nature ecology & evolution

ARTICLES

https://doi.org/10.1038/s41559-021-01471-7

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

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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 24 models. Forest species with low specific root length and high root tissue density (RTD) were more likely to occur in warm climates but species with high specific root length 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.

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 (the ALLOCATE model) is built on a single trait–environment trade-off[8]. 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 has been found in a variety of traits, including light compensation points along light gradients[9] and root angles along nutrient gradients[10]. However, in many cases, 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 (that is, 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 non-trivial because it cannot be observed through a simple trait–environment correlation[12].

A full list of affiliations appears at the end of the paper.

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, the effect of a trait on the 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 have 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 ($\mathrm{m\,g^{-1}}$); fine root length per unit mass) and root diameter (mm) that has evolved in concert with symbiosis with mycorrhizal fungi. Arbuscular mycorrhizal 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 or ericoid mycorrhizal 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. 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 ($\mathrm{mg\,mm^{-3}}$); fine root mass per unit volume) and acquisitive species construct more metabolically active tissue with low RTD and a high root nitrogen concentration (root N ($\mathrm{mg\,g^{-1}}$))[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 $r=-0.09$ (ref. [17]), which implies that plants have explored the expression of nearly all of the 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.

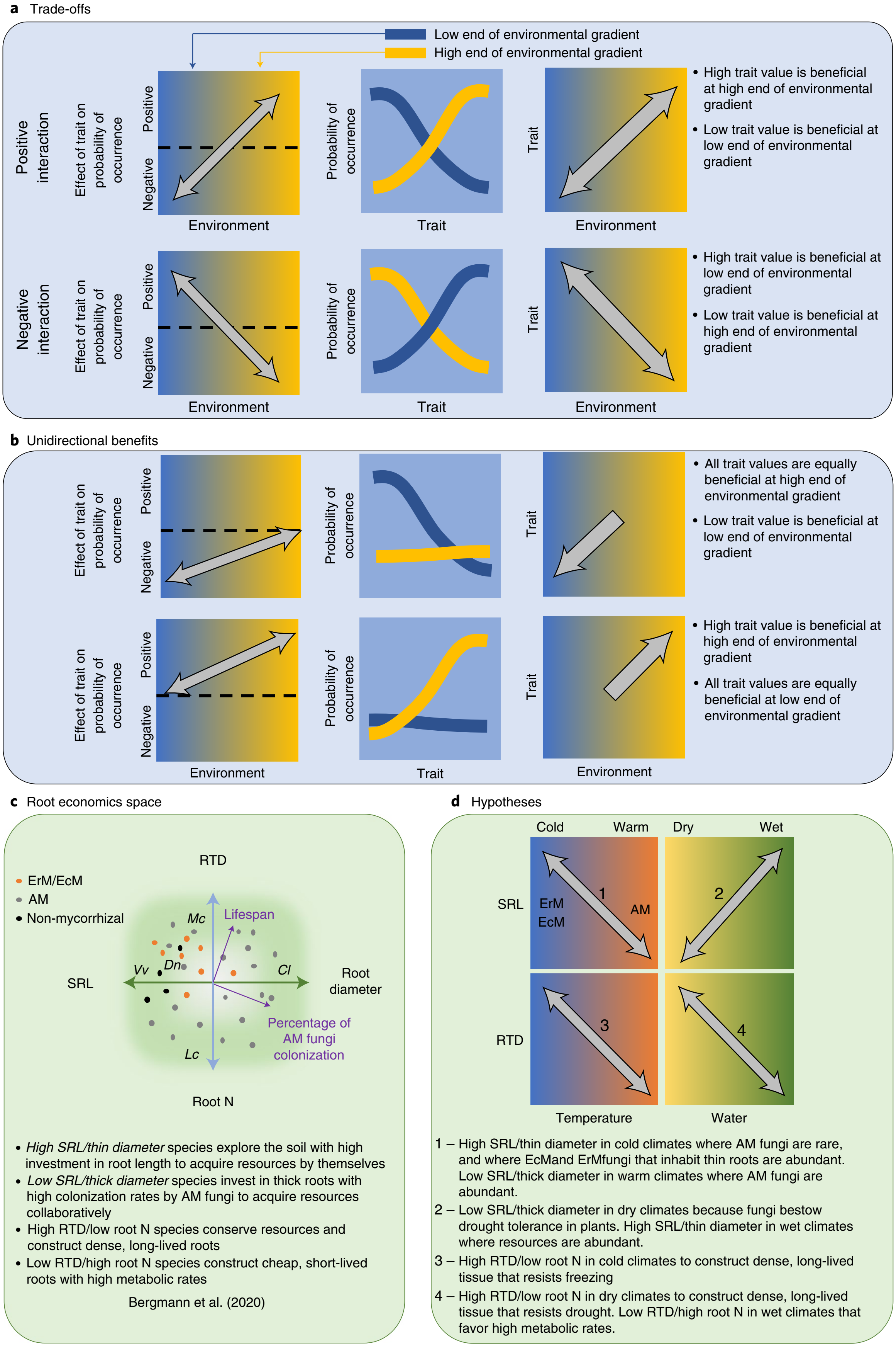
Hypotheses and methods

We developed four hypotheses about how SRL, root diameter, 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 root diameter 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 root diameter and temperature) for several reasons. Species with low SRL would be more prevalent in warm climates where arbuscular mycorrhizal 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) ericoid mycorrhizal and ectomycorrhizal 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 root diameter 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 arbuscular mycorrhizal fungi can be more drought tolerant

Fig. 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 (left). 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 (middle and right). **b**, Alternatively, if a statistical trait–environment interaction is detected, yet the trait only exhibits an effect at one end of the environmental gradient (that is, the effects do not switch direction along the gradient), this suggests there is only a unidirectional benefit. Evidence for a unidirectional benefit for two alternative cases is illustrated in 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 SRL versus large root diameter and the other axis is described by variation between investment in high RTD versus metabolically active roots with high root N. The locations 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 ericoid mycorrhizal (ErM) species; *Draba nemorosa* (*Dn*) is a high-SRL arbuscular mycorrhizal (AM) species with low colonization rates; *Cunninghamia 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. EcM, ectomycorrhizal. **d**, We developed four hypotheses for root trait–climate relationships using first principles about the adaptive value of these root traits along global climatic gradients, where temperature is illustrated as a gradient from blue to red (that is, cold to warm) and water availability is illustrated as a gradient from gold to green (that is, dry to wet).



