ ha}^{-1}$). Considering the tight allometric relationships that exist among tree structural components (stem, stump, branches, roots and so on)^{59–62}, we assumed that aboveground biomass was well

representative of stand total biomass. This dataset is based mainly on quite old common gardens (46 ± 3 years; 25–63 years between the first and third quartiles) for which generally only one survey of biomass measurements was available. When needed, stand aboveground biomass was estimated using specific or generic⁶³ allometric relationships. The estimated values were evaluated using an independent dataset⁶⁴ and showed satisfactory consistency (Supplementary Methods 5). The growth rate was calculated by dividing standing aboveground biomass by stand age. As there was no information about tree mortality, the SBD growth rate ($\text{in t ha}^{-1} \text{ yr}^{-1}$) was the mean rate of net biomass accumulation.

TED. While growth data were homogeneous in other datasets (that is, $\text{cm}_{\text{height}} \text{ yr}^{-1}$ for EAN + TDN, $\text{t ha}^{-1} \text{ yr}^{-1}$ for SBD), growth data for TED used several metrics (relative growth rate, $\text{cm}_{\text{height}} \text{ yr}^{-1}$, $\text{cm}_{\text{diameter}} \text{ yr}^{-1}$, $\text{kg}_{\text{tree}} \text{ yr}^{-1}$). This limitation implied that, contrary to other datasets (which could be used with original values and mixed linear modelling to explore growth–trait–site interactions; see the 'Data analyses' section), TED data were used mainly for growth–trait relationships.

Trait data

The functional traits that were studied in our four datasets are known to be key traits in plant functioning^{65–67}: plant maximal height (m), plant longevity (years), successional stage (integer from 1 to 5; from pioneer species to climax species), seed mass (mg; log-transformed to avoid data skewness), wood density (mg cm^{-3}), foliage and root element content (C, N, P, Ca; mg g^{-1}), SLA ($\text{mm}^2 \text{ mg}^{-1}$), maximum photosynthetic capacity (A_{max} ; $\mu\text{mol g}^{-1} \text{ s}^{-1}$) and SRL (mg g^{-1}). We used mass-based values of A_{max} and foliage composition but not area-based values because the former generally explain plant growth, and functioning in general, better than the latter^{27,68–70}.

Trait values were obtained from a previous global scale study of 178 different tree species⁵⁶. To fill the data gaps, we first complemented this database with trait values (if any) found in the publications containing our growth data, and in 76 publications and a few specialized websites (Supplementary Note 5). Wood carbon values were extracted from an open database⁷¹. When several values existed for a trait–species combination, we retained the mean value. In a second step, we measured traits for the 23 tree species of the EAN. To do this, we sampled one common garden (in south-western France) for mature foliage ($n = 36$ per species), living branches ($n = 3$ per species) and living fine roots ($n = 6$ soil cores; roots of <2 mm in diameter). Samples were analysed (C, N, P, Ca; for foliage and roots) and measured (wood density (WD), SLA, SRL) according to standard methods^{72,73}. Data obtained from field samplings showed satisfactory consistency with the initial database⁵⁶ ($r = +0.55$ to $+0.95$ for WD, SLA and element contents in leaves; regression slope values were close to 1) and we kept the measured values for our study. For four tree species of the EAN (*C. decurrens*, *C. atlantica*, *E. nitens*, *F. orientalis*), we had no A_{max} value so, in the field, we also measured their maximum photosynthetic capacity under good conditions (cumulated precipitation in the week before sampling = 34.5 mm; soil water content during measurements = 60–70% of the soil water holding capacity; vapour pressure deficit = 0.64–1.38 kPa; air temperature = 16–25 °C; photosynthetically active radiation > 1,500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$; data from the XyloSylve monitoring platform, 1.5 km from the common garden). Finally, for genera with several tree species, we complemented trait values by replacing missing values by the mean value of their genus, provided that at least two values were available and that they had a similar magnitude. This latter gap-filling represented a small proportion of trait values (proportion of estimated values for a given tree species: median = 0%; mean = 5%).

Trait values were generally highly interrelated (Supplementary Methods 6), which is a common pattern in functional ecology^{11,56,74,75} as plant functions are dependent on each other, implying trade-offs and high levels of correlation among traits^{33,65,67,76–79}. Owing to this strong

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interplay among functional traits^{24,80}, and because data about nutrient content of fine roots were scarce for tree species of TDN and SBD, we restrained the use of most root traits to EAN results. Trait value distribution was comparable among datasets (Supplementary Table 2).

Site data

We collected auxiliary data related to factors (hereafter, site properties) that may affect tree growth, notably climate, atmospheric N deposition, past land-use and soil properties. At the site scale, the collected information was: site name and location (longitude and latitude), elevation, mean annual values of temperature and precipitation (MAT, MAP), past land-use and fertilization history (information provided by the principal investigator of each site), soil name and soil parent material, topsoil clay or sand content, and other topsoil properties (for example, pH, cation-exchange capacity and its 'base' saturation value, total content of phosphorus, soil organic carbon content (SOC) and its ratio with total nitrogen (C/N), and soil water-holding capacity). Original site data were obtained differently for our four networks of common gardens: EAN site data were obtained using a shared protocol and soil analyses were carried out at a single laboratory. Data about TDN sites (and the few SBD sites that complemented the original dataset) were provided by the principal investigator of each site, when requested data were available. Data of most SBD-TED sites were extracted from publications⁵⁶, with the same availability limitation. This process of data acquisition implied that site data were homogeneous in the EAN dataset, whereas they contained a varying proportion of missing values and there were some heterogeneities in the methods used (for example, for soil phosphorus analyses) for TDN, SBD and TED.

Owing to missing auxiliary data in the TDN-SBD-TED datasets (climate, elevation and soil properties), we complemented them from external sources using the latitude-longitude coordinates of the sites. Similarly, we used global datasets to include variables that were never measured in the field (for example, atmospheric N deposition). The data sources used were taken from the literature (N deposition⁸¹; soil properties^{82,83}) or from large-scale databases. Elevation values were obtained from the Enhanced Shuttle Land Elevation Data (<https://www2.jpl.nasa.gov/srtm>). For climatic variables, we collected data for mean annual values of precipitation or temperature (MAP, MAT; <http://worldclim.org>), potential evapotranspiration and aridity index (<https://cgciarcsi.community>). For sites in Europe, we also collected climate data from the Climate Downscaling Tool (<https://www.ibbr.cnr.it/climate-dt>), from the B4EST European project (<https://b4est.eu>), which enables one to work with scale-free queries, customized periods (for this study, the period of tree growth in our datasets) and many other variables (for example, the sum of degree-days above 5 °C). The B4EST climate values were consistent with those obtained from other sources and were also consistent with data from the XyloSylve monitoring platform. The quality of the external sources was checked by comparing them with the measured values (when they existed) and showed acceptable consistency for most variables ($r = +0.67$ to $+0.90$ for MAT, MAP, soil pH and soil clay or sand content; regression slope values were close to 1) but not for some soil properties (for example, P content or cation-exchange capacity), which was consistent with previous large-scale studies^{18,84}. We observed a high level of covariation among several collected site variables. For example, MAT was highly correlated with potential evapotranspiration (PET; $r = +0.84$), sum of degree-days above 5 °C ($r = +0.85$) and mean temperature during the growing season ($r = +0.90$). Similarly, the soil water holding capacity was strongly controlled by soil clay content ($r = +0.86$) and sand content ($r = -0.82$). As highly correlated variables can bias methods of model selection⁸⁵, we retained only a few variables to describe climatic conditions: MAT and MAP (which are commonly used in ecology⁸⁶⁻⁸⁹) and the climate factor index (hereafter, f_{climate})⁹⁰. The climate factor index is based on monthly climatic conditions of a given site, and increases with concomitant water availability (that is, the precipitation:PET ratio)

and warm temperatures (Supplementary Methods 7), conditions that favour biological activity⁹¹ and tree growth¹⁸. This f_{climate} index is normalized to between 0 (harsh conditions) and 1 (optimal conditions)¹⁸ and has already been tested at national or global scales^{18,91,92}. We applied the same parsimonious approach for soil data, retaining clay content, SOC content, P content, C:N ratio and pH as explanatory variables. In addition to continuous climatic variables, we used a categorical approach to assess the influence of biomes on growth-trait relationships. In practice, we grouped all sites into three classes based on their latitude absolute value: tropical sites ($|\text{latitude}| \leq 23^\circ$), high-latitude sites ($|\text{latitude}| \geq 45^\circ$; generally cold sites⁹³) and intermediate sites (generally warm temperate sites).

With the scope of discussing our results in a global perspective, we finally collected data for all forests worldwide. Net primary production (NPP) of terrestrial ecosystems was retained using TERRA/MODIS data (https://neo.gsfc.nasa.gov/view.php?datasetId=MOD17A3H_Y_NPP). We averaged the annual NPP of all grid cells based on the 2010s decade. We also calculated the f_{climate} index at the global scale. To enable relevant comparisons with our results about forests, we retained in global data only cell grids with at least 90% of their surface area covered by forest ecosystems (land-use data)⁹⁴. At the global scale, the forest ecosystems are characterized by high NPP, caused by favourable climatic conditions, at low latitudes (Supplementary Methods 8).

Data analyses

Identifying the factors influencing site productivity. We first explored the drivers of tree growth with data from the EAN, because these are derived from common gardens sharing the same studied tree species and protocols (29 sites with enough data). The influence of functional traits (for example, leaf N content), site properties (for example, MAT, soil pH) and site productivity were assessed using three independent approaches (see below). We defined site productivity as the arithmetic mean value of the mean growth rate (cm yr^{-1}) of the n tree species studied in this site:

$$\text{site productivity} = \sum_{i=1}^{i=n} \text{species}_i \text{ mean growth rate}/n \quad (1)$$

The three approaches for data analysis were: (1) mixed linear models (lme4 R package⁹⁵; assigning the site identity as a random effect), (2) linear models based on the Akaike information criterion for the selection of the best model (ols_step_forward_aic function of the olsrr package⁹⁶) and (3) nonlinear random-forest analyses (randomForest package⁹⁷). For the latter, we followed a backward elimination method⁹⁸ to select by iterations the best random forest model, which consists of eliminating the least important variables until out-of-bag prediction accuracy drops. The importance of each variable in the retained model is assessed based on the percentage increase of mean squared error (%IncMSE). The threshold value above which a variable is considered as important is not consistent among studies using the random forest approach^{99,100} and, consequently, we defined four levels of confidence to interpret our results: low ($2\% \leq \% \text{IncMSE} < 5\%$), moderate ($5\% \leq \% \text{IncMSE} < 10\%$), high ($10\% \leq \% \text{IncMSE} < 20\%$) and very high ($\% \text{IncMSE} \geq 20\%$). Considering all tree species of the EAN together, the soil C:N ratio and f_{climate} were the most influential factors of site productivity (Extended Data Table 1).

