Laughlin, Daniel C.; Mommer, Liesje; Sabatini, Francesco Maria; [et al.]. «Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs». Nature Ecology & Evolution, Vol. 5 (June 2021), p. 1123-1134. DOI 10.1038/s41559-021-01471-7

Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs

Daniel C. Laughlin[1]*, Liesje Mommer[2], Francesco Maria Sabatini[4,3], Helge Bruelheide[4,3], Thom W. Kuyper[5], M. Luke McCormack[6], Joana Bergmann[7], Grégoire T. Freschet[8], Nathaly R. Guerrero-Ramírez[9], Colleen M. Iversen[10], Jens Kattge[11,3], Ina C. Meier[12], Hendrik Poorter[13,14], Catherine Roumet[15], Marina Semchenko[16,17], Christopher J. Sweeney[16], Oscar J. Valverde-Barrantes[18], Fons van der Plas[2,19], Jasper van Ruijven[2], Larry M. York[20], Isabelle Aubin[21], Olivia R. Burge[22], Chaeho Byun[23], Renata Ćušterevska[24], Jürgen Dengler[25,26,3], Estelle Forey[27], Greg R. Guerin[28,29], Bruno Hérault[30,31,32], Rob Jackson[33,34], Dirk Nikolaus Karger[35], Jonathan Lenoir[36], Tatiana Lysenko[37,38,39], Patrick Meir[40,41], Ülo Niinemets[42,43], Wim A. Ozinga[44], Josep Penuelas[45,46], Peter B. Reich[47,48], Marco Schmidt[49,50], Franziska Schrodt[51], Eduardo Velázquez[52], Alexandra Weigelt[19,3]

*Corresponding author: Daniel C. Laughlin daniel.laughlin@uwyo.edu

[1] Department of Botany, University of Wyoming, Laramie, Wyoming 82071, USA
[2] Plant Ecology and Nature Conservation Group, Wageningen University & Research, The Netherlands
[3] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany
[4] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Germany
[5] Soil Biology Group, Wageningen University & Research, The Netherlands
[6] Center for Tree Science, The Morton Arboretum, Lisle, USA
[7] Sustainable Grassland Systems, Leibniz Centre for Agricultural Landscape Research (ZALF), Paulinenaue, Germany
[8] Theoretical and Experimental Ecology Station (SETE), National Center for Scientific Research (CNRS), Moulis, France
[9] Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Göttingen, Germany
[10] Oak Ridge National Laboratory, Climate Change Science Institute and Environmental Sciences Division, Oak Ridge, Tennessee, USA
[11] Functional Biogeography, Max Planck Institute for Biogeochemistry, Jena, Germany
[12] Functional Forest Ecology, Department of Biology, Universität Hamburg, Germany
[13] Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, Jülich, Germany
[14] Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia
[15] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[16] Department of Earth and Environmental Sciences, The University of Manchester, UK
[17] Institute of Ecology and Earth Sciences, University of Tartu, Estonia
[18] Institute of Environment, Department of Biological Sciences, Florida International University, Miami, USA

[19] Systematic Botany and Functional Biodiversity, Institute of Biology, Leipzig University, Germany
[20] Noble Research Institute, LLC, Ardmore, OK 73401, USA
[21] Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sault Ste Marie, ON, Canada
[22] Ecosystems and Conservation, Manaaki Whenua - Landcare Research, Lincoln, New Zealand
[23] Department of Biological Sciences and Biotechnology, Andong National University, Andong, Republic of Korea
[24] Institute of Biology, University of Ss. Cyril and Methodius, Skopje, North Macedonia
[25] Vegetation Ecology, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland
[26] Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Germany
[27] Normandie Univ, UNIROUEN, INRAE, ECODIV, 76000 Rouen, France.
[28] Ecology and Evolutionary Biology, School of Biological Sciences, University of Adelaide, Australia
[29] Terrestrial Ecosystem Research Network (TERN), The University of Queensland, St. Lucia, Australia
[30] CIRAD, UPR Forêts et Sociétés, Yamoussoukro, Côte d'Ivoire
[31] Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France
[32] Institut National Polytechnique Félix Houphouët-Boigny, INP-HB, Yamoussoukro, Côte d'Ivoire
[33] Jackson Lab, Department of Earth System Science, Stanford University, USA
[34] Stanford Woods Institute for the Environment, Stanford, USA
[35] Biodiversity and Conservation Biology, Spatial Evolutionary Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland
[36] UMR CNRS 7058 « Ecologie et Dynamique des Systèmes Anthropisés » (EDYSAN), Université de Picardie Jules Verne, Amiens, France
[37] Laboratory of Vegetation Science, Komarov Botanical Institute RAS, Russian Academy of Sciences (RAS), Saint-Petersburg, Russia
[38] Laboratory of Phytodiversity Problems and Phytocoenology, Institute of Ecology of the Volga River Basin RAS - Branch of the Samara Scientific Center RAS, Russian Academy of Sciences (RAS), Togliatti, Russia
[39] Group of Ecology of living organisms, Tobolsk complex scientific station Ural Branch RAS, Russian Academy of Sciences (RAS), Tobolsk, Russia
[40] Research School of Biology, Australian National University, Canberra ACT, Australia
[41] School of Geosciences University of Edinburgh, Edinburgh UK
[42] Crop Science and Plant Biology, Estonian University of Life Sciences, Tartu, Estonia
[43] Estonian Academy of Sciences, Tallinn, Estonia
[44] Vegetation, Forest and Landscape Ecology, Wageningen Environmental Research, Wageningen University & Research, The Netherlands
[45] CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra (Catalonia) E-08193, Spain
[46] CREAF, Cerdanyola del Vallès (Catalonia) E-08193, Spain
[47] Department of Forest Resources, University of Minnesota, USA
[48] Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia

[49] Data and Modelling Centre, Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany
[50] Palmengarten, City of Frankfurt, Frankfurt am Main, Germany
[51] School of Geography, University of Nottingham, UK
[52] Production and Forest Resources, Institute for Research in Sustainable Forest Management (iuFOR), ETS Agricultural Engineering University of Valladolid, Palencia, Spain

Abstract

Ecological theory is built on trade-offs where trait differences among species evolved as adaptations to different environments. Trade-offs are often assumed to be bidirectional, where opposite ends of a gradient in trait values confer advantages in different environments. However, unidirectional benefits could be widespread if extreme trait values confer advantages at one end of an environmental gradient, whereas a wide range of trait values are equally beneficial at the other end. Here we show that root traits explain species occurrences along broad gradients of temperature and water availability, but model predictions only resembled trade-offs in two out of twenty-four models. Forest species with low specific root length (SRL) and high root tissue density (RTD) were more likely to occur in warm climates but species with high SRL and low RTD were more likely to occur in cold climates. Unidirectional benefits were more prevalent than trade-offs: for example, species with large-diameter roots and high RTD were more commonly associated with dry climates, but species with the opposite trait values were not associated with wet climates. Directional selection for traits consistently occurred in cold or dry climates, whereas a diversity of root trait values were equally viable in warm or wet climates. Explicit integration of unidirectional benefits into ecological theory is needed to advance our

understanding of the consequences of trait variation on species responses to environmental change.

The nature of ecological trade-offs

Ecological trade-offs underpin our conceptual understanding of global biodiversity distributions [1-6]. Species pools are filtered into local communities based on the matching of species' trait values to environmental conditions. Models that use traits to predict the success of a species in a given environment are actively being developed and tested. Ecological trade-offs arise as a consequence of the adaptive value of a trait, eloquently described as '*an evolutionary dilemma, whereby genetic change conferring increased fitness in one circumstance inescapably involves sacrifice of fitness in another*' [4]. As the term 'trade-off' implies, the trait effects are 'bidirectional', where, for example, low trait values of a species confer adaptive advantage at one end of an environmental gradient whereas high trait values confer benefits at the opposite end of the gradient (Fig 1A) [1].