- High trait value is beneficial at high end of environmental gradient
- Low trait value is beneficial at low end of environmental gradient

- High trait value is beneficial at low end of environmental gradient
- Low trait value is beneficial at high end of environmental gradient

- All trait values are equally beneficial at high end of environmental gradient
- Low trait value is beneficial at low end of environmental gradient

- High trait value is beneficial at high end of environmental gradient
- All trait values are equally beneficial at low end of environmental gradient

- *High SRL/thin diameter* species explore the soil with high investment in root length to acquire resources by themselves
- *Low SRL/thick diameter* species invest in thick roots with high colonization rates by AM fungi to acquire resources collaboratively
- High RTD/low root N species conserve resources and construct dense, long-lived roots
- Low RTD/high root N species construct cheap, short-lived roots with high metabolic rates

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1 – High SRL/thin diameter in cold climates where AM fungi are rare, and where EcMand ErMfungi that inhabit thin roots are abundant. Low SRL/thick diameter in warm climates where AM fungi are abundant.

2 – Low SRL/thick diameter in dry climates because fungi bestow drought tolerance in plants. High SRL/thin diameter in wet climates where resources are abundant.

3 – High RTD/low root N in cold climates to construct dense, long-lived tissue that resists freezing

4 – High RTD/low root N in dry climates to construct dense, long-lived tissue that resists drought. Low RTD/high root N in wet climates that favor high metabolic rates.

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) (Extended Data Fig. 1). We used the 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 (mm mm^{-1})) to represent chronic water limitation. The plots spanned a gradient of −10 to 25 °C mean annual temperature and 50–2,750 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 (Extended Data Fig. 1). 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 of 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 were negative in both forests and grasslands (Table 1 and Fig. 2a) and SRL was negatively correlated with species optimum minimum temperature (Extended Data Fig. 2a,b). Low-SRL species associated with arbuscular mycorrhizal fungi, such as Chinese fir (*Cunninghamia lanceolata*; Fig. 1c), were more likely to occur in warmer climates. High-SRL species associated with ericoid mycorrhizal 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 and 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 and Fig. 2c). Root diameter did not exhibit trade-offs with temperature in forests or grasslands (Table 1 and Fig. 2d–f). Large-diameter roots in forests were advantageous in warm climates, but thin roots were not clearly advantageous in cold climates (Table 1 and Fig. 2e). Thick roots thus exhibit a unidirectional benefit in forests with warm climates where arbuscular mycorrhizal 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 and Fig. 2g) and SRL was positively correlated with the species optimum P:PET ratio (Extended Data Fig. 2c,d). Species with low SRL were more likely to occur in dry environments, probably because arbuscular mycorrhizal fungi that inhabit thicker roots can confer drought tolerance to plants[28] (Fig. 2h,i). In contrast with expectations, species with any SRL value were equally likely to occur in wet environments (Fig. 2h,i), which may explain the lack of a 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 and Fig. 2k,l).

RTD influenced the probability of species occurrence along climatic gradients in forests and grasslands, but not in wetlands (Fig. 3a). In contrast with our third hypothesis and other studies[29,38–43], the RTD–temperature interaction was positive rather than negative (Table 1 and Fig. 3a), and RTD was positively correlated with species optimum minimum temperatures (Extended Data Fig. 2e,f). In forests, species with low RTD, such as honeysuckle (*Lonicera chrysantha*; Fig. 1c), were more likely to occur in cold climates and species with high RTD, such as common myrtle (*Myrtus communis*; Fig. 1c), were more likely to occur in warm climates (Table 1 and 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 to occur in warm climates (Table 1 and 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 and Fig. 3d–f).

RTD did not exhibit a trade-off in relation to water availability (Table 1 and Fig. 3g–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 the species optimum P:PET ratio (Extended Data Fig. 2g,h). In forests, species with a high RTD had greater chances of occurring in drier climates, probably 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 and 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. In contrast with our hypothesis, high root N appeared to be advantageous in dry forests (Table 1 and 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 analysed the largest root trait and vegetation datasets and found that, within forest ecosystems: (1) species with a low SRL, large root diameter or high RTD have a higher chance of occurring in warm climates, while species with a high SRL or low RTD have a higher chance of occurring in cold climates; and (2) species with a low SRL, large root diameter, high RTD and high root N have a