We quantified site productivity in other datasets using the same method as for EAN sites (equation (1)). As TDN data (and data from a few TED sites) had the same metric of tree growth as EAN data (that is, tree height growth, in cm yr^{-1}), we were able to present merged results (that is, EAN + TDN + TED). As the growth metric of SBD was different (in $\text{t ha}^{-1} \text{yr}^{-1}$), these results were consequently presented separately. Contrary to other datasets, we could not calculate site productivity in all TED sites because the growth metric varied from site to site. Thus, for some TED sites, only growth-trait relationships were investigated and no growth-trait-site interaction was tested.

Standardizing growth rate. The tree growth rate does not depend on functional traits alone, but is also strongly dependant on site properties (that is, local climate and soil fertility)^{19,30,101–104}. Indeed, when we investigated the main factors influencing tree growth, all of our results confirmed foresters' knowledge that site productivity was the main factor controlling species growth: site productivity was selected first by a mixed linear model ($\chi^2 = 63.2$), a predictive linear model (contribution to explained variance = 29.1%) and a non-linear random forest model (%IncMSE = 55.3%). In addition, site productivity was much more predictive than the other variables (e.g. leaf C:N, leaf C, wood density) selected by these three models ($\chi^2 = 22.0$; explained variance = 10.4%; %IncMSE = 34.2%). To remove the prominent influence of site productivity and hence to enable comparisons among species across all sites, we standardized the original values of tree species growth. To do so, we tested two different approaches: the z-score¹⁰⁵ and a log growth ratio (see equation 2). The two metrics were highly correlated to each other ($r = +0.86$), but the log growth ratio metric was more suitable for our data because (1) the z-score cannot be calculated for sites with only two tree species (Supplementary Note 6) and (2) the values transformed as log growth ratios showed better distributions as evaluated by normality tests (Lilliefors and Shapiro-Wilk tests¹⁰⁶) and QQ plots. We consequently standardized the original values using the log growth ratio metric, which consisted in dividing the absolute values of tree species growth by the site productivity value. This ratio was then log-transformed (natural logarithm)¹⁰⁷:

$$\begin{aligned} \text{log growth ratio} \\ = \log \left(\frac{\text{individual value}}{\text{population}_{\text{arithmetic.mean}}} \right) \\ = \log \left(\frac{\text{species growth rate}}{\text{site productivity}} \right) \end{aligned} \quad (2)$$

The log growth ratio metric is very similar to the centred log-ratio metric¹⁰⁸, the later using the geometric mean instead of the arithmetic mean. We preferred to use the arithmetic mean because (1) the geometric mean might be biased if one single value of the studied population is nil or very close to zero (which happens sometimes when comparing the growth rate of different plant species); and (2) the arithmetic mean is consistent with the site productivity metric (equation (1)).

Positive standardized growth rates (that is, log growth ratio values) indicate that these species had a higher growth rate than the average growth of the site, and negative standardized values indicate a lower growth rate than average for the site. For a few tree species that grew extremely slowly compared with the other species within the same site, this formula led to very negative values of standardized growth, with skewness problems of data distribution. Consequently, we corrected extreme values of standardized growth to -2.0 based on assessments of data distribution (histograms; Shapiro-Wilk tests).

An example of a data subset is presented, showing how the transformation of growth values removed the relationship between tree species growth and site productivity (Supplementary Methods 9a,c). An example of relationships between a functional trait and growth is also presented (Supplementary Methods 9b,d). Note that standardization of values was done for subsets of data with no missing value implying that, when there was a missing trait value for a tree species of a given site, the growth values of this site were standardized without taking into account this tree species (an example is provided in Supplementary Table 3). It is also noticeable that the method used for data standardization, while improving statistical power, enabled the study of interactions with possible confounding factors¹⁰⁹ (see below).

Defining acquisitive species and conservative species. As trait values constitute ecological gradients^{24,110,111}, continuous data analyses

are adequate to test our hypothesis (see the next section). Nevertheless, to test our hypothesis, we used in addition categorical analyses by classifying tree species into acquisitive species or conservative species based on their trait values. Tree species were considered to be acquisitive species if they have high values of photosynthetic capacity (A_{\max}), SLA and leaf N content^{10,24,27}. We prioritized A_{\max} to class tree species because this trait is integrative of plant functioning^{24,27,112}. For tree species without an A_{\max} value, we used the SLA value or the leaf N value instead. The procedure enabled the classification of 212 tree species, representing 98.3% of growth data (-87%, -10% and -1% of data based on A_{\max} , SLA and leaf N, respectively). However, in practice, there is no functional threshold value between acquisitive species and conservative species as they are distributed along trait gradients^{24,110,111}. Following previous studies¹¹³, we defined our species classes based on value distributions of our global database of functional traits. We defined acquisitive species and conservative species, with limit values close to median values ($A_{\max} = 0.1 \mu\text{mol g}^{-1} \text{s}^{-1}$; SLA = $13.3 \text{ mm}^2 \text{ mg}^{-1}$; leaf N content = 19.3 mg g^{-1}). Although these threshold values are consistent with the distributions reported in other studies carried out at the global scale (figure 2 in refs. 110,111), we performed a sensitivity analysis to assess to which extent changing the chosen values may affect our results (see below).

With this trait-based classification, acquisitive species tended to be represented more in broadleaf deciduous species than in needleleaf evergreen species, whereas conservative species included both broadleaf species and needleleaf species (Extended Data Table 3 and Supplementary Note 7). Similarly, both groups contained arbuscular mycorrhizal species and ectomycorrhizal species. Although there was no significant difference in shade tolerance and both groups contained early-successional species (for example, *Pinus* species and *Betula* species), acquisitive species were on average characteristic of earlier successional stages than conservative species. Finally, acquisitive species were shorter-lived than conservative species, which is consistent with how different ecological functions (that is, growth, survival, reproduction) are coordinated in woody plants⁴⁰.

Investigating site–trait interactive effects on tree growth. We expected that the role of functional traits in tree growth was neither unidirectional (that is, always positive or negative) nor systematic (that is, the traits correlated with tree growth were not systematically the same across different regions), but that it depended on environmental conditions^{12,15,36,58,114}. To investigate these possible site–trait interactions, we used three complementary approaches: (1) interactions were statistically tested using mixed models⁴⁵; (2) interactions were visually illustrated by regressing linear models between site productivity and growth–trait correlation values; and (3) the slope values of the regression between site productivity and standardized growth were compared for acquisitive species and conservative species.

(1) Mixed models were fitted on standardized values to remove the prominent effect of site productivity (equation (2)) and therefore enable comparisons among sites. The mixed models were built with site identity and tree species identity as random factors, as follows:

$$\text{growth} \sim \text{trait} + (\text{trait} \times \text{site}_{\text{prod}}) + (1|\text{site}_{\text{ID}}) + (1|\text{species}_{\text{ID}}) \quad (3)$$

where $\text{site}_{\text{prod}}$ is the site productivity (equation (1)), site_{ID} is the site identity and $\text{species}_{\text{ID}}$ is the species identity.

(2) For common gardens where it was possible to quantify a site productivity metric (in cm yr^{-1}) and that included at least ten different tree species, we graphically illustrated the extent to which the influence of trait values depended on site productivity by regressing a linear relationship between site productivity and the [species growth–trait value] correlation value of the same site:

$$\text{corr}\{\text{growth}_{\text{species}} - \text{trait}_{\text{species}}\} = f(\text{site productivity}) \quad (4)$$

with $\text{corr}\{\text{growth}_{\text{species}} - \text{trait}_{\text{species}}\}$ = correlation value (Pearson method) between species growth rate and species trait value; correlations being performed site by site.

This case corresponded to all EAN sites and a few sites from TDN and TED. Nevertheless, it was not possible to include TDN and TED *r* values to fit the linear regression because the probability of having by-random high *r* values tends to increase with decreasing size of data^{115,116}, implying that correlations obtained from TDN (10–12 species per site) or from TED (up to 34 species per site) were not directly comparable to correlations obtained from EAN (23 tree species per site). Nevertheless, even if TDN and TED *r* values were not used along with EAN *r* values to statistically test the interactions between site properties and $\text{growth}_{\text{species}} - \text{trait}_{\text{species}}$ relationships, in the graphs, we added the results from the TDN–TED sites that contained at least ten tree species.

(3) We tested whether the functional traits and site properties interactively influenced tree growth by comparing the slope value of the relationship between site productivity and tree growth (in standardized values), taking into account our two tree species classes (that is, acquisitive versus conservative, with respectively high and low values of A_{max} , SLA and leaf N). To do so, we built one linear regression model with interaction with site productivity, and a second model without interaction (using the *aov* function). Then, the two regression models were compared using covariance analysis (using the *anova* function). We concluded that a site–trait interaction existed if the slope of the regression was significantly different between the acquisitive tree species and the conservative tree species. For this approach, sites that included only acquisitive species, or only conservative species, were not taken into account in data analyses.

Analysing possible misleading effects or confounding effects in data analyses

Assessment of the datasets. The first three datasets that were built (EAN, TDN, SBD) are complementary in terms of tree age and climatic conditions. As the collected data lacked tropical data, a fourth dataset (TED) was built to supplement the three others, and the final data were representative of all climates (Supplementary Methods 10). Nevertheless, although the TED dataset was useful as complementary data, it is less homogeneous as it is based on several growth metrics (see above) and it includes sites with a very different number of tree species (Supplementary Methods 11). The TED results, when presented independently from other data, should consequently be interpreted with caution.