Classical ecological theory has long emphasized this bidirectional perspective on trait-environment relationships at the species level [7]. For example, resource ratio theory (ALLOCATE) is built on a single trait – environment trade-off. At the high end of the soil fertility gradient, plant species that allocate relatively more carbon aboveground than belowground are predicted to be better competitors for light. Whereas at the low end of the soil fertility gradient, plant species that allocate relatively more carbon belowground than aboveground are predicted to be better competitors for soil nutrients [8]. Empirical evidence for trade-offs have been found in a variety of traits including light compensation points along light gradients [9] and root angles along nutrient gradients [10]. In many cases, however, the empirical evidence for trade-offs in performance among species has been met with mixed success [6,11].

Empirical evidence for trade-offs at the species level would be provided by showing that the effect of a trait on the probability of species occurrence switches sign (*i.e.*, changes direction) along an environmental gradient (Fig. 1A) [12]. In other words, a positive relationship between a trait and an environmental gradient implies that the effect of the trait on the probability of species occurrence is negative at the low end of the gradient, but is positive at the high end of the gradient (Fig. 1A). This directional switch in sign is fundamental, but detecting the switch empirically is nontrivial because it cannot be observed through a simple trait-environment correlation [12]. The switch in sign can, however, be explicitly tested by comparing model-based predictions of trait effects on the probability of species occurrence at contrasting ends of the environmental gradient [13]. Specifically, if the first partial derivative with respect to traits crosses zero along the environmental gradient, then the effect of a trait on probability of occurrence switches sign (Fig 1A).

In contrast, the absence of a switch in sign of a trait's effect on the probability of species occurrence along an environmental gradient would indicate that a trait only confers an adaptive advantage at one end of this gradient, thereby exhibiting a mere 'unidirectional benefit' (Fig. 1B). The prevalence of unidirectional benefits at the species level has not been adequately tested, yet empirical research has provided hints that they exist. For example, plant communities in New Zealand exhibit trait convergence towards low leaf nitrogen concentration in phosphorus-poor soil, whereas in phosphorus-rich soil communities display wide divergence of leaf nitrogen concentration [14]. This suggests that low leaf nitrogen is adaptive in phosphorus-poor soil to maintain a balanced leaf nutrient stoichiometry, whereas high leaf nitrogen is not adaptive in phosphorus-rich soil. Thus, it is a unidirectional benefit, not a trade-off. Simulation results and empirical work in insect host use has suggested that the importance of trade-offs in the evolution of specialization may be overstated [11,15]. The prevailing view of trade-offs in ecological theory across all levels of organization [1,2] may thus have hindered the discovery of unidirectional benefits that could be widespread in nature. In particular at the species level, discerning the difference between trade-offs and unidirectional benefits would advance our understanding of how individual traits affect community assembly.

Belowground root traits

We tested the generality of ecological trade-offs in the context of plant root traits because these 'hidden' belowground organs are essential for water and nutrient uptake yet we still lack broad-scale empirical evidence for how they influence the filtering of species pools into local community assemblages [16]. To test the effects of root trait variation on species distributions along broad gradients in temperature and water availability we applied a new root trait framework consisting of two independent axes of variation [17] (Fig. 1C).

First, species span a trait axis defined by specific root length (SRL; fine root length per unit mass) and root diameter (RD) that has evolved in concert with symbiosis with mycorrhizal fungi. Arbuscular mycorrhizal (AM) plants comprise nearly 80% of plant species globally [18], and among them thick-rooted species are colonized at higher rates because of greater fungal habitat in the root cortex [17,19,20]. Most of the remaining mycorrhizal plant species associate with ectomycorrhizal (EcM) or ericoid mycorrhizal (ErM) fungi, which tend to colonize species with moderate to thin roots [17]. A small number of species in our dataset (described below) are non-mycorrhizal, and these species tend to have the thinnest roots to explore the soil for resources by themselves.

Second, species span another independent axis, where conservative species invest in high root tissue density (RTD; fine root mass per unit volume), and acquisitive species construct more metabolically active tissue with low RTD and high root nitrogen (root N) concentration [21,22]. This second axis is associated with the aboveground leaf economics spectrum [22], where species construct either short-lived leaves with high metabolic rates or long-lived leaves with thick cell walls [23]. Consequently, fast species construct cheaper fine roots with higher rates of root turnover [17]. The global correlation between SRL and RTD among species is r = -0.09 [17], which implies that plants have explored the expression of nearly all possible combinations of these two axes leading to a two-dimensional root economics space (Fig. 1C). Therefore, these two root trait axes provide a unique opportunity to scrutinize the evidence for ecological trade-offs and unidirectional benefits among species to advance our understanding of the role of traits in community assembly.

Hypotheses and methods

We developed four hypotheses about how SRL, RD, RTD, and Root N influence species distributions along broad gradients of temperature and water availability (Fig 1D). Our hypotheses are grounded in physiological and symbiotic mechanisms and we predict that trade-offs generate variation in species occurrences across climatic gradients (Fig 1D). Our predictions for SRL and RTD are opposite in sign to our predictions for RD and Root N, respectively, because they are negatively correlated [17].

(1) We predicted a negative relationship between SRL and temperature (and a positive relationship between RD and temperature) for several reasons. Species with low SRL would be more prevalent in warm climates where AM fungi are abundant [24-26].We also predicted species with high SRL to be more common in extremely cold climates because 1) non-mycorrhizal taxa dominate the high Arctic where mycorrhiza are limited by extremely low temperatures [27], and 2) ErM and EcM fungi are more common in moderately cold climates and tend to colonize species with moderate to high SRL [24-26].

(2) We predicted a positive relationship between SRL and water availability (and a negative relationship between RD and water availability) because species with high SRL can more efficiently acquire resources by themselves in wet environments, and species with low SRL that provide more cortical habitat for AM fungi can be more drought-tolerant through mycorrhizal symbiosis-enhanced stomatal conductance and water use efficiency [28].

(3) We predicted a negative relationship between RTD and temperature (and a positive relationship between root N and temperature) because 'slow' species with high RTD would tolerate low temperatures by limiting frost-induced cell lysis and resisting freezing-induced embolism formation, and because 'fast' species with low RTD and higher metabolic rates would be more productive than slow species in warmer climates [22,29].

(4) We predicted a negative relationship between RTD and water availability (and a positive relationship between root N and water availability) because conservative species would tolerate dry climates by resisting embolism formation and cellular collapse under extreme osmotic tension, and because acquisitive species with low RTD and higher metabolic rates would be more productive than slow species in wetter climates [22,30].

To test these four hypotheses, we combined the largest global vegetation database (sPlot) [31] with the global root trait database (GRooT) [32] (see Methods) (Fig. S1). We used long-term average minimum temperature of the coldest month to represent cold limitation and the long-term average precipitation-to-potential evapotranspiration ratio (P:PET) to represent chronic water limitation. The plots spanned a gradient of -10 to 25 °C mean annual temperature and 50 to 2,750 mm mean annual precipitation. Given the functional differences in vegetation dominated by woody and herbaceous plants with respect to traits such as height, root diameter, and root mass fractions [20,23,33-35], we took a conservative approach to prevent confounding the relationships by classifying each plot as forest, grassland, or wetland (Fig. S1). We predicted root trait-climate relationships to be absent in wetlands because plants that grow in anoxic soil conditions develop aerenchyma to maintain respiration rates, which would alter root morphology independent from the regional climate [36].

