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

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

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95

96 **Abstract**

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

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

114

115

116 **The nature of ecological trade-offs**

117 Ecological trade-offs underpin our conceptual understanding of global biodiversity distributions

118 ¹⁻⁶. Species pools are filtered into local communities based on the matching of species' trait

119 values to environmental conditions. Models that use traits to predict the success of a species in a

120 given environment are actively being developed and tested. Ecological trade-offs arise as a

121 consequence of the adaptive value of a trait, eloquently described as '*an evolutionary dilemma,*

122 *whereby genetic change conferring increased fitness in one circumstance inescapably involves*

123 *sacrifice of fitness in another*' ⁴. As the term 'trade-off' implies, the trait effects are

124 'bidirectional', where, for example, low trait values of a species confer adaptive advantage at one

125 end of an environmental gradient whereas high trait values confer benefits at the opposite end of

126 the gradient (Fig 1A) ¹.

127 Classical ecological theory has long emphasized this bidirectional perspective on trait-

128 environment relationships at the species level ⁷. For example, resource ratio theory

129 (ALLOCATE) is built on a single trait – environment trade-off. At the high end of the soil

130 fertility gradient, plant species that allocate relatively more carbon aboveground than

131 belowground are predicted to be better competitors for light. Whereas at the low end of the soil

132 fertility gradient, plant species that allocate relatively more carbon belowground than

133 aboveground are predicted to be better competitors for soil nutrients ⁸. Empirical evidence for

134 trade-offs have been found in a variety of traits including light compensation points along light

135 gradients⁹ and root angles along nutrient gradients¹⁰. In many cases, however, the empirical
136 evidence for trade-offs in performance among species has been met with mixed success^{6,11}.

137 Empirical evidence for trade-offs at the species level would be provided by showing that
138 the effect of a trait on the probability of species occurrence switches sign (*i.e.*, changes direction)
139 along an environmental gradient (Fig. 1A)¹². In other words, a positive relationship between a
140 trait and an environmental gradient implies that the effect of the trait on the probability of species
141 occurrence is negative at the low end of the gradient, but is positive at the high end of the
142 gradient (Fig. 1A). This directional switch in sign is fundamental, but detecting the switch
143 empirically is nontrivial because it cannot be observed through a simple trait-environment
144 correlation¹². The switch in sign can, however, be explicitly tested by comparing model-based
145 predictions of trait effects on the probability of species occurrence at contrasting ends of the
146 environmental gradient¹³. Specifically, if the first partial derivative with respect to traits crosses
147 zero along the environmental gradient, then the effect of a trait on probability of occurrence
148 switches sign (Fig 1A).

149 In contrast, the absence of a switch in sign of a trait's effect on the probability of species
150 occurrence along an environmental gradient would indicate that a trait only confers an adaptive
151 advantage at one end of this gradient, thereby exhibiting a mere 'unidirectional benefit' (Fig.
152 1B). The prevalence of unidirectional benefits at the species level has not been adequately tested,
153 yet empirical research has provided hints that they exist. For example, plant communities in New
154 Zealand exhibit trait convergence towards low leaf nitrogen concentration in phosphorus-poor
155 soil, whereas in phosphorus-rich soil communities display wide divergence of leaf nitrogen
156 concentration¹⁴. This suggests that low leaf nitrogen is adaptive in phosphorus-poor soil to
157 maintain a balanced leaf nutrient stoichiometry, whereas high leaf nitrogen is not adaptive in

158 phosphorus-rich soil. Thus, it is a unidirectional benefit, not a trade-off. Simulation results and
159 empirical work in insect host use has suggested that the importance of trade-offs in the evolution
160 of specialization may be overstated ^{11,15}. The prevailing view of trade-offs in ecological theory
161 across all levels of organization ^{1,2} may thus have hindered the discovery of unidirectional
162 benefits that could be widespread in nature. In particular at the species level, discerning the
163 difference between trade-offs and unidirectional benefits would advance our understanding of
164 how individual traits affect community assembly.

165

166 **Belowground root traits**

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

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

180 mycorrhizal, and these species tend to have the thinnest roots to explore the soil for resources by
181 themselves.

182 Second, species span another independent axis, where conservative species invest in high
183 root tissue density (RTD; fine root mass per unit volume), and acquisitive species construct more
184 metabolically active tissue with low RTD and high root nitrogen (root N) concentration ^{21,22}.