Moreover, even as a data supplement, we cautiously combined TED data with other data. In most cases, we found no risk of biasing the results. An exception was the study of the interaction between site productivity and growth–trait relationships in young sites. Indeed, two sites showed being much more productive than the rest of the studied population (Supplementary Methods 12). As outliers of a predictor variable may induce spurious correlations^{116,117}, these two sites were not used during data analyses implying possible interactions with site productivity.

Interactions with tree age. It is well-established that tree growth rate varies as a function of tree age¹¹⁸ and we consequently tested this possible effect. For the young stands (EAN and TDN datasets; age at tree measurement, 3–24 years), we found no significant effect ($P > 0.1$), neither considering site productivity (mixed model: $P = 0.555$, $t = +0.60$, $\text{d.f.} = 21.5$) nor considering tree growth at the stand scale ($P = 0.788$, $t = -0.27$, $\text{d.f.} = 31.0$). We also checked whether an interaction with tree species might exist by plotting the growth–age curve for each of them, and found no clear trend. We finally concluded that there was no substantial age effect in our data about young trees.

By contrast, data about mature stands showed a clear age effect on tree growth (Supplementary Methods 13a). This effect had no influence on results when data were standardized because the standardized values are species growth rate (or species trait value) that are relative

to the site productivity (equation (2)). Conversely, the age effect may affect the results when the site productivity is used as a predictor (equation (3), Table 1 and Fig. 3d), and we corrected growth values in these cases. To do so, we first fitted a nonlinear regression between forest age and productivity (Supplementary Methods 13a). The modelling efficiency value of the fitted regression was 0.46 (ref. 119). We then calculated a standardized growth rate, using 40 years old as a reference (which was close to the mean age value of SBD stands of 41.8 years):

$$\text{growth}_{40} = \text{growth}_{\text{fitted},40} \times \left(\frac{\text{growth}_{\text{original}}}{\text{growth}_{\text{fitted}}} \right) \quad (5)$$

where growth_{40} is the growth estimated at 40 years old, $\text{growth}_{\text{fitted},40}$ is value of the regression at age 40 years ($\text{growth}_{\text{fitted},40} = 4.446 \text{ t ha}^{-1} \text{ yr}^{-1}$), $\text{growth}_{\text{original}}$ is the growth original value and $\text{growth}_{\text{fitted}}$ is the value of the regression at the actual age of the stand.

The distribution of the corrected values is presented in the Supplementary Methods 13b.

Intraspecific differences. Different populations of a given tree species may differ in terms of trait values and growth rate due to genetic differences and plasticity to local conditions¹²⁰. In this study, the effect of intraspecific variability was not quantified, as the interspecific influence on growth was the main topic. Although it is well established that intraspecific variability exists, it is also observed that inter-specific variation can be much larger than the intraspecific variation^{121,122}. As such, retaining only the mean trait value of each plant species is considered to be a relevant and reliable approach in large scale studies^{2,110,111,122–124}, even with partly imputed data^{74,125}. In the present study dedicated to interspecific variation, the coefficient of variation (CV) of trait values was 25% for wood density and ranged from 42% to 78% for the acquisitive-conservative traits (A_{max} , SLA, SRL, leaf N and P). Conversely, intraspecific variation of traits was found to range from 9% to only 22% of CV for wood density, SLA, leaf N and leaf P^{126–128}, confirming that interspecific variability is larger than intraspecific variability in multispecies studies. Another possible problem is the variability of trait values over plant development¹²⁹ because some trait values found in the literature or trait databases were determined using seedlings and not adult trees¹³⁰. However, it was also shown that trait values at seedling stage are well correlated with trait values at adult stage¹³¹, implying that interspecific rankings are maintained over ontogenetic development¹³².

We used EAN data to evaluate the possible effect of intraspecific variability on tree growth. Indeed, each EAN site contains for each tree species up to eight different provenances. We found that intraspecific variability of tree growth was around fourfold lower than interspecific variability (CV = 17% and 66%, respectively), indicating that the interspecific effect on tree growth was much more important than intraspecific variations. This result is consistent with recent studies^{133,134} showing that provenance is generally a second-order driver of tree growth.

On the basis of these results, the literature results and on published guidelines¹³⁵, we concluded the intraspecific variability of trait values (or of growth rate values) probably had a minor effect on our results.

Ecological niches. One possible pitfall in studies based on common gardens is that some tree species might be planted outside their ecological niche (that is, unfavourable climatic/edaphic conditions), biasing the species growth dynamics. This possible bias was taken into account (1) during the design definition of most common gardens; (2) during data acquisition; and (3) after data acquisition:

At least for the common gardens of the EAN and TDN networks, the principal investigators (who are co-authors of this study) chose tree species not at random but based on their ecological requirements, implying that the planted tree species were expected to be adapted to local conditions.

During data acquisition, we excluded a few tree species with low survival rate (EAN-TDN common gardens) or described as unhealthy (SBD-TED; see the 'Experimental networks and tree species' section above).

Finally, we tested a possible niche effect using our data and quantitative information about ecological niches. To do so, we studied the 23 tree species of the EAN network, which is a network with a factorial design (that is, all tree species are present in all sites). For each tree species, we collected the surface area of the natural niche of the species and (for MAT, MAP and soil pH) the ranges of the species in natural conditions. This data collection was made based on information found in dedicated websites and publications (Supplementary Note 8). Then, for each species–site combination, we evaluated whether the trees were within or outside their niche by checking whether the site conditions (MAT, MAP, soil pH) were within or outside the range of values reported for the species in natural conditions. We also tested whether the ecological range of the tree species (as defined as $\{\text{MAT}_{\max} - \text{MAT}_{\min}\}$, and so on for MAP, soil pH) might explain tree growth. We found that (1) in a majority of cases, tree species were planted in sites where environmental conditions were suitable for them (see the percentage values in Supplementary Methods 14a–d); (2) trees planted in sites where conditions did not comply to the expected species requirements did not grow differently compared with trees planted in suitable conditions (Supplementary Methods 14a–d); (3) tree species with large ranges of ecological niche did not growth faster than tree species with narrow niches (Supplementary Methods 14e–g); (4) tree species with a large spatial niche did not perform better than tree species from small regions (Supplementary Methods 14h); and (5) there was a slight, but significant negative effect of the MAP range value on standardized tree growth (Supplementary Methods 14f). The latter result is mainly due to three tree species with a large MAP range (caused by very high MAP_{max} values; $>2,000 \text{ mm yr}^{-1}$) but having on average a lower standardized growth rate than the other tree species. Although this MAP range effect was significant, it explained less than 1% of the growth variance ($R^2 = 0.7\%$) and became not significant when considering tree species with $\text{MAP}_{\max} \leq 2,000 \text{ mm yr}^{-1}$ (compare with the red line in Supplementary Methods 14f), which is the most common case for temperate-boreal tree species. As a whole, we concluded that the ecological requirements of the studied tree species were fairly well respected and we consequently assumed that the results of the study were not severely biased.

Possible phylogenetic effect. Two tree species may be functionally very different because their most recent common ancestor existed in the far past, enabling its descendants to evolve differently for long times. As such, phylogeny may be a powerful predictor of plant species functioning^{123,136} and, in our case, may have explained tree growth better than functional traits. We tested this possible effect for the EAN dataset because this network has a factorial design. We built a phylogenetic tree for the 23 species of the dataset, which included closely related species (for example, species of the same genus) and evolutionary distant species (for example, angiosperms and gymnosperms). The phylogenetic distance between two species was estimated based on the approach of the most recent common ancestor. The distance between angiosperms and gymnosperms was fixed as 350 million years (Myr) and the distance between Cupressales and Pinales was set at 273 Myr (ref. 137). Within the gymnosperms, the distances among clades down to genera were estimated based on a dedicated study¹³⁸. Similarly, within the angiosperms, we used first the phylogenetic distances among families¹³⁹. For shorter phylogenetic distances (such as between genera of the same family or between two species of the same genus), we used the Angiosperm Phylogeny Website and relevant references^{138,140–142}. We calculated the phylogenetic distance of all possible pairs of tree species ($n = \sum_{i=1}^{i=23} (i - 1)$) and then we tested the extent to which this distance might explain tree growth and trait values. Using a linear plateau regression, we found that the phylogenetic distance had an effect for tree

species that were close to each other in the phylogenetic tree (that is, distance <98 –137 Myr). However, this effect was weak and explained only a very small proportion of the variance, from 1% (for leaf A_{\max} , wood density or SRL; data not shown) to 5–11% (for SLA or leaf N–P; Supplementary Methods 15). These results are consistent with previous studies showing that phylogeny often poorly explains functional traits, site properties or ecosystem functioning^{56,143,144}. On the basis of these results and on the literature, we concluded that, in our study, there was a significant but minor effect of the phylogeny on tree growth.

Possible spermatophyte effect. Our datasets comprise both angiosperm species and gymnosperm species. These two groups are evolutionary and functionally quite different^{145–149}, which might have induced apparent growth–trait correlations without any true functional relationships. We tested this possible effect by investigating the extent to which the growth–trait relationships were observable within a spermatophyte group (that is, only angiosperms or only gymnosperms). We found that growth–trait relationships were generally still significant for most traits (Supplementary Methods 16a,b,d). Similarly, within the angiosperm group, acquisitive species and conservative species showed the same growth trends as for the complete dataset, which was a significantly higher growth rate of the conservative species (Supplementary Methods 16f; not tested within the gymnosperm group due to an insufficient number of acquisitive species). Conversely, the growth–trait relationships were no longer significant, or significant only for angiosperms, for some other traits (Supplementary Methods 16c,e). These results are consistent with studies that explored plant functioning across plant functional types and found weaker or absent relationships for gymnosperms^{150–152}. This pattern can be explained by the level of functional diversity within each group: for six major traits (A_{\max} , SLA, SRL, wood density, and leaf N and P), the range of values was between 59% and 215% higher for angiosperm species than for gymnosperm species (see also supplementary figure 3 of ref. 150 and figure 1 of ref. 151). These ranges of values in the gymnosperm group were probably too narrow for some functional traits to enable isolating a significant growth–trait relationship. Besides, this explanation may also apply to leaf nitrogen (Supplementary Methods 16c) as the data dispersion showed that the overlap between angiosperm data and gymnosperm data was small (38% of the full range, as compared with 53–63% for SLA or leaf P), suggesting that the general effect observed for leaf nitrogen was induced by the comparison of two functionally different clades. As a whole we conclude that, in agreement with the literature^{124,150,151}, whereas the angiosperm–gymnosperm dichotomy strengthens existing function–trait relationships by enlarging the ranges of trait values, these relationships generally remain relevant within a spermatophyte group.