Root traits in relation to temperature and water

SRL was related to the probability of species occurrence along climatic gradients in forests and grasslands, but not in wetlands (Fig. 2). In agreement with our first hypothesis and regional studies [37-39], the interactive effects of SRL and temperature on species occurrence was negative in both forests and grasslands (Table 1, Fig. 2A), and SRL was negatively correlated with species optimum minimum temperature (Fig. S2A,B). Low-SRL species associated with AM fungi, such as Chinese fir (*Cunninghami lanceolata*, Fig. 1C), were more likely to occur in warmer climates. High-SRL species associated with ErM fungi, such as lingonberry (*Vaccinium vitis-idaea*, Fig. 1C), were more likely to occur in colder climates. Overall, the relationship between SRL and temperature in forests was an example of a classic trade-off (Table 1, Fig. 2B).

In grasslands, however, we only observed a unidirectional benefit (Fig. 2C). Species with high SRL, such as *Draba nemorosa* (Fig. 1C), were more likely to occur in colder climates, but species with any SRL value were equally likely to occur in warm climates (Table 1, Fig. 2C). Root diameter did not exhibit trade-offs with temperature in forests or grasslands (Table 1, Fig. 2D,E,F). Large-diameter roots in forests were advantageous in warm climates, but thin roots were not clearly advantageous in cold climates (Table 1, Fig. 2E). Thick roots thus exhibit a unidirectional benefit in forests with warm climates where AM fungi are most abundant [24-26].

SRL did not exhibit a trade-off in relation to water availability, but rather a unidirectional benefit (Table 1). In agreement with our second hypothesis, the SRL-water availability interaction was positive in both forests and grasslands (Table 1, Fig. 2G), and SRL was positively correlated with species optimum P:PET ratio (Fig. S2C,D). Species with low SRL were more likely to occur in dry environments likely because AM fungi that inhabit thicker roots can confer drought tolerance to plants [28] (Fig. 2H,I). Contrary to expectations, species with any SRL value were equally likely to occur in wet environments (Fig. 2H,I), which may explain a lack of clear linear relationship with water availability in previous studies [30,38]. Root diameter did not exhibit trade-offs with water availability in either forests or grasslands (Table 1, Fig. 2K,L).

RTD influenced the probability of species occurrence along climatic gradients in forests and grasslands, but not in wetlands (Fig. 3A). Contrary to our third hypothesis and other studies [29,38-43], the RTD-temperature interaction was positive rather than negative (Table 1, Fig. 3A) and RTD was positively correlated with species optimum minimum temperatures (Fig. S2E,F). In forests, species such as honeysuckle (*Lonicera chrysantha,* Fig. 1C) with low RTD were more likely to occur in cold climates and species such as common myrtle (*Myrtus communis,* Fig. 1C) with high RTD were more likely to occur in warm climates (Table 1, Fig. 3B). However, this trade-off was not observed in grasslands where we found that species with low RTD were more likely to occur in cold climates but species with any RTD value were equally likely in warm climates (Table 1, Fig. 3C). We predicted that 'slow' species with dense roots would be better adapted to low temperatures, but this was incorrect. Freeze-thaw dynamics of soil in cooler climates can physically disturb root systems, which introduces the risk of losing large investments in dense roots and may thus select for species that produce cheap low-density roots that can regrow quickly after disturbance [44,45]. We also predicted that 'fast' species with low RTD and higher metabolic rates would be more competitive in warm climates, but this too was incorrect. It may be that dense lignin-rich roots physically defend plants against plant pathogens, protozoan parasites, and insect herbivores whose effects can be more intense at higher temperature [24,46-49]. Root N did not exhibit clear trade-offs with temperature in either forests or grasslands (Table 1, Fig. 3D,E,F).

RTD did not exhibit a trade-off in relation to water availability (Table 1, Fig 3G,H,I). In partial agreement with our fourth hypothesis and regional studies [30,38,50], the RTD-water availability interaction was negative (Fig. 3G) and RTD was negatively correlated with species optimum P:PET ratio (Fig S2G,H). In forests, species with high RTD had greater chances of occurring in drier climates likely because denser root tissue enhances resistance to drought-induced cavitation [51]. However, species with any RTD value were equally likely to occur in wet climates (Table 1, Fig. 3H). No clear RTD-water availability trade-off was observed in grasslands (Fig. 3I), perhaps because short-lived herbaceous species escape drought by restricting their activity to brief pulses of ample water availability. Contrary to our hypothesis, high root N appeared to be advantageous in dry forests (Table 1, Fig 3K). This result is qualitatively consistent with the discovery that leaf N per area is higher in drought-tolerant plants because higher photosynthetic rates are possible at lower stomatal conductance [52]. Perhaps root N is higher in dry climates to provide drought-tolerant leaves with a greater supply of N.

Implications for ecological theory

The diversification of root morphology was pivotal to the evolutionary development of land plants in their quest to colonize the terrestrial biosphere [20,53], yet direct tests for how root traits may influence species distributions along climatic gradients have been lacking until now. We analyzed the largest root trait and vegetation datasets and found that within forest ecosystems 1) species with low SRL, large RD, or high RTD have a higher chance of occurring in warm climates, while species with high SRL or low RTD have a higher chance of occurring in cold climates; and 2) species with low SRL, large RD, high RTD, and high Root N have a higher chance of occurring in dry environments, but the probability of occurring in wet environments was not related to any of these root traits. These results demonstrate that root traits contribute to our understanding of the distribution of vegetation, and that unidirectional benefits may be more prevalent than trade-offs.

Ecological community assembly theory is grounded in trade-offs, but our study challenges our understanding of how individual continuous traits influence species distributions along environmental gradients. Of the 13 models in which a significant trait-by-environment interaction was detected, only two of these models supported a trade-off, whereas seven models supported unidirectional benefits and four exhibited no clear benefits in either direction (Table 1). This result demonstrates the importance of evaluating the model-based predictions at each end of the gradient (Fig. 2,3) rather than relying on trait-environment correlations or the significance of interaction coefficients alone as evidence of a trade-off. The predicted signs (*i.e.*, direction) of the relationships were supported 67% of the time (16 out of the 24 models), but the model predictions only resembled trade-offs 8% of the time (2 out of 24 models) (Table 1). Our results agree with Grubb's insight that '*the concept of a trade-off, which implies that being suited to one condition necessarily involves not being suited to the opposite, is widely diffused in the current literature but is not universally applicable*'.[54]

Our work suggests that community assembly models and plant strategy theories that use continuous variation in functional traits should be explicit about whether a trait exhibits trade-offs with environmental gradients or unidirectional benefits. Patterns of aboveground trait variation have been shown to exhibit trait convergence in resource-poor environments and trait divergence in productive environments [14,55], suggesting that unidirectional benefits may also occur in aboveground traits. Our analysis focused on determining the contributions of individual traits to species distributions, but plant strategy theories are built on sets of multiple traits. Plant strategies are likely generated by a combination of trade-offs for some traits (e.g., light compensation point along light gradients[9]) and unidirectional benefits for others (e.g. leaf nutrient concentrations along soil fertility gradients[14,55]), which inevitably makes the task of predicting species responses using continuous traits more difficult than previously anticipated. Predictive models that use sets of continuous traits as predictors of species responses need to know whether a trait exhibits trade-offs or unidirectional benefits along an environmental gradient. Strong trait-environment interaction coefficients in linear models will, by default, predict a trait-environment trade-off, but our results show that these are less prevalent than unidirectional benefits. In the case of unidirectional benefits, the predictive power of a trait for species occurrences would vary with the particular values of that trait, giving one end of the range in trait values higher importance than the other end. Such information could perhaps enter models as priors within a hierarchical model framework. An expanded theory of trait-environment interactions that incorporates unidirectional benefits will advance our understanding of the adaptive value of traits in community assembly and may improve predicted responses to climate change. For example, in regions projected to become warmer and drier rather than warmer and wetter [56], plant communities may converge toward lower SRL and higher RTD. This would make other trait combinations less viable and put species with higher SRL or lower RTD at a higher risk of local extinction in these drier regions.