185 This second axis is associated with the aboveground leaf economics spectrum ²², where species
186 construct either short-lived leaves with high metabolic rates or long-lived leaves with thick cell
187 walls ²³. Consequently, fast species construct cheaper fine roots with higher rates of root turnover
188 ¹⁷. The global correlation between SRL and RTD among species is $r = -0.09$ ¹⁷, which implies
189 that plants have explored the expression of nearly all possible combinations of these two axes
190 leading to a two-dimensional root economics space (Fig. 1C). Therefore, these two root trait axes
191 provide a unique opportunity to scrutinize the evidence for ecological trade-offs and
192 unidirectional benefits among species to advance our understanding of the role of traits in
193 community assembly.

194

195 **Hypotheses and methods**

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

202 (1) We predicted a negative relationship between SRL and temperature (and a positive
203 relationship between RD and temperature) for several reasons. Species with low SRL would be
204 more prevalent in warm climates where AM fungi are abundant²⁴⁻²⁶. We also predicted species
205 with high SRL to be more common in extremely cold climates because 1) non-mycorrhizal taxa
206 dominate the high Arctic where mycorrhiza are limited by extremely low temperatures²⁷, and 2)
207 ErM and EcM fungi are more common in moderately cold climates and tend to colonize species
208 with moderate to high SRL²⁴⁻²⁶.

209 (2) We predicted a positive relationship between SRL and water availability (and a
210 negative relationship between RD and water availability) because species with high SRL can
211 more efficiently acquire resources by themselves in wet environments, and species with low SRL
212 that provide more cortical habitat for AM fungi can be more drought-tolerant through
213 mycorrhizal symbiosis-enhanced stomatal conductance and water use efficiency²⁸.

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

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

224 To test these four hypotheses, we combined the largest global vegetation database (sPlot)
225 ³¹ with the global root trait database (GRooT) ³² (see Methods) (Fig. S1). We used long-term
226 average minimum temperature of the coldest month to represent cold limitation and the long-
227 term average precipitation-to-potential evapotranspiration ratio (P:PET) to represent chronic
228 water limitation. The plots spanned a gradient of -10 to 25 °C mean annual temperature and 50 to
229 2,750 mm mean annual precipitation. Given the functional differences in vegetation dominated
230 by woody and herbaceous plants with respect to traits such as height, root diameter, and root
231 mass fractions ^{20,23,33-35}, we took a conservative approach to prevent confounding the
232 relationships by classifying each plot as forest, grassland, or wetland (Fig. S1). We predicted root
233 trait-climate relationships to be absent in wetlands because plants that grow in anoxic soil
234 conditions develop aerenchyma to maintain respiration rates, which would alter root morphology
235 independent from the regional climate ³⁶.

236

237 **Root traits in relation to temperature and water**

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

247 In grasslands, however, we only observed a unidirectional benefit (Fig. 2C). Species with high
248 SRL, such as *Draba nemorosa* (Fig. 1C), were more likely to occur in colder climates, but
249 species with any SRL value were equally likely to occur in warm climates (Table 1, Fig. 2C).
250 Root diameter did not exhibit trade-offs with temperature in forests or grasslands (Table 1, Fig.
251 2D,E,F). Large-diameter roots in forests were advantageous in warm climates, but thin roots
252 were not clearly advantageous in cold climates (Table 1, Fig. 2E). Thick roots thus exhibit a
253 unidirectional benefit in forests with warm climates where AM fungi are most abundant ²⁴⁻²⁶.

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

263 RTD influenced the probability of species occurrence along climatic gradients in forests
264 and grasslands, but not in wetlands (Fig. 3A). Contrary to our third hypothesis and other studies
265 ^{29,38-43}, the RTD-temperature interaction was positive rather than negative (Table 1, Fig. 3A) and
266 RTD was positively correlated with species optimum minimum temperatures (Fig. S2E,F). In
267 forests, species such as honeysuckle (*Lonicera chrysantha*, Fig. 1C) with low RTD were more
268 likely to occur in cold climates and species such as common myrtle (*Myrtus communis*, Fig. 1C)
269 with high RTD were more likely to occur in warm climates (Table 1, Fig. 3B). However, this

270 trade-off was not observed in grasslands where we found that species with low RTD were more
271 likely to occur in cold climates but species with any RTD value were equally likely in warm
272 climates (Table 1, Fig. 3C). We predicted that ‘slow’ species with dense roots would be better
273 adapted to low temperatures, but this was incorrect. Freeze-thaw dynamics of soil in cooler
274 climates can physically disturb root systems, which introduces the risk of losing large
275 investments in dense roots and may thus select for species that produce cheap low-density roots
276 that can regrow quickly after disturbance^{44,45}. We also predicted that ‘fast’ species with low
277 RTD and higher metabolic rates would be more competitive in warm climates, but this too was
278 incorrect. It may be that dense lignin-rich roots physically defend plants against plant pathogens,
279 protozoan parasites, and insect herbivores whose effects can be more intense at higher
280 temperature^{24,46-49}. Root N did not exhibit clear trade-offs with temperature in either forests or
281 grasslands (Table 1, Fig. 3D,E,F).