Sensitivity of results to the retained threshold values. We tested the extent to which changing the threshold values retained for classifying tree species (acquisitive species versus conservative species, based on A_{\max} , SLA or leaf N content) would change our results. First, for each of these three traits, we quantified the difference between the percentile 40% and the percentile 60%, which represents the part of a normal distribution where values change most (maximum change range, MCR). In a second step, we defined the ranges of sensitivity analyses by adding or subtracting the MCR value to the threshold value initially retained. This resulted in large changes to the population size of the species classes (up to 3.0-fold; $n = 250$ –747 stands of conservative tree species). These results explain why we did not use larger ranges of sensitivity analyses because the compared classes would have been extremely unbalanced in size, with deleterious effects on the stability of the results. The large changes to the population size of the species classes also highlight that the acquisitive–conservative status of the tree species of the present study should not be used alone for management decisions. Indeed, if

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a dichotomous classification was useful for data analyses, tree species are distributed along ecological and functional gradients, with many species having intermediate positions.

We finally performed the sensitivity analyses by testing the difference between tree species (acquisitive species versus conservative species) with varying threshold values ($n = 5$, including the value initially retained as median value). The results showed that the results were satisfactory, with quite stable slope values (Supplementary Table 4a) and a constant difference of growth rate between acquisitive species and conservative species (Supplementary Table 4b).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The datasets generated in this study (EAN, TDN, SBD, TED) have been deposited in the <https://entrepot.recherche.data.gouv.fr> database (<https://doi.org/10.57745/3OIGHB>; Etalab Open License 2.0, compatible CC-BY 2.0). Data supporting Figs. 1–4 and Table 1 are provided in the Article and its Supplementary Information. There is no restriction on data availability. Source data are provided with this paper.

Code availability

Data were analysed using code developed by authors (R language, v.9.4 and v.4.2.3) and common statistical methods: random forest (randomForest R package, v.4.7-1.1), linear models (olsrr R package, v.0.5.3), mixed models (lme4 R package, v.1.1-32), Kruskal–Wallis test (R core). All analyses are fully described in the Methods. The main R procedures that were used have been deposited in the <https://entrepot.recherche.data.gouv.fr> database (<https://doi.org/10.57745/3OIGHB>). Complementary information is available from the authors on request.

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Competing interests R.B. is employed by a company that works with landowners to implement projects of reforestation or afforestation worldwide. F.J.S.-P. and M.J.R.-L. occasionally advise foresters or landowners. The other authors declare no competing interests.

Additional information

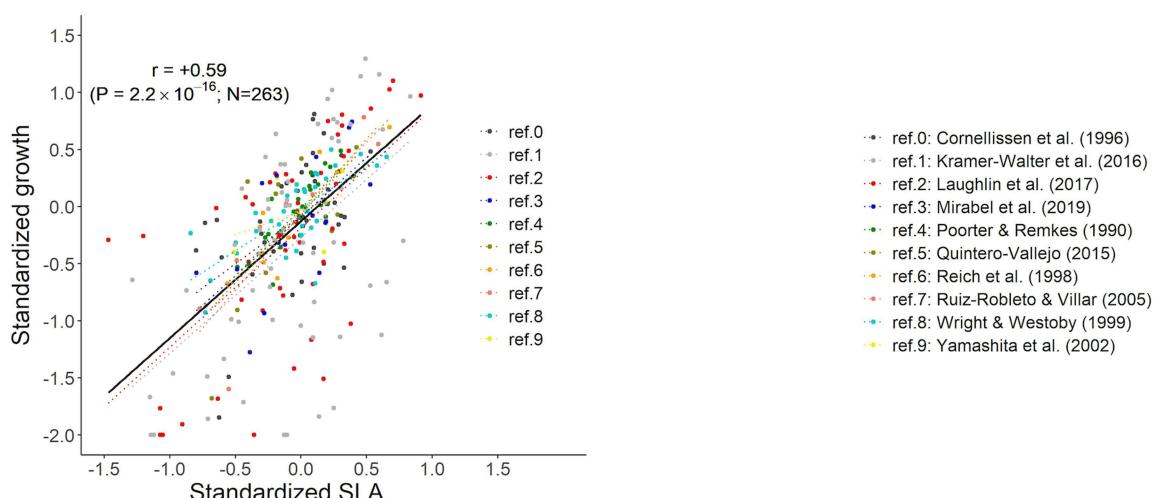
Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-025-08692-x>.

Correspondence and requests for materials should be addressed to L. Augusto and M. Charru.

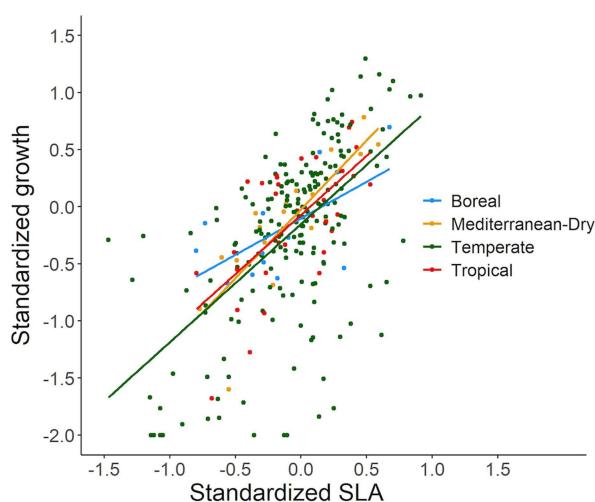
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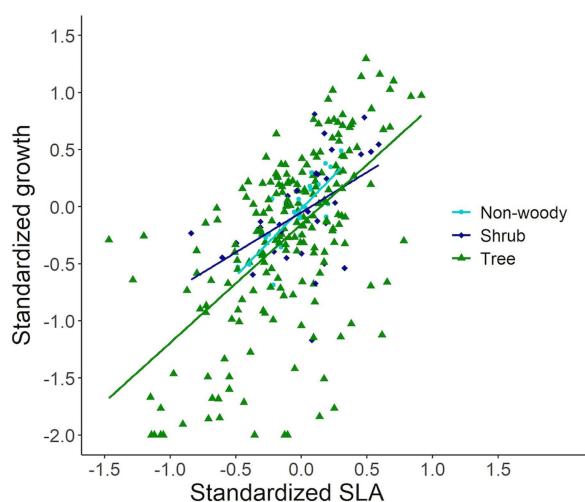
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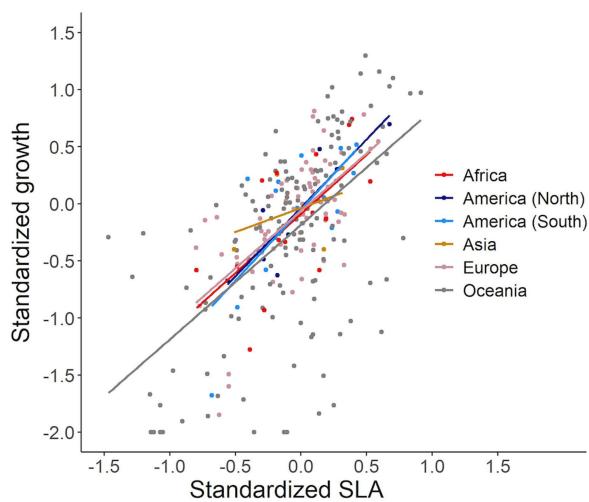
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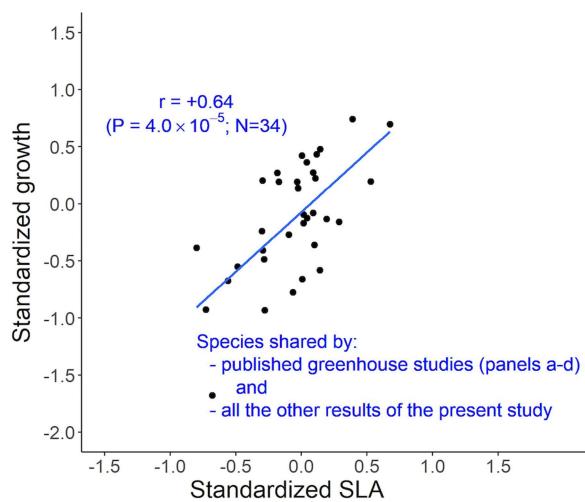
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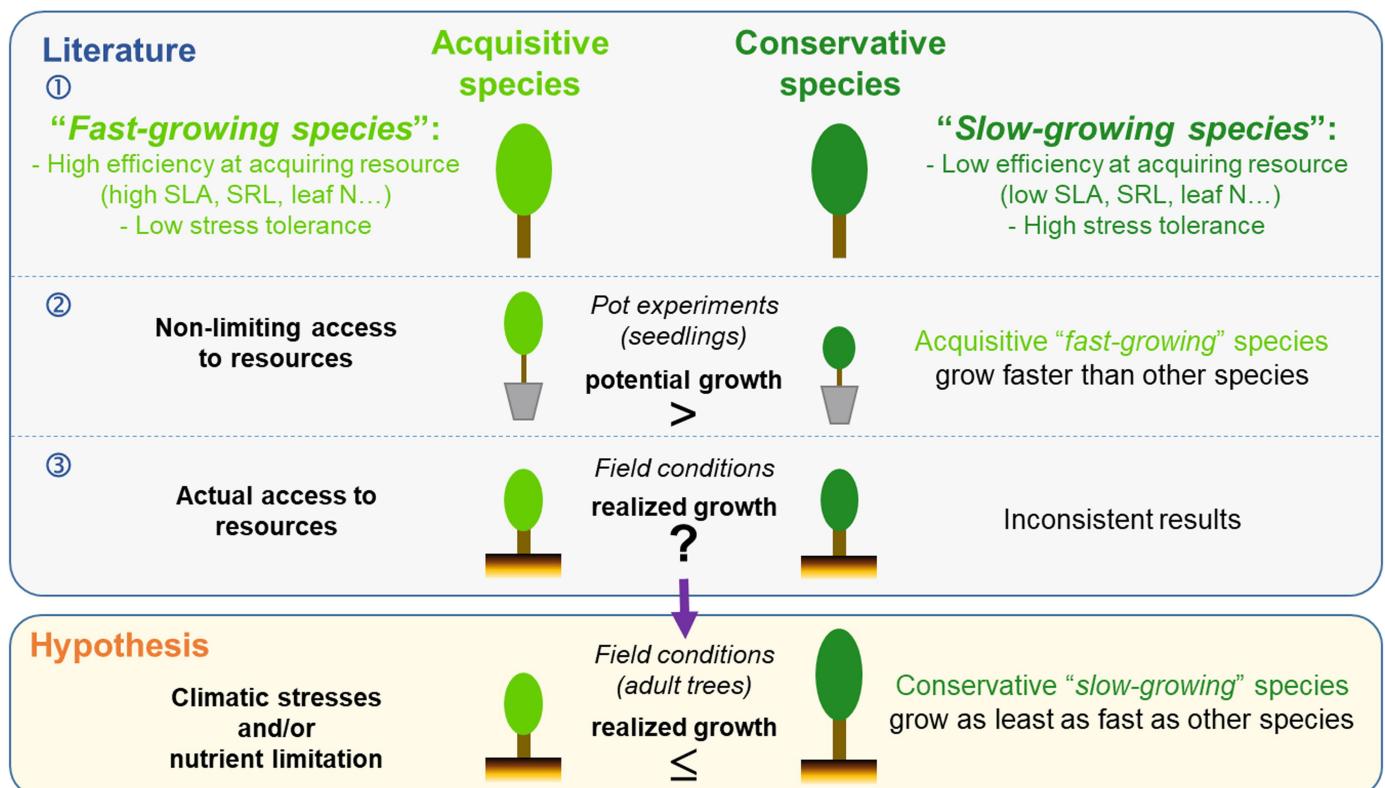