Forests exhibited the strongest trade-offs among species, grasslands were dominated by unidirectional benefits, and root trait-climate interactions were absent in wetlands (Table 1). The lack of trade-offs in wetlands was expected because anoxic water-logged soils select for species with aerenchyma which would confound root trait-climate relationships. The co-occurrence and higher functional diversity of both woody and herbaceous plants in forests may partly explain the evidence for stronger trade-offs in forests. Forests contain a higher proportion of woody species and these exhibit a higher variability in fine root traits than herbs, both because the clades of land plants that are characterized by large root diameter are mostly trees and because there is a greater diversity of mycorrhizal types among woody plants [17]. Woody plants host not only AM mycorrhizal fungi, but also the evolutionarily younger EcM and ErM fungi (which are associated with thinner roots) [20], whereas non-woody plants mostly host AM fungi with only a minority of genera being noted for hosting EcM fungi (e.g., *Kobresia*). Many of the grasslands in our dataset are semi-natural and occur because of human management, which may also weaken trait-environment relationships. Our analysis was also limited to species-level average trait values, and it is possible that evidence for trade-offs may be stronger in general if intraspecific trait plasticity could be explicitly incorporated into the model.

We also found that trade-offs were stronger along temperature gradients than along gradients in water availability, and we consider two possible reasons for this. First, weaker moisture effects could have resulted from a larger mismatch between modelled and actual climatic conditions for moisture than for temperature. The difference between macro- and microclimate might be comparably small for temperature, whereas soil moisture is more strongly modified by soil conditions and topography, resulting in local deviations of water supply from our predictions. This interpretation is supported by the lack of trait-environment interactions in wetlands where water availability is driven by hydrological processes rather than climate. Second, this may be related to observations that shifts in mycorrhizal dominance occur on temperature gradients, but not so consistently with water [57]. At large scales, AM species tend to dominate warm regions (tropical dipterocarps being notable exceptions), whereas EcM and ErM tend to dominate cold regions, and root traits should respond to differences in mycorrhizal dominance [24,25]. However, it is still uncertain whether the shift in mycorrhizal dominance is due to temperature induced shifts in root morphology, or if the shift in root morphology is driven by temperature induced shifts in mycorrhizal dominance, or both.

The expectation of trade-offs holds across different levels of organization from individuals, populations, and to species [1], but may become masked in species because of multiple trade-offs in complex environments [2]. Indeed, there are many factors that confound the detection of broad-scale relationships between interspecific trait variation and climate: the high range of species trait values within communities relative to the global range [58,59], the high plasticity of traits within species across environments and the importance of other traits [60], the stochastic nature of disturbance regimes and land-use change [58], the spatially heterogeneous variation in microclimate and soil properties such as moisture and texture at small spatial scales [38], dispersal limitation, and biotic interactions (e.g., competition, facilitation) [61]. While root traits only explained a fraction of the variation in species occurrences (Table 1), similar to studies focused on aboveground traits [58], it is therefore remarkable that such clear root trait-climate relationships were discovered here. This suggests that the root economics space framework is important for understanding plant community assembly.

Trade-off theory assumes that selection is bidirectional and that constraints occur at both ends of the environmental gradient [1], but relaxing these assumptions may explain when and where trade-offs occur among species. Importantly, unidirectional benefits were consistently associated with the more extreme cold and dry climates that are more resource-limited than warm and wet climates (Figs. 2 and 3). This supports the idea that environmental filtering increases in intensity where resources are more limited [62]. Single optimum traits were observed in cold and dry climates, while single trait optima were not observed in warmer and wetter climates. In other words, warm and wet climates exerted no clear directional selection on root traits. This may also partially explain why biodiversity is higher in warm and wet climates and lower in cold and dry climates. Given the prevalence of unidirectional benefits, revisiting evidence for trade-offs between aboveground traits and environmental gradients using model-based predictions is a research priority.

References

1 Agrawal, A. A. A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology* **101**, e02924, (2020).

2 Agrawal, A. A., Conner, J. K. & Rasmann, S. in *Evolution since Darwin: the First 150 Years* Vol. 150 243-268 (2010).

3 Futuyma, D. J. & Moreno, G. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* **19**, 207-233, (1988).

4 Grime, J. P. & Pierce, S. *The Evolutionary Strategies that Shape Ecosystems*. (John Wiley & Sons, 2012).

5 Fry, J. D. Detecting ecological trade-offs using selection experiments. *Ecology* **84**, 1672-1678, (2003).

6 Grubb, P. J. Trade-offs in interspecific comparisons in plant ecology and how plants overcome proposed constraints. *Plant Ecology & Diversity* **9**, 3-33, (2016).

7 Kneitel, J. M. & Chase, J. M. Trade- offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* **7**, 69-80, (2004).

8 Tilman, D. *Plant strategies and the dynamics and structure of plant communities*. (Princeton University Press, 1988).

9 Lusk, C. H. & Jorgensen, M. A. The whole-plant compensation point as a measure of juvenile tree light requirements. *Functional Ecology* **27**, 1286-1294, (2013).

10 Ho, M. D., Rosas, J. C., Brown, K. M. & Lynch, J. P. Root architectural tradeoffs for water and phosphorus acquisition. *Functional Plant Biology* **32**, 737-748, (2005).

11 Forister, M. L. & Jenkins, S. H. A Neutral Model for the Evolution of Diet Breadth. *The American Naturalist* **190**, E40-E54, (2017).

12 Laughlin, D. C., Strahan, R. T., Adler, P. B. & Moore, M. M. Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. *Ecology Letters* **21**, 411-421, (2018).

13 Pollock, L. J., Morris, W. K. & Vesk, P. A. The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* **35**, 716-725, (2012).

14 Mason, N. W. H. *et al.* Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology* **100**, 678-689, (2012).

15 Gompert, Z. *et al.* The evolution of novel host use is unlikely to be constrained by trade-offs or a lack of genetic variation. *Molecular Ecology* **24**, 2777-2793, (2015).

16 Laliberté, E. Below-ground frontiers in trait-based plant ecology. *New Phytologist* **213**, 1597-1603, (2017).

17 Bergmann, J. *et al.* The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**, eaba3756, (2020).

18 Tedersoo, L., Bahram, M. & Zobel, M. How mycorrhizal associations drive plant population and community biology. *Science* **367**, eaba1223, (2020).

19 Kong, D. *et al.* Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* **203**, 863-872, (2014).

20 Ma, Z. *et al.* Evolutionary history resolves global organization of root functional traits. *Nature* **555**, 94-97, (2018).

21 Weemstra, M. *et al.* Towards a multidimensional root trait framework: a tree root review. *New Phytologist* **211**, 1159-1169, (2016).

22 Kramer-Walter, K. R. *et al.* Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* **104**, 1299-1310, (2016).

23 Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167-171, (2016).