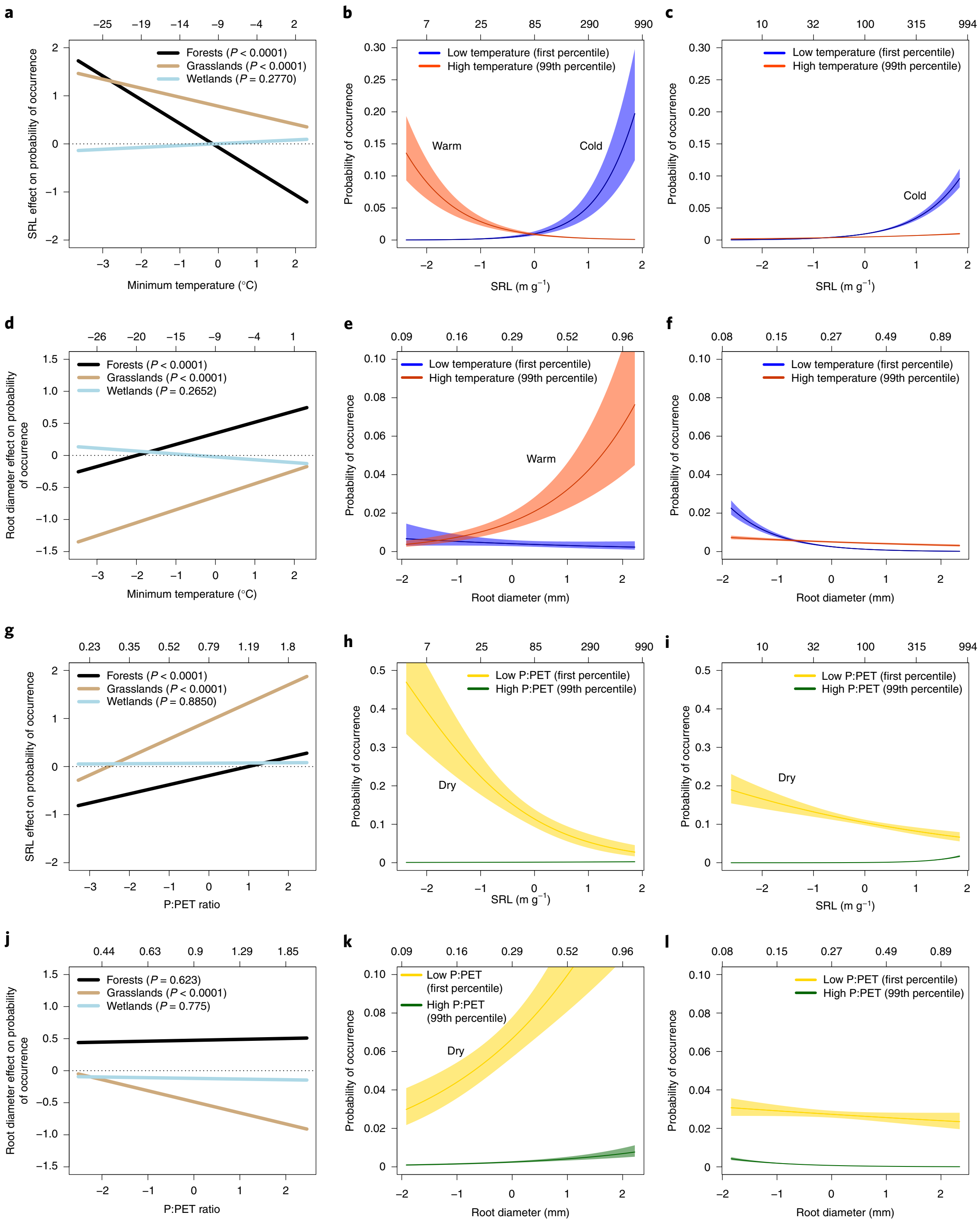

Fig. 2 | Specific root length and root diameter are related to species occurrences along climatic gradients. a,**d**,**g**,**j**, Interactions between root traits and temperature (**a** and **d**) and the precipitation-to-potential evapotranspiration (P:PET) ratio (**g** and **j**) are illustrated as the signs of the relationships between the traits and the probability of occurrence along climatic gradients in forests, grasslands and wetlands. The *y* axes show the partial derivative of the probability of occurrence with respect to traits ($\partial y/\partial T$), to demonstrate whether the effect of the trait on the 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. **b**,**c**,**e**,**f**,**h**,**i**,**k**,**l**, Model predictions (including 95% confidence intervals) of SRL (**b**, **c**, **h** and **i**) and root diameter (**e**, **f**, **k** and **l**) as a function of temperature (**b**, **c**, **e** and **f**) or P:PET ratio (**h**, **i**, **k** and **l**) for forests (**b**, **e**, **h** and **k**) and grasslands (**c**, **f**, **i** and **l**). Wetlands are not shown because no interactions were significant. A trade-off was only evident in **b**, where trait values exhibited different effects on occurrences at different ends of the environmental gradients. In contrast, unidirectional benefits were evident in **c**, **e**, **h** and **i**. No interaction was found in **f**, **k** and **l**. 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 (that is, zeros) comprise ~99% of the dataset. All bottom *x* axes are scaled to unit variance. The top *x* axes are scaled to either the native scale (**a** and **d**) or the log scale (**b**, **c** and **e**–**l**).

Table 1 | Model support and summary of the results for root trait–climate interactions

Trait and climate variables	Vegetation type	Generalized linear mixed-effects model results				Comparison with environment-only model		Interpretation	
		Trait–environment interaction coefficient (s.e.)	P value for interaction coefficient	R^2_m [a]	R^2_c [b]	ΔAIC[c]	LRT χ^2 with d.f. = 2[d] (P value)	Hypothesized direction supported?	Nature of trade-off
SRL–temperature[e]	Forests	−0.50 (0.03)	$P<2\times10^{-16}$	0.06	0.77	−36	39.6 ($P=2.556\times10^{-9}$)	Yes	Trade-off
	Grasslands	−0.19 (0.01)	$P<2\times10^{-16}$	0.05	0.79	−51	55.0 ($P=1.144\times10^{-12}$)	Yes	Unidirectional
	Wetlands	0.04 (0.04)	$P=0.277$	0.01	0.48	+3	1.1 ($P=0.5694$)	Yes	No interaction
Root diameter–temperature[e]	Forests	0.17 (0.04)	$P=3.79\times10^{-5}$	0.06	0.77	−22	26.5 ($P=1.731\times10^{-6}$)	Yes	Unidirectional
	Grasslands	0.20 (0.01)	$P<2\times10^{-16}$	0.04	0.82	−21	25.5 ($P=2.885\times10^{-6}$)	Yes	No interaction[f]
	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)	$P=2.31\times10^{-7}$	0.05	0.75	−31	35.1 ($P=2.422\times10^{-8}$)	Yes	Unidirectional
	Grasslands	0.38 (0.01)	$P<2\times10^{-16}$	0.11	0.79	−74	78.0 ($P<2.2\times10^{-16}$)	Yes	Unidirectional
	Wetlands	0.005 (0.03)	$P=0.88498$	0.01	0.49	+3	0.7 ($P=0.708$)	Yes	No interaction
Root diameter–P:PET	Forests	0.01 (0.03)	$P=0.623$	0.08	0.70	−37	41.2 ($P=1.132\times10^{-9}$)	No	No interaction
	Grasslands	−0.17 (0.01)	$P<2\times10^{-16}$	0.06	0.78	−12	16.2 ($P=0.000308$)	Yes	No interaction[f]
	Wetlands	−0.01 (0.04)	$P=0.775$	0.02	0.55	+3	1.8 ($P=0.4121$)	Yes	No interaction
RTD–temperature[e]	Forests	0.41 (0.05)	$P=2.45\times10^{-14}$	0.07	0.74	−34	38.3 ($P=4.772\times10^{-9}$)	No	Trade-off
	Grasslands	0.26 (0.02)	$P<2\times10^{-16}$	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–temperature[e]	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 ($P=6.54\times10^{-6}$)	Yes	Unidirectional
	Grasslands	−0.12 (0.02)	$P=1.6\times10^{-11}$	0.04	0.77	−4	8.0 ($P=0.01788$)	Yes	No interaction[f]
	Wetlands	0.01 (0.03)	$P=0.8406$	0	0.48	+2	2.0 ($P=0.3729$)	Yes	No interaction
Root N–P:PET	Forests	−0.14 (0.03)	$P=7.01\times10^{-6}$	0.04	0.74	−2	6.1 ($P=0.04621$)	No	Unidirectional
	Grasslands	−0.15 (0.03)	$P=2.96\times10^{-9}$	0.04	0.79	−4	7.8 ($P=0.01977$)	No	No interaction[f]
	Wetlands	−0.14 (0.05)	$P=0.00994$	0.07	0.55	−2	6.4 ($P=0.04018$)	No	No interaction

Each of the eight models was evaluated for its support for a trait–environment interaction in forests, grasslands and wetlands. Statistical evidence was evaluated by inspecting: the significance of the coefficient in the model; model R^2 values; the AIC difference (ΔAIC) between models accounting for the environment alone versus models accounting for both the environment and traits (see full model description in the Methods); and the LRT χ^2 value. The numbers of observations for the various tests are provided in Supplementary Table 1. [a]Deviance explained by fixed effects. [b]Deviance explained by fixed and random effects (see Methods for list of random effects). [c]$\Delta\mathrm{AIC}=\mathrm{AIC}_{\mathrm{T\times E}}-\mathrm{AIC}_{\mathrm{E}}$ (that is, the AIC of model T×E minus the AIC of model E; see Methods). Models with a value of ΔAIC more negative than −4 are more supported than the simpler model E. [d]Chi-squared statistic for an LRT comparing models T×E and E with 2 d.f. [e]Minimum temperature in the coldest month (°C). [f]Models (described in the main text) that exhibited significant trait–environment interaction coefficients and LRTs, yet the illustrated model predictions in Figs. 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.