282 RTD did not exhibit a trade-off in relation to water availability (Table 1, Fig 3G,H,I). In
283 partial agreement with our fourth hypothesis and regional studies^{30,38,50}, the RTD-water
284 availability interaction was negative (Fig. 3G) and RTD was negatively correlated with species
285 optimum P:PET ratio (Fig S2G,H). In forests, species with high RTD had greater chances of
286 occurring in drier climates likely because denser root tissue enhances resistance to drought-
287 induced cavitation⁵¹. However, species with any RTD value were equally likely to occur in wet
288 climates (Table 1, Fig. 3H). No clear RTD-water availability trade-off was observed in
289 grasslands (Fig. 3I), perhaps because short-lived herbaceous species escape drought by
290 restricting their activity to brief pulses of ample water availability. Contrary to our hypothesis,
291 high root N appeared to be advantageous in dry forests (Table 1, Fig 3K). This result is
292 qualitatively consistent with the discovery that leaf N per area is higher in drought-tolerant plants

293 because higher photosynthetic rates are possible at lower stomatal conductance⁵². Perhaps root
294 N is higher in dry climates to provide drought-tolerant leaves with a greater supply of N.

295

296 **Implications for ecological theory**

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

308 Ecological community assembly theory is grounded in trade-offs, but our study
309 challenges our understanding of how individual continuous traits influence species distributions
310 along environmental gradients. Of the 13 models in which a significant trait-by-environment
311 interaction was detected, only two of these models supported a trade-off, whereas seven models
312 supported unidirectional benefits and four exhibited no clear benefits in either direction (Table
313 1). This result demonstrates the importance of evaluating the model-based predictions at each
314 end of the gradient (Fig. 2,3) rather than relying on trait-environment correlations or the
315 significance of interaction coefficients alone as evidence of a trade-off. The predicted signs (*i.e.*,

316 direction) of the relationships were supported 67% of the time (16 out of the 24 models), but the
317 model predictions only resembled trade-offs 8% of the time (2 out of 24 models) (Table 1). Our
318 results agree with Grubb's insight that *'the concept of a trade-off, which implies that being suited*
319 *to one condition necessarily involves not being suited to the opposite, is widely diffused in the*
320 *current literature but is not universally applicable'*.⁵⁴

321 Our work suggests that community assembly models and plant strategy theories that use
322 continuous variation in functional traits should be explicit about whether a trait exhibits trade-
323 offs with environmental gradients or unidirectional benefits. Patterns of aboveground trait
324 variation have been shown to exhibit trait convergence in resource-poor environments and trait
325 divergence in productive environments^{14,55}, suggesting that unidirectional benefits may also
326 occur in aboveground traits. Our analysis focused on determining the contributions of individual
327 traits to species distributions, but plant strategy theories are built on sets of multiple traits. Plant
328 strategies are likely generated by a combination of trade-offs for some traits (e.g., light
329 compensation point along light gradients⁹) and unidirectional benefits for others (e.g. leaf
330 nutrient concentrations along soil fertility gradients^{14,55}), which inevitably makes the task of
331 predicting species responses using continuous traits more difficult than previously anticipated.
332 Predictive models that use sets of continuous traits as predictors of species responses need to
333 know whether a trait exhibits trade-offs or unidirectional benefits along an environmental
334 gradient. Strong trait-environment interaction coefficients in linear models will, by default,
335 predict a trait-environment trade-off, but our results show that these are less prevalent than
336 unidirectional benefits. In the case of unidirectional benefits, the predictive power of a trait for
337 species occurrences would vary with the particular values of that trait, giving one end of the
338 range in trait values higher importance than the other end. Such information could perhaps enter

339 models as priors within a hierarchical model framework. An expanded theory of trait-
340 environment interactions that incorporates unidirectional benefits will advance our understanding
341 of the adaptive value of traits in community assembly and may improve predicted responses to
342 climate change. For example, in regions projected to become warmer and drier rather than
343 warmer and wetter ⁵⁶, plant communities may converge toward lower SRL and higher RTD. This
344 would make other trait combinations less viable and put species with higher SRL or lower RTD
345 at a higher risk of local extinction in these drier regions.