24 Tedersoo, L. *et al.* Global diversity and geography of soil fungi. *Science* **346**, 1256688, (2014).

25 Steidinger, B. S. *et al.* Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**, 404-408, (2019).

26 Soudzilovskaia, N. A. *et al.* Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications* **10**, 5077, (2019).

27 Kytöviita, M.-M. Asymmetric symbiont adaptation to Arctic conditions could explain why high Arctic plants are non-mycorrhizal. *FEMS Microbiology Ecology* **53**, 27-32, (2005).

28 Augé, R. M., Toler, H. D. & Saxton, A. M. Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. *Mycorrhiza* **25**, 13-24, (2015).

29 Gill, R. A. & Jackson, R. B. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**, 13-31, (2000).

30 Butterfield, B. J., Bradford, J. B., Munson, S. M. & Gremer, J. R. Aridity increases below-ground niche breadth in grass communities. *Plant Ecology* **218**, 385-394, (2017).

31 Bruelheide, H. *et al.* sPlot – A new tool for global vegetation analyses. *Journal of Vegetation Science* **30**, 161-186, (2019).

32 Guerrero-Ramírez, N. R. *et al.* Global root traits (GRooT) database. *Global Ecology and Biogeography* **30**, 25-37, (2021).

33 Valverde-Barrantes, O. J., Freschet, G. T., Roumet, C. & Blackwood, C. B. A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist* **215**, 1562-1573, (2017).

34 Kong, D. *et al.* Nonlinearity of root trait relationships and the root economics spectrum. *Nature Communications* **10**, 2203, (2019).

35 Fort, F. & Freschet, G. T. Plant ecological indicator values as predictors of fine-root trait variations. *Journal of Ecology*, (2020).

36 Purcell, A. S. T., Lee, W. G., Tanentzap, A. J. & Laughlin, D. C. Fine Root Traits Are Correlated with Flooding Duration while Aboveground Traits Are Related to Grazing in an Ephemeral Wetland. *Wetlands* **39**, 291-302, (2019).

37 Laughlin, D. C., Fulé, P. Z., Huffman, D. W., Crouse, J. & Laliberté, E. Climatic constraints on trait-based forest assembly. *Journal of Ecology* **99**, 1489-1499, (2011).

38 Simpson, A. H., Richardson, S. J. & Laughlin, D. C. Soil–climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography* **25**, 964-978, (2016).

39 Chen, W., Zeng, H., Eissenstat, D. M. & Guo, D. Variation of first-order root traits across climatic gradients and evolutionary trends in geological time. *Global Ecology and Biogeography* **22**, 846-856, (2013).

40 Freschet, G. T. *et al.* Climate, soil and plant functional types as drivers of global fine-root trait variation. *Journal of Ecology* **105**, 1182-1196, (2017).

41 Ostonen, I. *et al.* Adaptive root foraging strategies along a boreal–temperate forest gradient. *New Phytologist* **215**, 977-991, (2017).

42 Wang, R. *et al.* Different phylogenetic and environmental controls of first-order root morphological and nutrient traits: Evidence of multidimensional root traits. *Functional Ecology* **32**, 29-39, (2018).

43 Craine, J. M. & Lee, W. G. Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia* **134**, 471-478, (2003).

44 Craine, J. M., Lee, W. G., Bond, W. J., Williams, R. J. & Johnson, L. C. Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology* **86**, 12-19, (2005).

45 Zadworny, M. *et al.* Patterns of structural and defense investments in fine roots of Scots pine (Pinus sylvestris L.) across a strong temperature and latitudinal gradient in Europe. *Global Change Biology* **23**, 1218-1231, (2017).

46 Oliverio, A. M. *et al.* The global-scale distributions of soil protists and their contributions to belowground systems. *Science Advances* **6**, eaax8787, (2020).

47 Bennett, A. E., Grussu, D., Kam, J., Caul, S. & Halpin, C. Plant lignin content altered by soil microbial community. *New Phytologist* **206**, 166-174, (2015).

48 Moore, B. D. & Johnson, S. N. Get Tough, Get Toxic, or Get a Bodyguard: Identifying Candidate Traits Conferring Belowground Resistance to Herbivores in Grasses. *Frontiers in Plant Science* **7**, (2017).

49 Delgado-Baquerizo, M. *et al.* The proportion of soil-borne pathogens increases with warming at the global scale. *Nature Climate Change*, (2020).

50 de la Riva, E. G. *et al.* Root traits across environmental gradients in Mediterranean woody communities: are they aligned along the root economics spectrum? *Plant and Soil* **424**, 35-48, (2018).

51 Hacke, U. G., Sperry, J. S. & Pittermann, J. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology* **1**, 31-41, (2000).

52 Wright, I. J., Reich, P. B. & Westoby, M. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* **15**, 423-434, (2001).

53 Wang, B. *et al.* Presence of three mycorrhizal genes in the common ancestor of land plants suggests a key role of mycorrhizas in the colonization of land by plants. *New Phytologist* **186**, 514-525, (2010).

54 Grubb, P. in *The population structure of vegetation* Vol. Handbook of Vegetation Science Vol 3 (ed J. White) 595-621 (Dr. W. Junk Publishers, 1985).

55 Laughlin, D. C. *et al.* Quantifying multimodal trait distributions improves trait-based predictions of species abundances and functional diversity. *Journal of Vegetation Science* **26**, 46-57, (2015).

56 Pfahl, S., O’Gorman, P. A. & Fischer, E. M. Understanding the regional pattern of projected future changes in extreme precipitation. *Nature Climate Change* **7**, 423-427, (2017).

57 Read, D. J. Mycorrhizas in ecosystems. *Experientia* **47**, 376-391, (1991).

58 Bruelheide, H. *et al.* Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* **2**, 1906-1917, (2018).

59 Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821-827, (2004).

60 Kumordzi, B. B. *et al.* Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants. *Functional Ecology* **33**, 1771-1784, (2019).

61 Velázquez, E., Paine, C. E. T., May, F. & Wiegand, T. Linking trait similarity to interspecific spatial associations in a moist tropical forest. *Journal of Vegetation Science* **26**, 1068-1079, (2015).

62 Butterfield, B. J. Environmental filtering increases in intensity at both ends of climatic gradients, though driven by different factors, across woody vegetation types of the southwest USA. *Oikos* **124**, 1374-1382, (2015).

63 Iversen, C. M. *et al.* A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist* **215**, 15-26, (2017).

64 Kattge, J. *et al.* TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**, 119-188, (2020).

65 Pakeman, R. J. & Quested, H. M. Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science* **10**, 91-96, (2007).

66 Karger, D. N. *et al.* Climatologies at high resolution for the earth's land surface areas. *Scientific Data* **4**, 170122, (2017).

67 Zomer, R. J., Trabucco, A., Bossio, D. A. & Verchot, L. V. Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment* **126**, 67-80, (2008).

68 Olson, D. M. *et al.* Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933-938, (2001).

69 Jamil, T., Ozinga, W. A., Kleyer, M. & ter Braak, C. J. F. Selecting traits that explain species–environment relationships: a generalized linear mixed model approach. *Journal of Vegetation Science* **24**, 988-1000, (2013).

70 Miller, J. E. D., Damschen, E. I. & Ives, A. R. Functional traits and community composition: a comparison among community-weighted means, weighted correlations, and multilevel models. *Methods in Ecology and Evolution* **10**, 415-425, (2018).

71 R Development Core Team. *R 3.6.1: A language and environment for statistical computing*, <http://www.R-project.org/> (2019).

72 Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag, 2016).

73 Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1-48, (2015).

74 Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* **82**, 1-26, (2017).