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–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 (Figs. 2 and 3), rather than relying on trait–environment correlations or the significance of interaction coefficients alone as evidence of a trade-off. The predicted signs (that is, 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 the 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 probably generated by a combination of trade-offs for some traits (for example, light compensation point along light gradients[9]) and unidirectional benefits for others (for example, leaf nutrient concentrations along soil fertility gradients[14,55]), which inevitably makes the task of predicting species responses using continuous traits more difficult than was previously anticipated. When using predictive models that use sets of

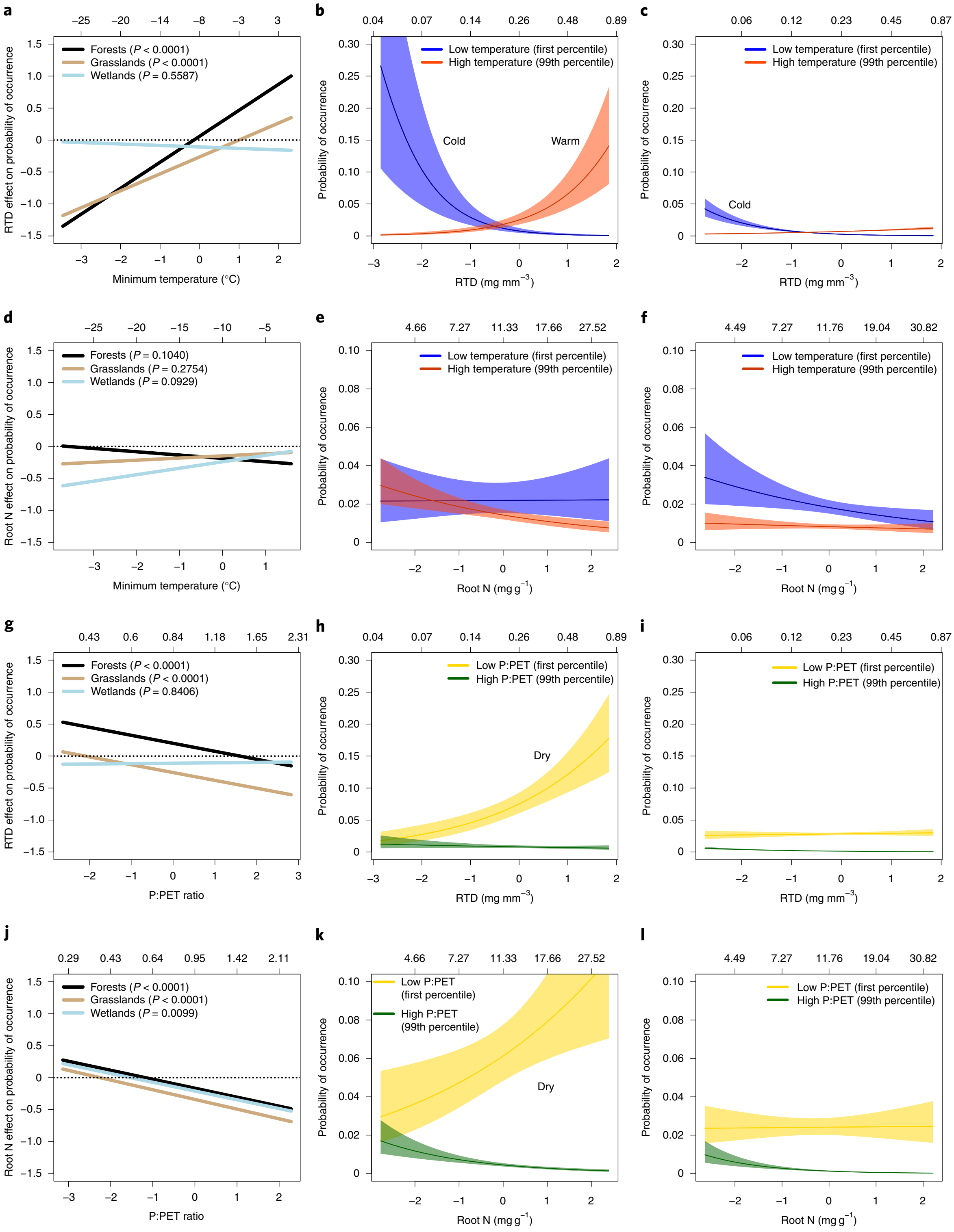

Fig. 3 | RTD and root N are related to species occurrences along climatic gradients. a,**d**,**g**,**j**, Interactions between root traits and temperature (**a** and **d**) and the precipitation-to-potential evapotranspiration (P:PET) ratio (**g** and **j**) are illustrated as the signs of the relationships between the traits and the probability of occurrence along climatic gradients in forests, grasslands, and wetlands. The *y* axes show the partial derivative of the probability of occurrence with respect to traits ($\partial y/\partial T$), to demonstrate whether the effect of the trait on the 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. **b**,**c**,**e**,**f**,**h**,**i**,**k**,**l**, Model predictions (including 95% confidence intervals) of RTD (**b**, **c**, **h** and **i**) and root N (**e**, **f**, **k** and **l**) as a function of temperature (**b**, **c**, **e** and **f**) or P:PET ratio (**h**, **i**, **k** and **l**) for forests (**b**, **e**, **h** and **k**) and grasslands (**c**, **f**, **i** and **l**). Wetlands are not shown because no interactions were significant. A trade-off was only evident in **b**. In contrast, unidirectional benefits were evident in **c**, **h** and **k**. No interaction was found in **e**, **f**, **i** and **l**. 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 (that is, zeros) comprise ~99% of the dataset. All bottom *x* axes are scaled to unit variance. The top *x* axes are scaled to either the native scale (**a** and **d**) or the log scale (**b**, **c** and **e**–**l**).

continuous traits as predictors of species responses, we 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 towards a lower SRL and higher RTD. This would make other trait combinations less viable and put species with a higher SRL or lower RTD at 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 a 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 arbuscular mycorrhizal fungi, but also the evolutionarily younger ectomycorrhizal and ericoid mycorrhizal fungi (which are associated with thinner roots)[20], whereas non-woody plants mostly host arbuscular mycorrhizal fungi, with only a minority of genera being noted for hosting ectomycorrhizal fungi (for example, *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, arbuscular mycorrhizal species tend to dominate warm regions (tropical dipterocarps being notable exceptions), whereas ectomycorrhizal and ericoid mycorrhizal species 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 to populations 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 regimens 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 (for example, competition and 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, whereas 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.