Extended Data Fig. 1 | Effect of specific leaf area (SLA) on seedling growth under favourable conditions. Data were collected from 10 independent publications that reported seedling growth representing 263 species-experiments combinations and 212 distinct plant species (a), different forest biomes (b), plant types (c), and forested continents (d). A subset of values representing the tree species shared by the 10 publications about seedling

growth and by the present study about trees is shown (e). Data are standardized to enable comparisons among sites (see Methods). Linear regressions were fitted by class of values. The SLA trait was chosen because it was studied in all the 10 publications (Supplementary Note 1) and because SLA is a key trait in the plant economics spectrum (ref. 24).

Forest-based solutions for climate change mitigation

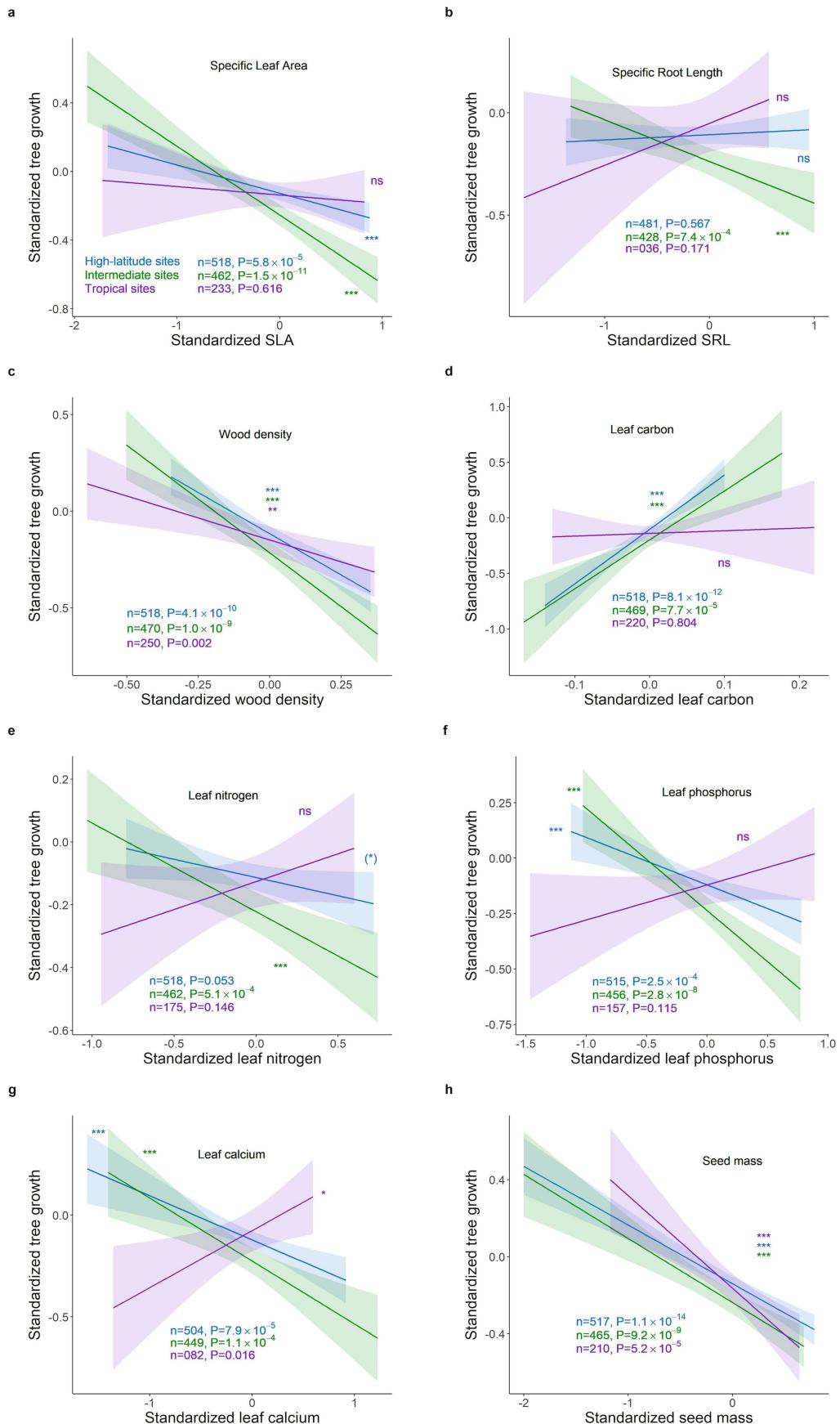
Need for tree species that efficiently fix CO₂ through long-term fast growth



Sources

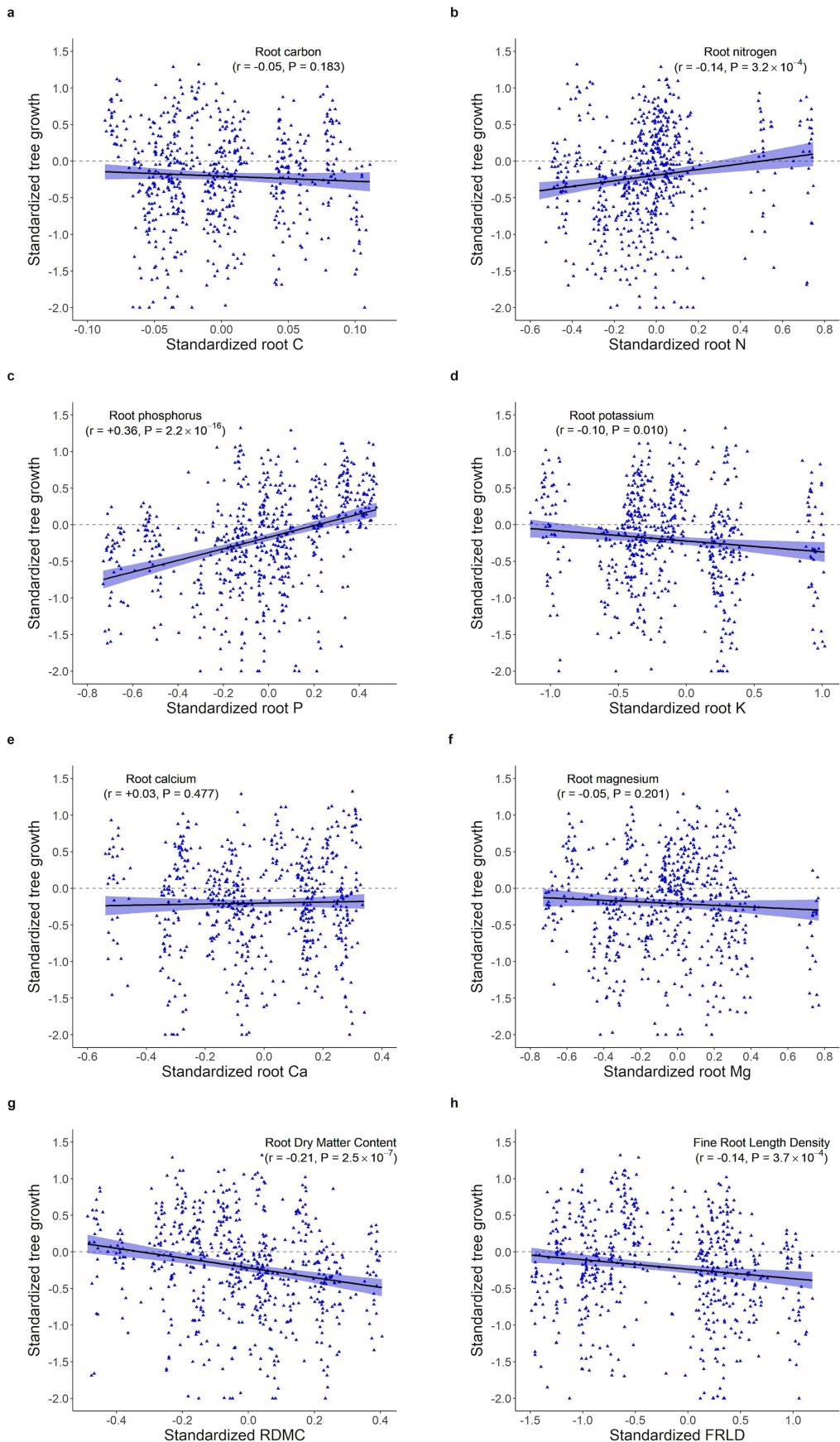
1. *Definition of ecological strategies*: Lambers & Poorter (1992). Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. In *Advances in Ecol. Res.* (Vol. 23, pp. 187-261). Academic Press.
2. *Pot experiments*: Extended Data Fig. 1
3. *Field observations*: Paine *et al.* (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology*, 103(4), 978-989.