75 Lüdecke, D., Makowski, D. & Waggoner, P. performance: Assessment of Regression Models Performance. R package version 0.4.2. (2019).

76 Stefan, V. & Levin, S. plotbiomes: Plot Whittaker biomes with ggplot2. R package version 0.0.0.9001., (2020).

77 Roberts, D. W. labdsv: Ordination and Multivariate Analysis for Ecology. R package version 1.8.0. https://CRAN.R-project.org/package=labdsv. (2016).

78 Anderson, D. R. *Model based inference in the life sciences: a primer on evidence*. (Springer Science & Business Media, 2008).

Acknowledgements:

We thank the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig for supporting the sRoot and sPlot working groups and the University of Wyoming Advanced Research Computing Center for their technical support. sPlot was initiated by sDiv and funded by the German Research Foundation (FZT 118), and now is a platform of iDiv. The sRoot workshops and LM were also supported by NWO-Vidi grant 864.14.006. CMI and FRED were supported by the Biological and Environmental Research program in the U.S. Department of Energy's Office of Science. JB was supported by Deutsche Forschungsgemeinschaft (DFG) - project 432975993. NG-R thanks the Dorothea Schlözer Postdoctoral Programme of the Georg-August-Universität.

Author contributions:

AW, LM, HB and DCL conceived the idea for the project; all authors were involved in collecting datasets, developing the conceptual framework and interpreting the results; DCL, FMS and HB performed the statistical analyses; DCL wrote the first draft of the manuscript; all authors commented on and agreed with the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Table 1. Model support and summary of results for root trait-climate interactions. Each of the eight models were evaluated for their support for a trait-by-environment interaction in forests, grasslands, and wetlands. Statistical evidence was evaluated by inspecting the significance of the coefficient in the model, the model R^2, the *AIC* difference (ΔAIC) between models with the environment alone versus models with both environment and traits (see full model description in Methods), and a likelihood ratio test (LRT). Number of observations for each test are provided in Table S1.

		Generalized Linear Mixed Effects Model Results				**Comparison with Environment-only model**		**Interpretation**	
Trait and climate variables	**Vegetation type**	**Trait-Env interaction coefficient (Std. Error)**	***P*-value for interaction coefficient**	R^2_m	R^2_c	ΔAIC	***LRT*** χ^2 **with** $df=2$ **(*P*-value)**	**Hypothesized direction supported?**	**Nature of Trade-off**
SRL - Temp	Forests	-0.50 (0.03)	$P < 2e-16$	0.06	0.77	-36	39.6 (P=2.556e-09)	Yes	Trade-off
	Grasslands	-0.19 (0.01)	$P < 2e-16$	0.05	0.79	-51	55.0 (P=1.144e-12)	Yes	Unidirectional
	Wetlands	0.04 (0.04)	$P = 0.277$	0.01	0.48	+3	1.1 (P=0.5694)	Yes	No interaction
RD - Temp	Forests	0.17 (0.04)	$P = 3.79e-05$	0.06	0.77	-22	26.5 (P=1.731e-06)	Yes	Unidirectional
	Grasslands	0.20 (0.01)	$P < 2e-16$	0.04	0.82	-21	25.5 (P=2.885e-06)	Yes	No interaction*
	Wetlands	-0.04 (0.04)	$P = 0.2652$	0.01	0.55	2	1.3 (P=0.5224)	Yes	No interaction
SRL - P:PET	Forests	0.19 (0.04)	$P = 2.31e-07$	0.05	0.75	-31	35.1 (P=2.422e-08)	Yes	Unidirectional
	Grasslands	0.38 (0.01)	$P < 2e-16$	0.11	0.79	-74	78.0 (P<2.2e-16)	Yes	Unidirectional
	Wetlands	0.005 (0.03)	$P = 0.88498$	0.01	0.49	+3	0.7 (P=0.708)	Yes	No interaction
RD - P:PET	Forests	0.01 (0.03)	$P = 0.623$	0.08	0.70	-37	41.2 (P=1.132e-09)	No	No interaction
	Grasslands	-0.17 (0.01)	$P < 2e-16$	0.06	0.78	-12	16.2 (P=0.000308)	Yes	No interaction*
	Wetlands	-0.01 (0.04)	$P = 0.775$	0.02	0.55	3	1.8 (P=0.4121)	Yes	No interaction
RTD - Temp	Forests	0.41 (0.05)	$P = 2.45e-14$	0.07	0.74	-34	38.3 (P=4.772e-09)	No	Trade-off
	Grasslands	0.26 (0.02)	$P < 2e-16$	0.03	0.82	-8	12.0 (P=0.0025)	No	Unidirectional
	Wetlands	-0.02 (0.04)	$P = 0.5587$	0.01	0.49	+3	1.8 (P=0.4072)	Yes	No interaction
Root N - Temp	Forests	-0.05 (0.03)	$P = 0.1040$	0.02	0.69	-2	6.5 (P=0.03947)	No	No interaction
	Grasslands	0.03 (0.03)	$P = 0.27539$	0.01	0.74	2	2.4 (P=0.2956)	No	No interaction
	Wetlands	0.10 (0.06)	$P = 0.0929$	0.08	0.60	0	4.1 (P=0.1296)	Yes	No interaction

RTD - P:PET	Forests	-0.13 (0.04)	*P* = 0.000503	0.04	0.63	-20	23.9 (*P*=6.54e-06)	Yes	Unidirectional
	Grasslands	-0.12 (0.02)	*P* = 1.6e-11	0.04	0.77	-4	8.0 (*P*=0.01788)	Yes	No interaction*
	Wetlands	0.01 (0.03)	*P* = 0.8406	0.00	0.48	+2	2.0 (*P*=0.3729)	Yes	No interaction
Root N - P:PET	Forests	-0.14 (0.03)	*P* = 7.01e-06	0.04	0.74	-2	6.1 (*P*=0.04621)	No	Unidirectional
	Grasslands	-0.15 (0.03)	*P* = 2.96e-09	0.04	0.79	-4	7.8 (*P*=0.01977)	No	No interaction*
	Wetlands	-0.14 (0.05)	*P* = 0.00994	0.07	0.55	-2	6.4 (*P*=0.04018)	No	No interaction

R^2_m = deviance explained by fixed effects

R^2_c = deviance explained by fixed and random effects (see Methods for list of random effects)

$\Delta AIC = AIC_{TxE} - AIC_E$; that is, AIC of model *TxE* minus AIC of model *E* (see Methods). Models with ΔAIC that are more negative than -4 are more supported than the simpler model E

χ^2 = chi-square statistic for likelihood ratio test (LRT) comparing models *TxE* and *E* with 2 *df*

SRL = specific root length (m g^{-1})

RTD = root tissue density (mg mm^{-3})

RD = root diameter (mm)

Root N = root nitrogen concentration (mg g^{-1})

Temp = minimum temperature in the coldest month (degree C)

P:PET = Precipitation : Potential Evapotranspiration ratio (mm mm^{-1})

*Four models marked by an asterisk (described in text) exhibited significant trait-by-environment interaction coefficients and likelihood ratio tests, yet the illustrated model predictions in Figures 2 and 3 did not exhibit clear trade-off or unidirectional benefits, so we classify them as “no interaction” here because of our conservative criterion