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[63] with root data in TRY[64], as well as additional incorporated literature. This dataset has strong representation of arbuscular mycorrhizal, ectomycorrhizal and ericoid 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 analyse average trait values of species. RTD values reported to be $>1.0\,\mathrm{mg\,mm^{-3}}$ were excluded from this study. This resulted in a dataset of 1,767 species with SRL, 1,426 species with RTD, 1,283 species with root N and 1,623 species with root diameter. 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 root diameter 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 (Extended Data Fig. 1a). 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 (Extended Data Fig. 1b). 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 ($r = -0.12$) (Extended Data Fig. 1d). Model results were qualitatively similar if the mean annual temperature was used instead of the minimum temperature of the coldest month. Water availability was expressed as the P:PET ratio 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 the Supplementary Information). 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 was >0.5, it was classified as wetland; if the relative cover of species with forest affinities was >0.3, it was classified as forest; if the relative cover of species with either grassland, savanna, heathland or steppe was >0.7, it was classified as grassland. These three if–else conditions were sequential, so that a plot assigned to wetland could not also be assigned to forest or grassland. We selected the thresholds iteratively, 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 (Extended Data Fig. 1d). 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 effect on the results because the directions 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 numbers of plots used in the various models are listed in Supplementary Table 1.

Data analysis. We fit hierarchical models using generalized linear mixed-effects models to test whether root traits explained 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 modelled 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 4 weeks were required to achieve model convergence. We used the following packages in R version 3.6.1 (ref. [71]) to conduct our analyses: stats[71], ggplot2 (ref. [72]), lme4 (ref. [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 in the number of plots in European ecoregions. In summary, for each climatic factor, we fit the following environment-only hierarchical model (model E):

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

where y is binomial presence and absence, β_0 is the global intercept, β_1 is the fixed-effect term describing the main effect of the climatic gradient, β_2 is the fixed-effect term describing the main effect of the squared climatic term (which allowed us to model optimum environments for each species), γ_{j0} is a random intercept for each of j species drawn from a normal distribution $N\left(0,\ \sigma^2_{\gamma_{j0}}\right)$, δ_{k0} is a random intercept for each of k ecoregions drawn from a normal distribution $N\,(0,\ \sigma^2_{\delta_{k0}})$, γ_{j1} is a random slope for each of j species drawn from a normal distribution $N\left(0,\ \sigma^2_{\gamma_{j1}}\right)$ and γ_{j2} is a random slope for each of j species drawn from a normal distribution $N\left(0,\ \sigma^2_{\gamma_{j2}}\right)$. We used the quadratic polynomial random effects from this model to compute the optimum temperature and water availability for each species (that is, 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 abundances of each species in the dataset were used as weights in the regression (see Extended Data Fig. 2). The lme4 syntax for this model was glmer(occurrence ~ climate + climate² + (climate + climate²|species) + (1|ecoregion), family = binomial).

Second, we fit trait–environment interaction models, which included one root trait and its interaction with climate, to test whether traits explained 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 trait × environment interaction hierarchical model (model T×E):

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

where β_3 is the fixed-effect term describing the main effect of traits and β_4 is 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 T×E with model E. Given the statistical power of the large dataset, we used three criteria to assess the evidence for whether species occurrences could be explained by trait–environment interactions: (1) differences in the Akaike information criterion (ΔAIC) between the two models (that is, $\mathrm{AIC}_{\mathrm{T\times E}} - \mathrm{AIC}_{\mathrm{E}}$) of less than −4 (that is, an absolute difference of >4)[78]; (2) significant likelihood ratio tests (LRTs) using a chi-squared 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 an 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). To be considered a trade-off, the effect of traits on the 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 the probability of occurrence changes along the climatic gradient. A significant positive interaction would be illustrated as a line with a positive slope that passes through $\partial y/\partial T = 0$ (Fig. 1a). In contrast, unidirectional benefits were interactions where a trait exhibited an effect on the probability of occurrence at one end of the gradient but had no effect on the 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 (first percentile) and high end (99th percentile) of each climatic gradient. Given the size of the datasets, these percentiles included 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%, we considered this to be a unidirectional benefit. Given the large number of absences that are typical with sparse community datasets, the average probability of species detection was approximately 0.01; thus, a 5% probability would be a fivefold 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 (Extended Data Fig. 2). 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 occurrences of species-level average trait values are plotted along each climate gradient in Extended Data Figs. 3 and 4.

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

Data availability

All of the data needed to reproduce the model results can be accessed at https://doi.org/10.25829/idiv.3475-8-2316.

Code availability

All of the code needed to reproduce the model results can be accessed at https://doi.org/10.25829/idiv.3475-8-2316.

Received: 16 November 2020; Accepted: 20 April 2021;

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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 technical support. sPlot was initiated by sDiv and funded by the German Research Foundation (FZT 118) and is now a platform of iDiv. The sRoot workshops and L.M. were also supported by NWO-Vidi grant 864.14.006. C.M.I. and the Fine-Root Ecology Database were supported by the Biological and Environmental Research program in the US Department of Energy's Office of Science. J.B. was supported by Deutsche Forschungsgemeinschaft (DFG) project 432975993. N.R.G.-R. thanks the Dorothea Schlözer Postdoctoral Programme of the Georg-August-Universität.

Author contributions

A.W., L.M., H.B. and D.C.L. conceived of the idea for the project. All authors were involved with collecting datasets, developing the conceptual framework and interpreting the results. D.C.L., F.M.S. and H.B. performed the statistical analyses. D.C.L. 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.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-021-01471-7.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-021-01471-7.