Extended Data Fig. 2 | Context, rationale and hypothesis of the present study.



Extended Data Fig. 3 | Effect of functional traits on tree growth. Data were standardized to enable comparisons among sites (see Methods). Linear regressions were fitted (level of confidence of the error band = 0.95) by latitudinal class (limit values = 23° and 45°). P values of correlations are

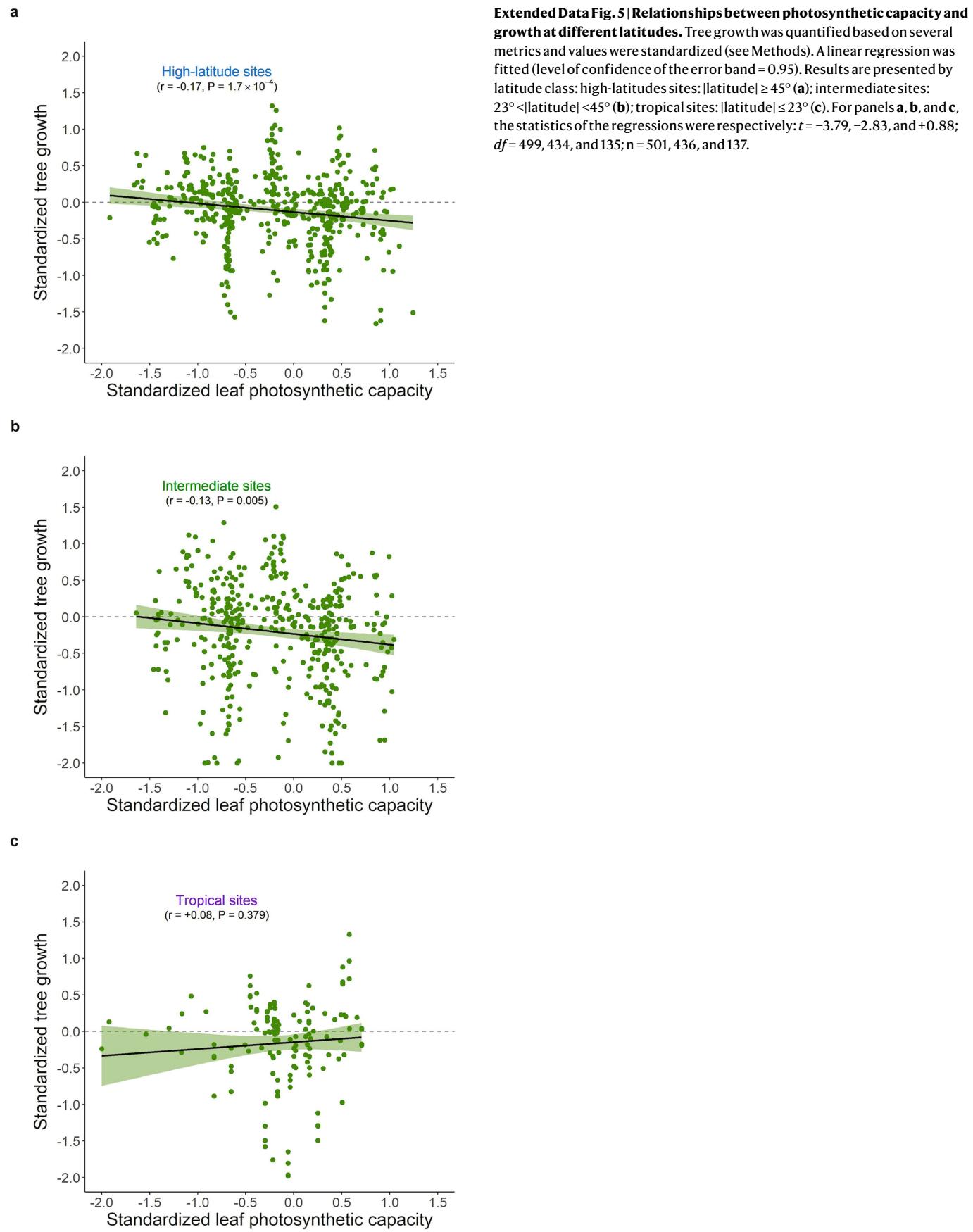
symbolized as follows: *** ($P < 0.001$), ** ($P < 0.010$), * ($P < 0.050$), (*) ($P < 0.100$), ns ($P \geq 0.100$). For the scope of readability, a regression line and its data points are not presented together when several lines are shown in a given panel.

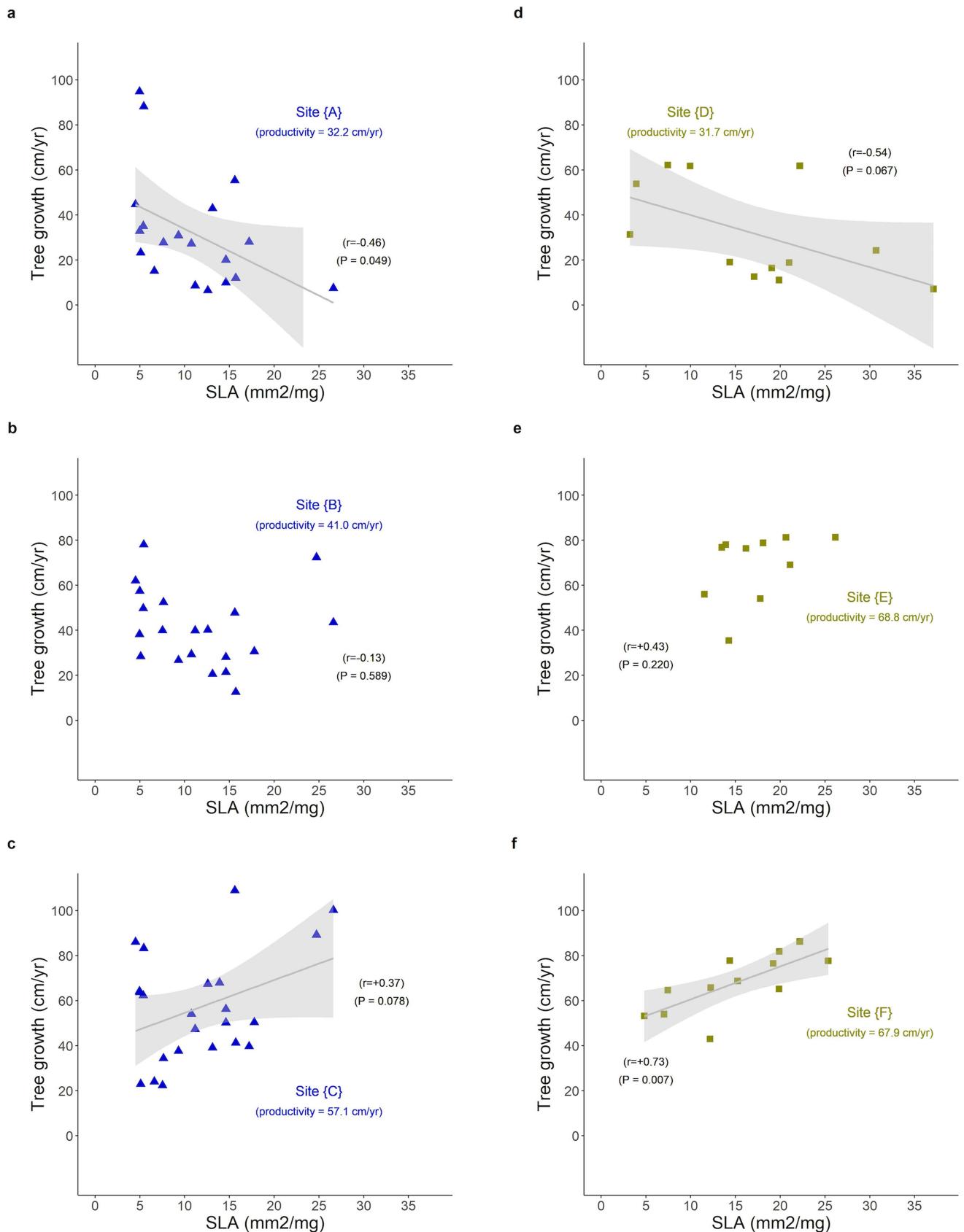


Extended Data Fig. 4 | Effect of fine root traits on tree growth in the European Atlantic Network.

Fine roots are roots with a diameter ≤ 2 mm. Data are standardized to enable comparisons among sites (see Methods). For panels from **a** to **h**, the statistics of the regressions (level of confidence of the error

band = 0.95) were: $t = -1.3, +3.6, +9.6, -2.6, +0.7, -1.3, -5.2$ and -3.6 ; $df = 617$ and $n = 619$ in all cases. Specific root length (SRL) results are presented in Extended Data Fig. 3. Original units: fine root content in carbon and nutrients (mg g^{-1}), fine root dry matter content (g g^{-1}), and fine root length density ($\text{cm}_{\text{root}} \text{cm}^{-3}_{\text{soil}}$).