Figure Captions

Figure 1. The ecological consequences of trait variation on species distributions along climatic gradients. (A) Empirical evidence for an ecological trade-off requires the existence of a strong trait-environment interaction [1,12]. Here we illustrate examples for both positive and negative trait-environment interactions driving species occurrences. In the case of a positive interaction between a trait and an environmental gradient, the effect of the trait on the probability of species occurrence at the low end of an environmental gradient would be negative, but this effect will switch directions and become positive at the high end of the gradient (see left-hand column). This result would imply that a high trait value is beneficial at the high end of the gradient and a low trait value is beneficial at the low end of the gradient (see middle and right-hand columns). (B) Alternatively, if a statistical trait-environment interaction is detected, yet the trait only exhibits an effect at one end of the environmental gradient (i.e., the effects do not switch direction along the gradient), then this suggests there is only a 'unidirectional benefit'. Evidence for a unidirectional benefit for two alternative cases are illustrated for the positive interaction scenario. (C) We scrutinized the existence of trade-offs using plant roots, which have recently been shown to vary among species along two independent trait axes [17]. One axis is described by variation in investment in high specific root length (SRL) versus large root diameter (RD), and the other axis is described by variation between investment in high root tissue density (RTD) versus metabolically-active roots with high root nitrogen (root N). The location in the root economics space of five species discussed in the main text are shown on the biplot: *Vaccinium vitis-idaea (Vv)* is a high-SRL ErM species*, Draba nemorosa (Dn)* is a high-SRL AM species with low colonization rates*, Cunninghami lanceolata (Cl)* is a low-SRL AM species*, Lonicera chrysantha (Lc)* is a low-RTD species*,* and *Myrtus communis (Mc)* is a high-RTD

species. (D) We developed four hypotheses using first principles about the adaptive value of these roots traits along global climatic gradients, where temperature is illustrated as a gradient from blue to red (*i.e.*, cold to warm) and water availability is illustrated as a gradient from gold to green (*i.e.*, dry to wet).

Figure 2. Specific root length (SRL) and root diameter (RD) are related to species occurrences along climatic gradients. The left-hand column illustrates how the sign of the relationship between the trait and the probability of occurrence changes along gradients of mean minimum temperature of the coldest month and the precipitation-to-potential evapotranspiration ratio (P:PET) in forests, grasslands, and wetlands. The y-axis of the left-hand column is the partial derivative of probability of occurrence with respect to traits ($\partial y / \partial T$) to demonstrate whether the effect of the trait on probability of occurrence changes sign along the climatic gradient. Biologically meaningful interactions switch sign, which is indicated if the lines cross the horizontal dotted line. The middle and right-hand columns illustrate model predictions (including 95% confidence intervals) for forests and grasslands, respectively (wetlands are not shown because no interactions were significant). A trade-off was only evident in panel B, where trait values exhibited different effects on occurrences at different ends of the environmental gradients. In contrast, unidirectional benefits were evident in panels C, E, H, and I. Note that the flat lines that hover close to zero probability are interpreted as ‘equally likely to occur across the root trait gradient’ because the average probability of occurrence is near zero; this is because absences (i.e., zeros) comprise ~99% of the dataset.

Figure 3. Root tissue density (RTD) and root nitrogen concentration (Root N) are related to species occurrences along climatic gradients. The left-hand column illustrates how the sign of the relationship between the trait and the probability of occurrence changes along gradients of mean minimum temperature of the coldest month and the precipitation-to-potential evapotranspiration ratio (P:PET) in forests, grasslands, and wetlands. The y-axis of the left-hand column is the partial derivative of probability of occurrence with respect to traits ($\partial y/\partial T$) to demonstrate whether the effect of the trait on probability of occurrence changes sign along the climatic gradient. Biologically meaningful interactions switch sign, which is indicated if the lines cross the horizontal dotted line. The middle and right-hand columns illustrate model predictions (and 95% confidence intervals) for forests and grasslands, respectively (wetlands are not shown because no interactions were significant). A trade-off was only evident in panel B. In contrast, unidirectional benefits were evident in panels C, H, and K. Note that the flat lines that hover close to zero probability are interpreted as 'equally likely to occur across the root trait gradient' because the average probability of occurrence is near zero; this is because absences (i.e., zeros) comprise ~99% of the dataset.

Methods

Data synthesis

To test the adaptive value of root traits along gradients in temperature and water availability, we joined the global vegetation plot database (sPlot) [31] with the global root trait database (GRooT) [32], which combines observations from the Fine-Root Ecology Database (FRED) [63] with root data in TRY [64], as well as additional incorporated literature. This dataset has strong representation of AM, EcM, and ErM mycorrhizal types but only a few non-mycorrhizal species.

We computed species-level averages of the most commonly measured fine root traits by first calculating the mean value of a species within a study and then averaging those values for a species across studies. We cannot say anything about plasticity or intraspecific trait variation in this study given that we were only able to analyze average trait values of species. RTD values reported to be > 1.0 mg mm^{-3} were excluded from this study. This resulted in a dataset of 1,767 species with specific root length (SRL; m g^{-1}) and 1,426 species with root tissue density (RTD; mg mm^{-3}), 1,283 species with root nitrogen concentration (root N, mg g^{-1}), and 1,623 species with root diameter (RD; mm). Out of the 2,122 species in GRooT, 1,638 species were present in sPlot for a total of 998,669 vegetation records. We discarded all plots that contained < 80% trait coverage based on relative cover [65] for a total of 152,771 plots with SRL data, 154,192 plots with RD data, 107,325 plots with RTD data, and 109,494 plots with root N data.

The majority of plots were located in Europe, Asia, North America, and Australia (Fig S1A). Plots were found within all global biomes except tropical rainforests but were most representative of temperate seasonal forest, boreal forest, woodland-shrubland, and temperate grassland-desert biomes (Fig S1B). The paucity of root trait data in tropical forests prevented us from including these biomes in our analysis, highlighting the importance of new data collection in tropical ecosystems. We used the geographical coordinates of each plot to compile climate data and ecoregion classification. The average minimum temperature in the coldest month was downloaded from CHELSA (~1 km resolution) [66]. The correlation between minimum temperature and P:PET was weak and negative (r = -0.12) (Fig. S1D). Model results were qualitatively similar if mean annual temperature was used instead of minimum temperature of the coldest month. Water availability was expressed as the precipitation-to-potential evapotranspiration ratio (P:PET) using the global Aridity index raster (~1 km resolution) [67].

Information on vegetation types was only available for a subset of plots in sPlot, and most of these classified plots were located in Europe. To have all plots consistently assigned to vegetation types, we ran one classification based on species' affinities to forest, grassland, savanna, heathland, steppe, wetland, and other, as assigned based on expert opinion (available in Supplementary Material). Based on the relative cover of each species within a given plot, we summarized species based on their habitat affinities, and summed their relative cover. We then assigned each plot to a habitat based on the following if-else conditions: if the pooled relative cover of species with wetland affinities > 0.5, then it was classified as "Wetland", if the relative cover of species with forest affinities > 0.3, then it was classified as "Forest", if the relative cover of species with either grassland, savanna, heathland, or steppe > 0.7, then we classified it as "Grassland". These three if-else conditions were sequential, so that a plot assigned to "Wetland", could not be also assigned to "Forest" or "Grassland". We selected the thresholds iteratively, in order to maximize the overall accuracy of the classification based on species' habitat affinity, when tested against sPlot's native habitat classification. Out of the 202,942 plots we considered, 23,885 were assigned to "Wetland", 65,618 to "Forest" and 103,009 to "Grassland". Another 10,420 remained unassigned and were removed from the analysis. The overall accuracy of the classification was 0.67 and the Kappa statistic was 0.49. Compositional differences among the three vegetation types are illustrated by a Principal Coordinates Analysis using Bray-Curtis distances (Fig S1D). We included savanna species within grasslands and did not include a 'savanna' category for two main reasons: 1) no plots in our dataset occurred in the savanna regions of South America or Africa, and 2) the compositional data available to us could not be used to reliably discern a savanna from a forest or grassland. This decision had no appreciable affect on the results because the direction of the trait-environment interactions detected in this study were relatively consistent between grassland and forest, so adding additional vegetation types that are intermediary between the two would not have affected the results.