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Peer review information *Nature Ecology & Evolution* thanks Benjamin Delory and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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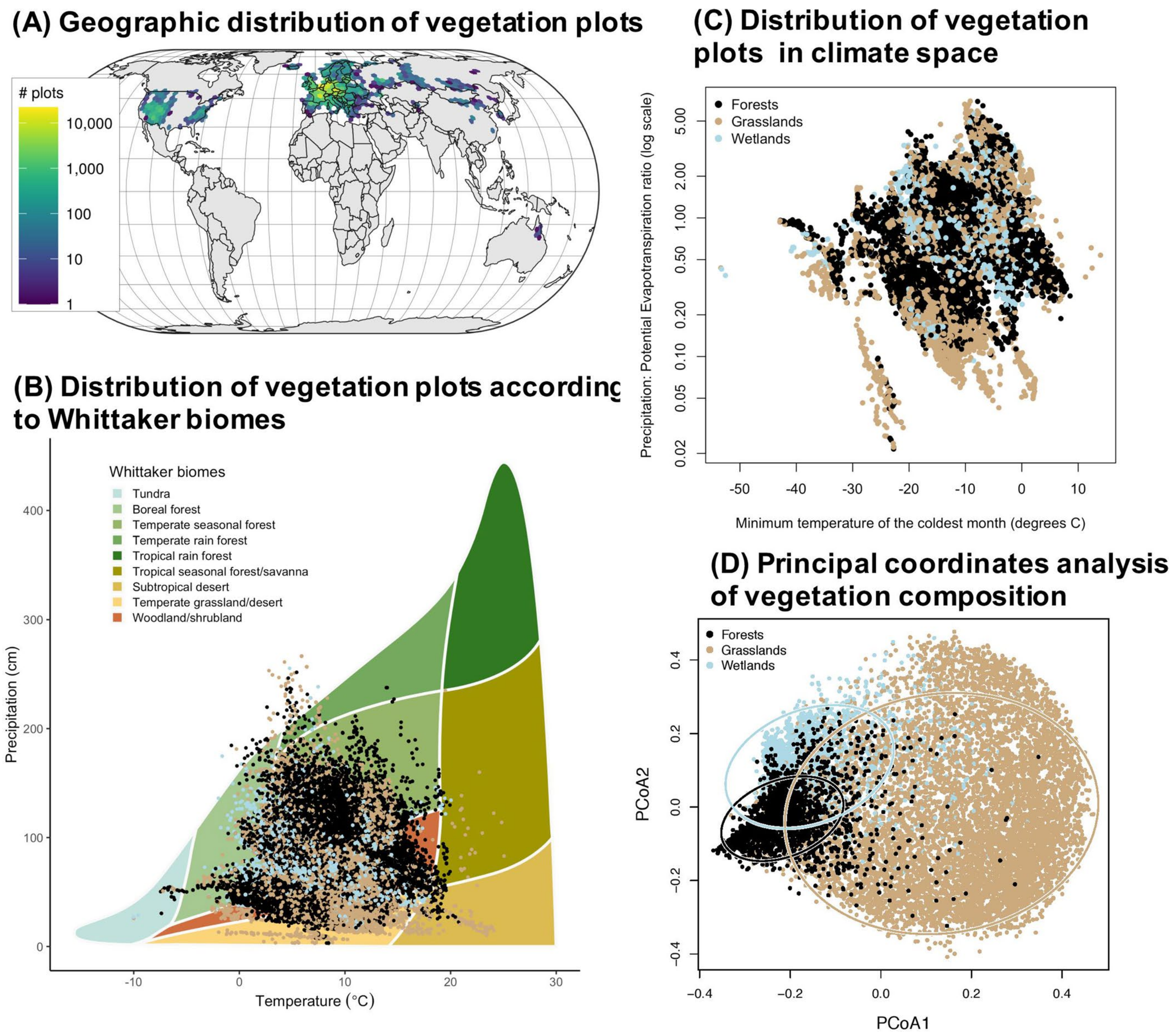


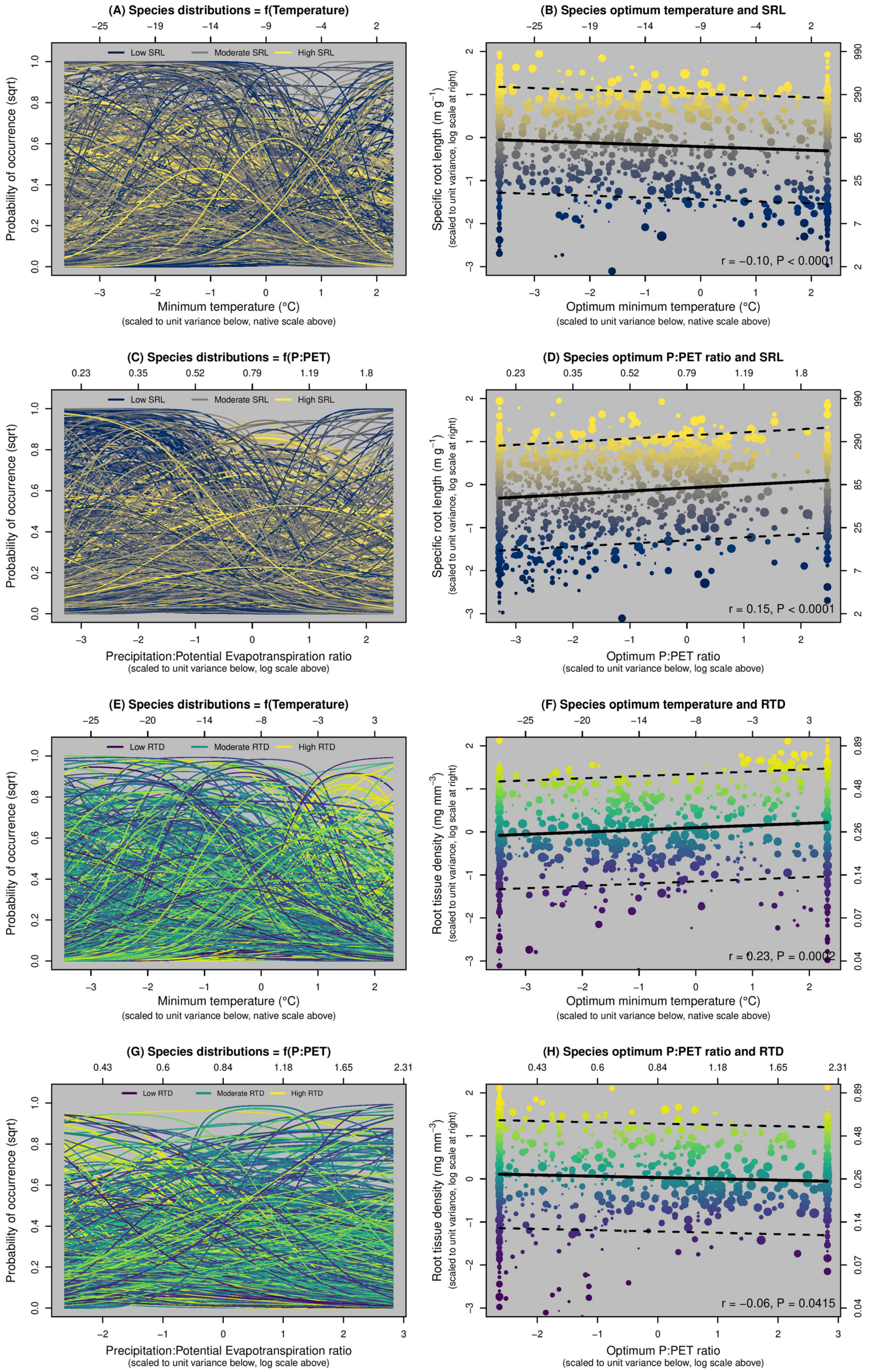
(A) Geographic distribution of vegetation plots