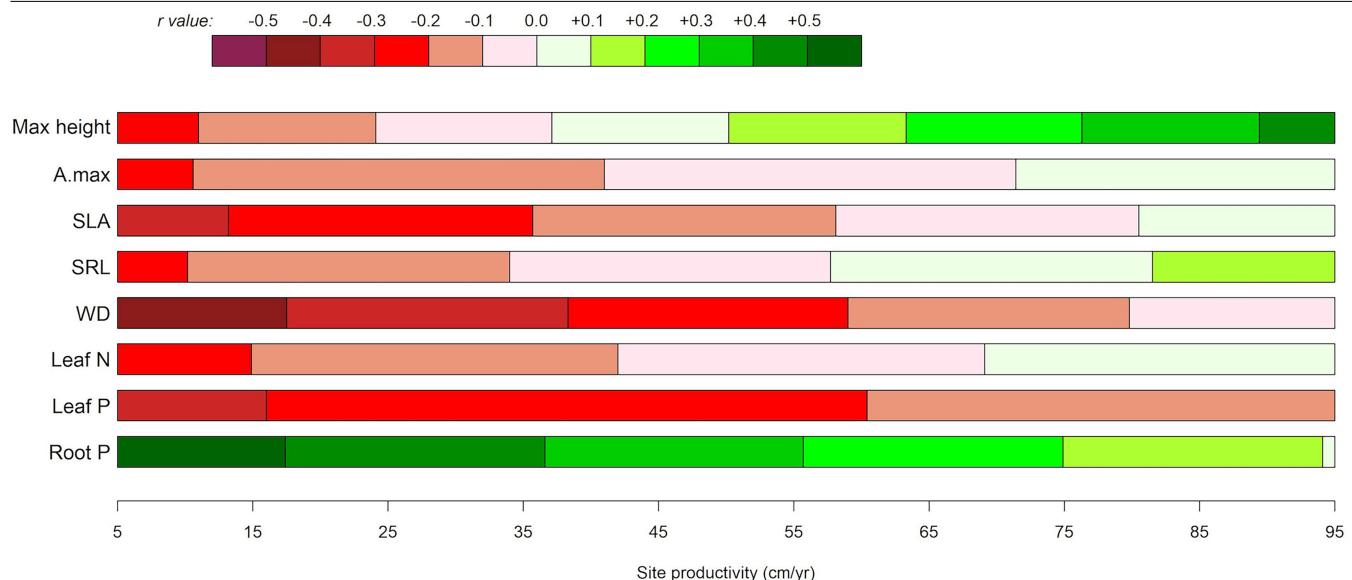




Extended Data Fig. 6 | Examples of relationships between a functional trait and tree species growth. Each panel presents the relationship between the Specific Leaf Area (SLA) value and the growth rate value of different tree species growing in a given common garden. Scatter plots present three sites of the European Atlantic Network (a, b, c) and three sites of the Tree Diversity

Network (d, e, f). These sites are also identified in Fig. 2b. For panels from a-f, the statistics of the regressions (level of confidence of the error band = 0.95) were respectively: $t = -2.13, -0.55, +1.85, -2.05, +1.33$, and $+3.40$; $df = 17, 18, 21, 10, 8$, and 10 ; $n = 19, 20, 23, 12, 10$, and 12 .

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Extended Data Fig. 7 | Influence of soil and climate on growth-trait relationships in the European Atlantic Network. Linear regressions between growth rate and trait value were fitted for each site of the European Atlantic Network (see panels **abc** of Extended Data Fig. 6 for three examples of SLA-growth relationships). The correlation values (r) were then regressed to site productivity (*i.e.* the mean value of growth per site; Fig. 2). The fitted linear regression between site productivity and r values was finally used to draw the graph: for instance, the correlation between growth and trait value was

systematically negative for wood density (WD; fitted linear regression in Fig. 2a), but switched from being negative at low productivity sites to positive at high productivity sites for SRL (Fig. 2d). Functional traits: Max height = tree species maximum height (m); A_{\max} = maximum photosynthetic capacity ($\mu\text{mol g}^{-1}\text{s}^{-1}$); SLA = specific leaf area ($\text{mm}^2\text{mg}^{-1}$); SRL = specific root length (mg g^{-1}); WD = wood density (mg cm^{-3}); Leaf N, Leaf P, and Root P = organ content in nitrogen or phosphorus (mg g^{-1}).

Extended Data Table 1 | Site drivers of tree growth in the European Atlantic Network (EAN)

Species	MAT	f_{climate}	N dep.	Soil C:N	Soil P	Soil pH	Soil clay
all EAN species pooled	??	↗↗↗	↗↗	↖↖↖	↗	↘↘	??
<i>Acer pseudoplatanus</i>	↘	-	↗↗↗	↖↖↖	-	-	-
<i>Betula pendula</i>	??	???	↗↗↗	↖↖↖	↗	↘↘	↘↘
<i>Calocedrus decurrens</i>	-	↗	??	↖↖	↗↗↗	-	-
<i>Castanea sativa</i>	-	-	-	↖↖↖	-	↘	↘↘
<i>Cedrus atlantica</i>	??	??	↗↗	↖↖↖	↗↗	↖↖↖	-
<i>Cupressus sempervirens</i>	??	-	(?)	↖↖	↗↗↗	?	-
<i>Eucalyptus nitens</i>	↘	?	?	(?)	-	?	-
<i>Fagus orientalis</i>	?	-	↗↗	↖↖↖	↗	↘↘	-
<i>Larix decidua</i>	↖↖↖	?	↗↗↗	↖↖↖	-	↖↖↖	?
<i>Liquidambar styraciflua</i>	(↗)	-	-	(↖)	↗↗	-	↘
<i>Pinus nigra</i>	↗↗	↗↗↗	↗↗↗	↖↖↖	(↗)	↘	?
<i>Pinus pinaster</i>	↗↗↗	↗↗↗	↗↗↗	↖↖	-	↖↖↖	??
<i>Pinus sylvestris</i>	↗	↗↗↗	↗↗↗	↖↖↖	-	↖↖↖	??
<i>Pinus taeda</i>	↗↗↗	↗↗↗	???	↖↖↖	-	↖↖	-
<i>Pseudotsuga menziesii</i>	↖↖↖	??	↗↗↗	↖↖	??	↖↖↖	-
<i>Quercus ilex</i>	??	↗↗	??	↖↖↖	↗↗↗	-	↘↘
<i>Quercus petraea</i>	-	↗	-	↖↖↖	↗↗	-	-
<i>Quercus robur</i>	↗↗	↗↗	↗↗	↖↖↖	↗↗	↖↖↖	??
<i>Quercus rubra</i>	↗↗	↗↗↗	↗↗↗	↘	↗↗	↘↘	??
<i>Robinia pseudoacacia</i>	↗	↗↗	-	↖↖↖	↗↗	-	-
<i>Sequoia sempervirens</i>	?	-	-	↖↖	↗↗	-	-
<i>Thuja plicata</i>	?	-	-	↖↖↖	↗↗	↘↘	-

MAT = Mean Annual Temperature, f_{climate} = climatic factor (concomitant sufficient moisture and temperature for biological activity; see Methods), N dep. = nitrogen atmospheric deposition, soil C:N = soil C:N ratio, soil P = soil phosphorus content (Olsen method), soil pH = soil pH value, soil clay = soil clay content. Data were first analysed using random forest modelling, enabling to identify the site drivers of tree growth with a backward elimination approach (see Methods). The percentage increase of Mean Squared Error (%IncMSE) was used as metric for this identification, with four levels of confidence: low ($2\% \leq \%IncMSE < 5\%$; noted as “↗” in case of positive relationship; see below), moderate ($5\% \leq \%IncMSE < 10\%$; noted as “↗”), high ($10\% \leq \%IncMSE < 20\%$; “↗↗”), and very high ($\%IncMSE \geq 20\%$; “↗↗↗”). When the %IncMSE value was less than 2%, the relationship was considered as negligible (noted as “.”). In a second step, for the relationships that were selected by the random forest models (i.e. $\%IncMSE \geq 2\%$), the direction of these effects was identified based on Spearman correlation values: the symbols “↗”, “?” and “↘” indicate positive ($r \geq +0.20$), unclear ($|r| < 0.20$) and negative ($r \leq -0.20$) effects on tree growth, respectively. Results are presented for all species pooled together, and per tree species. No results are presented for *Fagus sylvatica* (lack of data in several sites).

Article

Extended Data Table 2 | Influence of functional traits on tree growth in the European Atlantic Network (EAN)

Sites	H_{\max}	A_{\max}	SLA	LC	LN	LP	WD	SRL	RC	RN	RP
all sites	???	???	???	↗↗↗	???	???	↘↘↘	???	???	???	↗↗↗
UK-03	↗↗	.	?	↗	.	(↘)	.	(?)	.	(?)	.
UK-02	.	.	.	↗↗	(?)	.	↘↘	.	.	.	↗↗
UK-01	.	(?)	(?)	↗↗	↘	↘	.	?	.	.	.
FR-14	.	(?)	(↗)	↗↗↗	(↗)	.	.	↗	.	↗↗↗	↗↗↗
FR-13	.	???	.	↗↗↗	?	(↗)
FR-12	.	(?)	↗↗↗	.	.	.	↘	.	↗↗	↗↗↗	.
FR-11	(↗)	↘	???	↗↗↗	↘	↘	↘
FR-10	.	.	?	↗↗	.	↘
FR-09	.	.	↘	(↗)	.	↘	↘↘↘	.	.	.	↗↗
FR-08	.	(↘)	?	↗↗↗	.	.	↘	.	.	.	↗↗
FR-07	.	(?)	???	↗↗	.	?	(?)	.	.	.	↗
FR-06	.	?	?	↗↗↗	(↗)	.	.	.	↗	↗↗↗	.
FR-05	.	?	?	↗↗	(?)	.	?	(?)	.	.	.
FR-04	.	.	↘↘	↗	.	↘	↘↘↘	.	.	?	↗↗
FR-03	.	.	↘↘	↗↗	.	.	↘↘	.	.	???	↗↗↗
FR-02	.	.	???	↗	.	.	↘↘	(?)	.	.	↗
FR-01	(↘)	↗	↘↘	(↗)	.	.	↗↗
SP-06	.	.	↘↘↘	↗↗	(?)	↘	↘↘	↘	.	.	↗↗↗
SP-05	.	(↘)	↘↘	↗↗↗	.	.	↘↘	.	↗↗	↗↗	.
SP-04	.	.	.	↗↗↗	.	.	↘↘↘	.	↗↗	↗↗↗	.
SP-03	.	↘	.	↗↗↗	(?)	.	↘	.	↗↗↗	↗↗↗	.
SP-02	↘↘	(?)	↘	↗↗	?	.	↘↘↘	↗	.	↗↗	.
SP-01	.	.	↘	.	.	(↗)	↘↘
PT-04	.	(?)	↘↘↘	↗↗	(?)	↘	↘	.	(↘)	.	↗↗
PT-03	.	.	↘↘↘	↗	↘↘	↘	↘	.	(↘)	.	.
PT-02	.	.	↘↘↘	↗↗	↗↗	↗↗	.
PT-01	.	(?)	↘	↗↗	.	↘
AI-02	.	.	↘↘	(?)	.	↘↘	↘	.	(↘)	(?)	.
AI-01	?	.	↘↘	↗↗	.	↘	?	?	.	.	?