Each plot was categorized into ecoregions using Olson et al's ecoregion classification system [68] to account for the spatial structure of the data and to define regional species pools. Regional species pools were defined as all species detected in plots within an ecoregion, and we defined species absences based on these regional species pools. Species that were not detected on plot *x* but were found on other plots within the ecoregion were considered absent in plot *x*. We did this to prevent a situation where a species has zero probability of being in a plot; for example, we prevented a subtropical species from being considered 'absent' from a plot in the taiga. This method accounts for the fact that species may be absent from a plot because of biogeographical dispersal limitation, not just because of environmental filtering. We removed all ecoregions with < 200 observations, which eliminated observations from South America and Africa. The final number of plots used in each model is listed in Table S1.

Data analysis

We fit hierarchical models using Generalized Linear Mixed Effects Models to test whether root traits explain species occurrences by their interactions with climatic gradients [13,69], which is the most appropriate method for evaluating how trait-environment interactions drive species occurrences [70]. We modeled binomial species presence-absence data using a logit link function and binomial error structure. Given the size of the dataset, all models were fit in parallel using an Intel compiled version of R on the high-performance computer cluster at the University of Wyoming, where several days to four weeks were required to achieve model convergence. We used the following packages in R version 3.6.1 [71] to conduct our analyses: stats [71], ggplot2 [72], lme4 [73], lmerTest [74], performance [75], plotbiomes [76], and labdsv [77].

First, we fit an 'environment-only model', which fit quadratic polynomials to all species simultaneously with respect to the climate factor. The quadratic polynomial was especially important to accurately capture the broad variation in species environmental optima across such vast climatic gradients. We also controlled for variation in occurrences within each ecoregion by modelling ecoregions as random intercepts, which was important given the strong bias of number of plots in European ecoregions. In summary, for each climatic factor we fit the following hierarchical model ('model *E*'):

$$logit(y) = \beta_0 + \gamma_{j0} + \delta_{k0} + \left(\beta_1 + \gamma_{j1}\right) climate + \left(\beta_2 + \gamma_{j2}\right) climate^2$$

where y was binomial presence and absence, β_0 was the global intercept, $\beta_1$was the fixed effect term describing the main effect of the climatic gradient, $\beta_2$was the fixed effect term describing the main effect of the squared-climatic term, which allowed to model optimum environments for each species, γ_{j0} was a random intercept for each of j species drawn from a normal distribution $N(0,\sigma^2_{\gamma j0})$, δ_{k0} was a random intercept for each of k ecoregions drawn from a normal distribution $N(0,\sigma^2_{\delta k0})$, γ_{j1} was a random slope for each of j species drawn from a normal distribution $N(0,\sigma^2_{\gamma j1})$, and γ_{j2} was a random slope for each of j species drawn from a normal distribution $N(0,\sigma^2_{\gamma j2})$. We used the quadratic polynomial random effects from this model to compute the optimum temperature and water availability for each species, *i.e.*, the value of the climatic variables where the species attains its highest probability of occurrence. We regressed these on the trait values of each species, where the relative abundance of each species in the dataset were used as weights in the regression (see Fig. S2). The lme4 syntax for this model was `glmer(occurrence ~ climate + climate² + (climate + climate²|species) + (1|ecoregion), family=binomial).`

Second, we fit 'trait-by-environment interaction models', which included one root trait and its interaction with climate, to test if traits explain any additional information about the changing probabilities of species occurrences along the climatic gradients. For each trait and climatic factor combination we fit the following hierarchical model ('model *TxE'*):

$$logit(y) = \beta_0 + \gamma_{j0} + \delta_{k0} + (\beta_1 + \gamma_{j1})climate + (\beta_2 + \gamma_{j2})climate^2 + (\beta_3)trait + (\beta_4)trait \cdot climate$$

where $\beta_3$was the fixed effect term describing the main effect of traits, and β_4 was the fixed effect term describing the interaction between the trait and the climatic gradient. The lme4 syntax for this model was `glmer(occurrence ~ climate + climate² + trait + trait:climate + (climate + climate²|species) + (1|ecoregion), family=binomial).`

To evaluate the empirical support for the trait-environment interaction, we compared model '*TxE'* model to model '*E*'. Given the statistical power of the large dataset, we used three criteria to assess the evidence of whether species occurrences can be explained by trait-environment interactions: 1) differences in *AIC* between the two models (i.e., $AIC_{TxE} - AIC_E$) that were < -4 (i.e., an absolute difference > 4) [78], 2) significant likelihood ratio tests using a chi-square statistic, and 3) a significant fixed effect interaction term in the linear predictor. All three criteria needed to be met to consider these to be important interactions. We used a threshold of AIC differences more negative than -4 following suggested rules of thumb for model comparison [78].

We further classified these significant interactions into two general types: 1) "trade-offs" and 2) "unidirectional benefits". Trade-offs occur where certain trait values confer adaptive advantage at one end of an environmental gradient and other trait values confer benefits at the opposite end of the gradient (Fig. 1A). Unidirectional benefits occur when a trait confers an adaptive advantage at only one end of an environmental gradient (Fig. 1B). In order to be considered a 'trade-off', the effect of traits on probability of occurrence had to switch signs between each end of the environmental gradient [12]. To test this, we illustrate the first partial derivative of the model with respect to the trait ($\partial y/\partial T$) to demonstrate how the effect of the trait on probability of occurrence changes along the climatic gradient. A significant positive interaction would be illustrated as a line with positive slope that passes through $\partial y/\partial T = 0$ (Fig. 1A). In contrast, 'unidirectional benefits' were interactions where a trait exhibits an effect on probability of occurrence at one end of the gradient but has no effect on probability of occurrence at the other end of the gradient (Fig. 1B). To operationalize this distinction, we plotted model-predicted probabilities as a function of each trait at the low end (1st percentile) and high end (99th percentile) of each climatic gradient. Given the size of the datasets, these percentiles include thousands of observations. If the probability of occurrence at one end of the gradient did not exceed 5% whereas the probability of occurrence at the other end of the gradient exceeded 5%, then we considered this to be a 'unidirectional benefit'. Given the large number of absences that is typical with sparse community datasets, the average probability of species detection was approximately 0.01, thus a 5% probability would be a five-fold increase from the average. Using these criteria, the nature of each trade-off is listed in Table 1 and Figs. 2 and 3.

We limited our analyses to models with one trait and one climate gradient rather than fitting more complex models with multiple traits and multiple climate gradients. We took this choice to make our work more comparable to other recent work [58] and to achieve a more straightforward interpretation of interactions. We also limited our models to one climate gradient because model convergence was problematic even for the environment-only models (model *E*). These models included hundreds of random slopes and intercepts with respect to climate variables and squared variables to fit quadratic polynomials to account for each species' nonlinear response to climate (Fig. S2). Adding a second climate variable would add hundreds more coefficients to account for each species' nonlinear response to that gradient, and we would need to include their interaction. Finally, we limited models to only one trait because including two traits reduced the number of species with data for both traits that could be included in the model. The occurrence of species-level average trait values are plotted along each climate gradient in Figs. S3 and S4.

Data Availability

All code and data needed to reproduce the model results can be accessed at https://idata.idiv.de/ddm/Data/ShowData/3475