(B) Distribution of vegetation plots according to Whittaker biomes

(C) Distribution of vegetation plots in climate space

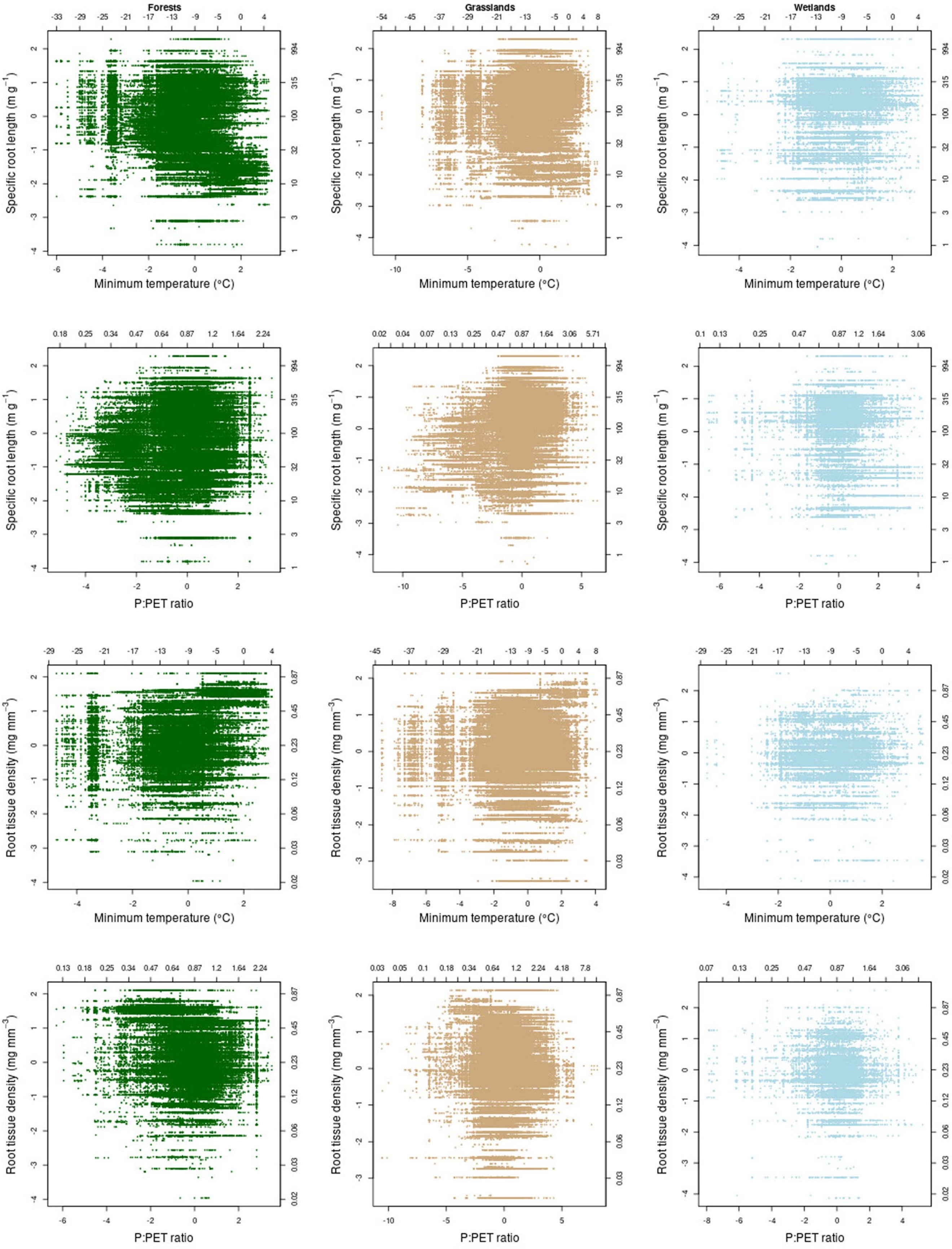
(D) Principal coordinates analysis of vegetation composition

Extended Data Fig. 1 | Geographic and climatic distribution of vegetation plots. Distribution of vegetation plots (A) across the globe, and (B) in climate space represented by mean annual temperature (MAT) and mean annual precipitation (MAT) superimposed onto Whittaker biomes[78]. The legend for color codes of vegetation types (black=forest, gold=grassland, blue=wetland) can be seen in panels C and D. Note the heavy bias toward North America, Europe, and Asia. Plots are located in all major biomes except tropical rainforest, but the majority of plots are found in temperate grasslands, temperate forests and woodlands, and boreal forest biomes. Note that we do not use the Whittaker biomes in our classification of plots into forest, grassland, and wetlands but rather use the composition data to do so (see Methods). These three vegetation types span a broad range of climate space and it is common to find grassland plots in a forest biome and forest plots within a grassland biome. (C) Plots in climate space using the climate variables that were used in the models (minimum temperature of the coldest month, and the precipitation-to-potential evapotranspiration ratio). (D) Principal coordinates analysis (PCoA) of vegetation composition using Bray-Curtis distances. The first axis explains 12% of the variation and the second axis explains 5%. Plots are color-coded according to how they were classified (that is, forest, grassland, wetland) and we illustrate 80% confidence ellipses for each vegetation type. This plot illustrates a random sample of 15,461 plots because analysis of >100,000 observations with >600 species was not computationally feasible within the time limits imposed by high-performance computer clusters.