H_{\max} = Plant maximum height; A_{\max} = photosynthetic maximum capacity; SLA = specific leaf area; LC, LN and LP = leaf carbon (C), nitrogen (N) and phosphorus (P) content, respectively; WD = wood density; SRL = specific root length; RC, RN and RP = root C, N and P content. Data were first analysed using random forest modelling, enabling to identify the site drivers of tree growth with a backward elimination approach (see Methods). The percentage increase of Mean Squared Error (%IncMSE) was used as metric for this identification, with four levels of confidence (notes as from “↗” to “↗↗↗”; see Extended Data Table 1). When the %IncMSE value was less than 2%, the relationship was considered as negligible (noted as “.”). In a second step, for the relationships that were selected by the random forest models, the direction of these effects was identified based on Spearman correlation values: the symbols “↗”, “?” and “↘” indicate positive ($r \geq +0.20$), unclear ($|r| < 0.20$) and negative ($r \leq -0.20$) effects on growth, respectively. Results are presented for all sites pooled together, and per site. Sites are presented from North to South (UK = United Kingdom, FR = France, SP = Spain, PT = continental Portugal, AI = Azores islands).

Extended Data Table 3 | Distribution of trait values between acquisitive species and conservative species

Descriptors	Conservative species (n = 93)	Acquisitive species (n = 119)	Difference
Leaf shape			$P < 0.001^{***}$ ($\chi^2=84.2$; df=1)
Broadleaf	38	116	
Needleleaf	55	3	
Leaf phenology			$P < 0.001^{***}$ ($\chi^2=42.6$; df=1)
Deciduous	17	69	
Evergreen	71	35	
Mycorrhizal symbiosis			$P < 0.001^{***}$ ($\chi^2=16.3$; df=2)
Arbuscular	39	72	
Mixed	7	17	
Ectomycorrhizal	47	29	
N symbiotic fixation			$P = 0.003^{**}$ ($\chi^2=8.4$; df=1)
Non-fixers	84	89	
Fixers	9	30	
Tree max height (m)	43 ± 2 [30–50] (n=85)	36 ± 1 [30–44] (n=102)	$P = 0.031^*$ ($\chi^2=4.7$; df=1)
Tree lifespan (years)	392 ± 38 [188–501] (n=56)	222 ± 26 [96–294] (n=59)	$P < 0.001^{***}$ ($\chi^2=16.3$; df=1)
Successional stage (1–5)	3.3 ± 0.1 [3.0–4.0] (n=59)	2.5 ± 0.1 [1.5–3.0] (n=55)	$P < 0.001^{***}$ ($\chi^2=14.3$; df=1)
Shade tolerance (1–5)	2.5 ± 0.2 [1.4–3.6] (n=40)	2.6 ± 0.2 [1.8–3.6] (n=38)	$P = 0.474$ ($\chi^2=0.5$; df=1)
Seed mass (log{mg})	3.2 ± 0.2 [1.6–4.5] (n=89)	3.8 ± 0.3 [2.3–5.5] (n=102)	$P = 0.028^*$ ($\chi^2=4.8$; df=1)
Leaf A_{max} ($\mu\text{mol g}^{-1} \text{s}^{-1}$)	0.057 ± 0.003 [0.035–0.079] (n=59)	0.195 ± 0.012 [0.136–0.207] (n=73)	$P < 0.001^{***}$ ($\chi^2=97.2$; df=1)
SLA ($\text{mm}^2 \text{mg}^{-1}$)	9.2 ± 0.5 [5.8–11.7] (n=87)	18.0 ± 0.6 [13.9–19.9] (n=117)	$P < 0.001^{***}$ ($\chi^2=94.0$; df=1)
Leaf N (mg g^{-1})	14.8 ± 0.6 [11.4–17.2] (n=89)	23.1 ± 0.8 [17.7–25.6] (n=96)	$P < 0.001^{***}$ ($\chi^2=62.4$; df=1)
Leaf P (mg g^{-1})	1.26 ± 0.06 [0.89–1.50] (n=83)	1.63 ± 0.08 [1.10–1.98] (n=88)	$P < 0.001^{***}$ ($\chi^2=11.5$; df=1)
Leaf Ca (mg g^{-1})	8.7 ± 0.9 [4.1–9.6] (n=69)	9.4 ± 0.6 [6.4–10.7] (n=62)	$P = 0.030^*$ ($\chi^2=4.7$; df=1)
Wood C (mg g^{-1})	492 ± 3 [481–506] (n=55)	465 ± 3 [450–481] (n=59)	$P < 0.001^{***}$ ($\chi^2=37.3$; df=1)
Wood density (mg cm^{-3})	501 ± 12 [429–565] (n=93)	563 ± 12 [467–650] (n=118)	$P < 0.001^{***}$ ($\chi^2=12.8$; df=1)
SRL (m g^{-1})	24.7 ± 2.1 [13.6–32.9] (n=50)	44.7 ± 3.8 [25.0–52.4] (n=44)	$P < 0.001^{***}$ ($\chi^2=21.4$; df=1)

Tree species strategy (i.e. conservative or acquisitive) was a priori defined based on A_{max} (leaf photosynthetic maximum capacity) and to a lesser extent on SLA and leaf N content (see Methods). Leaf N, P, and Ca: leaf content of nitrogen, phosphorus and calcium; SLA and SR: specific leaf area and specific root length. Seed mass values were log-transformed to avoid data skewness. Successional stage and shade tolerance are coded from 1 (pioneer species; shade intolerant species) to 5 (climax species; shade tolerant species). There were some non-determined values for several traits (e.g. n=21 for seed mass). Categorical traits are presented in numbers (excluding species with missing trait values), whereas continuous traits are presented as mean values ± 1 standard error, with the range between first quartile and third quartile in square brackets. Differences between acquisitive species and conservative species were tested with a χ^2 test (categorical traits) or a Kruskal & Wallis two-sided test (continuous traits).

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Software and code

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Data collection No computer code was used for data collection.

Data analysis Data were analysed using code developed by authors (R language, version 9.4 and 4.2.3) and common statistical methods : random forest (randomForest R package, version 4.7-1.1), linear models (olsrr R package, version 0.5.3), mixed models (lme4 R package, version 1.1-32), Kruskall & Wallis test (R core). All analyses are fully described in the Methods section. The main R procedures that were used have been deposited in the <https://entrepot.recherche.data.gouv.fr> database under accession link <https://doi.org/10.57745/3OIGHB>. Complementary information can be provided by authors on request.

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The datasets generated in this study (EAN, TDN, SBD, TED) have been deposited in the <https://entrepot.recherche.data.gouv.fr> database under accession link <https://doi.org/10.57745/3OIGHB> (Etalab Open License 2.0, compatible CC-BY 2.0). Figures 1 to 4, and Table 1, have associated raw data that are available online along with the article files. There is no restriction on data availability.

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Study description

We evaluated to what extent the tree properties (known as functional traits) can explain tree growth, in interactions with local environment (soil properties, climate).

Research sample

To be able to study the influence of functional traits on tree growth, independently from variations of environmental conditions, we studied tree growth in common gardens. In such experimental sites, different tree species were growing in the same conditions, enabling us to explore any growth-trait relationship. To study the possible interactions with local environment, we included in our study as many common gardens as possible (n=160). Trait data were compiled, using published works and our own samplings.

Sampling strategy

Data about tree growth were collected mainly by mobilising existing experimental networks: REINFORCE (re-named EAN in this study) and TreeDivNet. We complemented these datasets with data from the literature and from individual common gardens (by contacting their PI). Data about traits were in majority already existing (see above). We complemented them by sampling 23 tree species in common gardens of the REINFORCE network (see Methods).

Data collection

The growth data was provided by all networks (or PIs in case of individual common gardens). The checking, structuration, homogenisation and curation of all data were done by Laurent Augusto, Remi Borelle, Marie Charru, and Lucie Bon. Trait data were at first mobilised from a published work (Augusto & Boca, 2022). This dataset was complemented by specific bibliographic requests (WoS, Google Scholar), looking for trait values that were identified as missing. Finally, leaf, root, and wood samples were collected from on-going common gardens, brought to laboratory and measured/analysed.

Timing and spatial scale

Data collection for tree growth and functional traits was carried out from January 2020 (beginning of the study) to June 2023 (date at which the last growth subsets of data were made available). Data analyses began as soon as 2021, and were regularly updated based on the arrival of new data.
Data collection for plant traits was initiated in January 2020 and was closed in October 2021 (when the last chemical analyses were finished).
Most trees were measured at age between 3 years-old and 90 years-old.
The studied sites are distributed throughout the world, with a higher concentration in Western Europe.

Data exclusions

There was no data exclusion for functional traits. For tree growth, we excluded experimental plots that had not enough alive trees to avoid biasing the results.

Reproducibility

The results can be reproduced as the core dataset of the study is available online (see Data availability in the manuscript). The numerous code scripts (in R) are available from the corresponding authors upon request.

Randomization

Most of the TreeDivNet common gardens had randomised blocks. In the EAN common gardens, four tree species were in replicated plots, enabling the quantification of internal variability. Some of the SBD common gardens also had replicated blocks.

Blinding

All data (tree growth, traits, site descriptors) were collected by many different operators, working independently. In addition, data were acquired in on-going common gardens led by different PIs. As such, it is very unlikely that all operators could influence each other while collecting data.

Did the study involve field work? Yes No

Field work, collection and transport

Field conditions

Root and wood samples were collected at the end of the winter season in a EAN common garden (SW France; cold, rainy conditions). Leaf samples and measurements of photosynthetic capacity were carried out in early summer during a sunny and warm period (but not dry period; see Methods).

Location

Two common gardens were used for samplings, both being in SW France (approx. 45°N, 1°W). They are characterised by temperate conditions (MAT=12.8-12.9°C; MAP=904-930 mm/yr) and coarse-textured acidic soil conditions (podzol and cambisol).

Access & import/export

Both sites are experimental sites, outside any protected area. Access was done by car, following existing roads and paths. No waste was left in situ

Disturbance

Vegetation and soil were left as much as possible untouched. We collected the strictly necessary amount of matter to enable representativeness (see Methods).

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