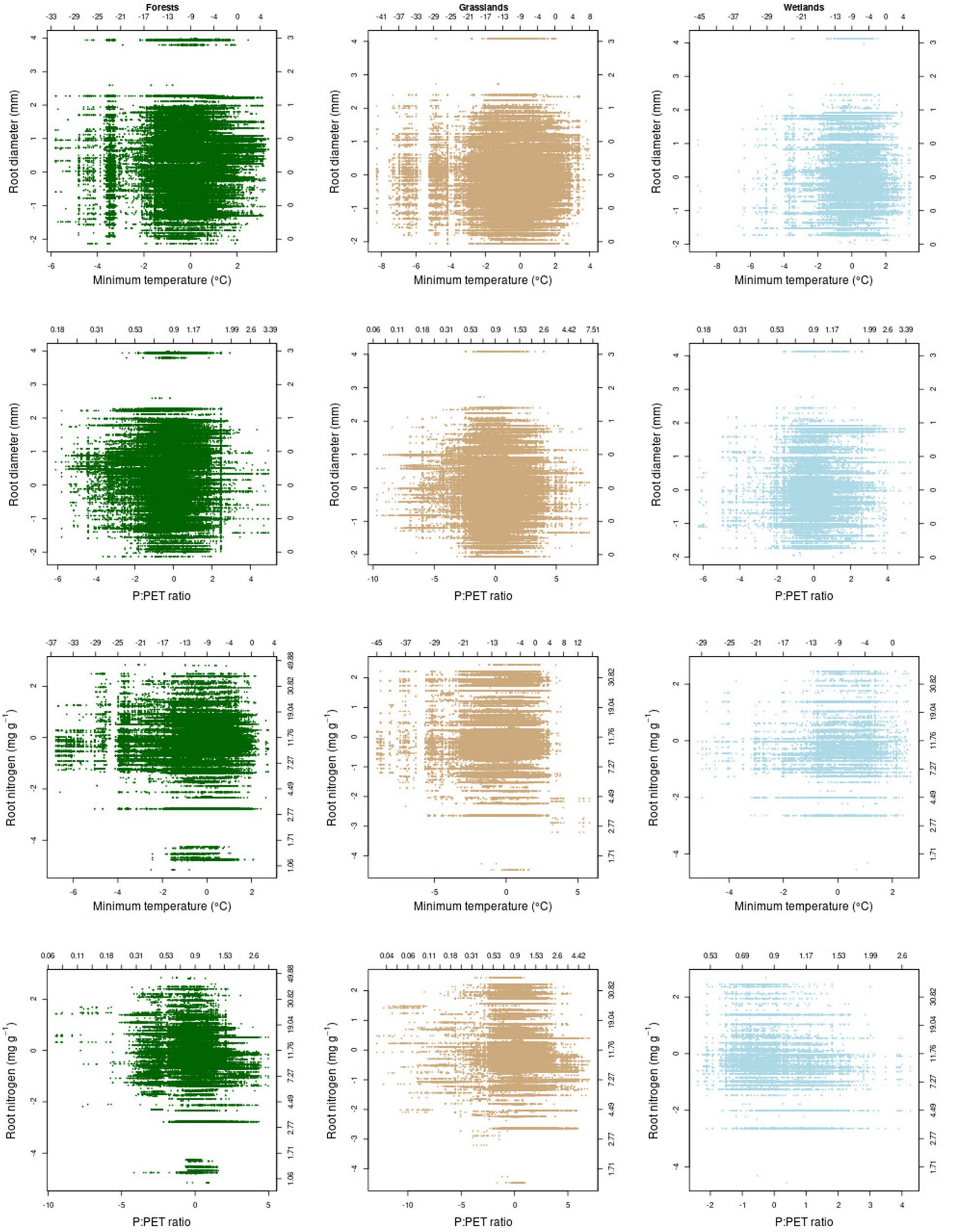
Extended Data Fig. 2 | See next page for caption.

Extended Data Fig. 2 | Species distributions along climatic gradients in relation to their specific root length (SRL) and root tissue density (RTD) in forests and grasslands combined. The left-column illustrates the modelled distributions of species using quadratic polynomials in the random effects. The *y*-axis of modeled probabilities of occurrence were square root transformed to amplify distributions of less common species to make them more visible. The right-column illustrates the relationship between optimum climatic conditions and root functional traits for each species, where the dark line illustrates the fitted regression line and the dotted lines represent 95% confidence intervals. Trait values for each species are color-coded using two different color ramps for each trait where dark colors are low trait values and light colors are high trait values. Size of the species symbols is proportional to their occurrence in the dataset. See Supplementary Table 1 for numbers of species in each model.



Extended Data Fig. 3 | See next page for caption.

Extended Data Fig. 3 | The occurrences of species-level average trait values of specific root length and root tissue density along two climatic gradients. Illustration of occurrences of specific root length and root tissue density along the gradients of minimum temperature in the coldest month and the precipitation-to-potential evapotranspiration ratio. The climate gradients are scaled to unit variance below and plotted in their native scale above. The traits are scaled to unit variance on the left and plotted in their native scale to the right.



Extended Data Fig. 4 | See next page for caption.

Extended Data Fig. 4 | The occurrences of species-level average trait values of root diameter and root nitrogen along two climatic gradients. Illustration of occurrences of root diameter and root nitrogen along the gradients of minimum temperature in the coldest month and the precipitation-to-potential evapotranspiration ratio. The climate gradients are scaled to unit variance below and plotted in their native scale above. The traits are scaled to unit variance on the left and plotted in their native scale to the right.

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Research sample	To test the adaptive value of root traits along gradients in temperature and water availability, we combined the global vegetation plot database (sPlot) with the global root trait database (GRooT), which subsets observations from the Fine-Root Ecology Database (FRED) with root data in TRY, as well as additional incorporated literature. These data were mostly collected in the field by the primary data sources, but we conducted no field work for this data synthesis.
Sampling strategy	We included all species for which root trait data was available, and all vegetation plots that included these species.
Data collection	We combined the global vegetation plot database (sPlot) with the global root trait database (GRooT), which subsets observations from the Fine-Root Ecology Database (FRED)
Timing and spatial scale	The analysis is nearly global in extent.
Data exclusions	We excluded root tissue density values that were > 1.0 mg/mm^3, because they are likely incorrect measurements.
Reproducibility	This is a descriptive analysis of data. All of our analyses can be reproduced with the R code that is provided. However, please note that it takes 3-8 weeks for the models to converge on a supercomputer.
Randomization	Our analysis was dependent on what species and plot data was available for analysis. We did not randomly choose from the data, we included all data that was available.
Blinding	Blinding is not relevant to our analysis.

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