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

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

377 The expectation of trade-offs holds across different levels of organization from
378 individuals, populations, and to species ¹, but may become masked in species because of multiple
379 trade-offs in complex environments ². Indeed, there are many factors that confound the detection
380 of broad-scale relationships between interspecific trait variation and climate: the high range of
381 species trait values within communities relative to the global range ^{58,59}, the high plasticity of
382 traits within species across environments and the importance of other traits ⁶⁰, the stochastic
383 nature of disturbance regimes and land-use change ⁵⁸, the spatially heterogeneous variation in
384 microclimate and soil properties such as moisture and texture at small spatial scales ³⁸, dispersal

385 limitation, and biotic interactions (e.g., competition, facilitation) ⁶¹. While root traits only
386 explained a fraction of the variation in species occurrences (Table 1), similar to studies focused
387 on aboveground traits ⁵⁸, it is therefore remarkable that such clear root trait-climate relationships
388 were discovered here. This suggests that the root economics space framework is important for
389 understanding plant community assembly.

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

402

403

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585

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597

598 **Author contributions:**

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

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605 **Competing interests**

606 The authors declare no competing interests.

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610 **Table 1. Model support and summary of results for root trait-climate interactions.** Each of the eight models were evaluated for
611 their support for a trait-by-environment interaction in forests, grasslands, and wetlands. Statistical evidence was evaluated by
612 inspecting the significance of the coefficient in the model, the model R^2 , the AIC difference (ΔAIC) between models with the
613 environment alone versus models with both environment and traits (see full model description in Methods), and a likelihood ratio test
614 (LRT). Number of observations for each test are provided in Table S1.
615

		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

616 R^2_m = deviance explained by fixed effects

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

618 $\Delta AIC = AIC_{TxE} - AIC_E$; that is, AIC of model TxE minus AIC of model E (see Methods). Models with ΔAIC that are more negative
619 than -4 are more supported than the simpler model E

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

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

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

623 RD = root diameter (mm)

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

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

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

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

630

631

632 **Figure Captions**

633 **Figure 1. The ecological consequences of trait variation on species distributions along**

634 **climatic gradients.** (A) Empirical evidence for an ecological trade-off requires the existence of a

635 strong trait-environment interaction^{1,12}. Here we illustrate examples for both positive and

636 negative trait-environment interactions driving species occurrences. In the case of a positive

637 interaction between a trait and an environmental gradient, the effect of the trait on the probability

638 of species occurrence at the low end of an environmental gradient would be negative, but this

639 effect will switch directions and become positive at the high end of the gradient (see left-hand

640 column). This result would imply that a high trait value is beneficial at the high end of the

641 gradient and a low trait value is beneficial at the low end of the gradient (see middle and right-

642 hand columns). (B) Alternatively, if a statistical trait-environment interaction is detected, yet the

643 trait only exhibits an effect at one end of the environmental gradient (i.e., the effects do not

644 switch direction along the gradient), then this suggests there is only a ‘unidirectional benefit’.

645 Evidence for a unidirectional benefit for two alternative cases are illustrated for the positive

646 interaction scenario. (C) We scrutinized the existence of trade-offs using plant roots, which have

647 recently been shown to vary among species along two independent trait axes¹⁷. One axis is

648 described by variation in investment in high specific root length (SRL) versus large root diameter

649 (RD), and the other axis is described by variation between investment in high root tissue density

650 (RTD) versus metabolically-active roots with high root nitrogen (root N). The location in the

651 root economics space of five species discussed in the main text are shown on the biplot:

652 *Vaccinium vitis-idaea* (*Vv*) is a high-SRL ErM species, *Draba nemorosa* (*Dn*) is a high-SRL AM

653 species with low colonization rates, *Cunninghamia lanceolata* (*Cl*) is a low-SRL AM species,

654 *Lonicera chrysantha* (*Lc*) is a low-RTD species, and *Myrtus communis* (*Mc*) is a high-RTD

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

659

660

661 **Figure 2. Specific root length (SRL) and root diameter (RD) are related to species**

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

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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.

696 **Methods**

697

698 *Data synthesis*

699 To test the adaptive value of root traits along gradients in temperature and water
700 availability, we joined the global vegetation plot database (sPlot)³¹ with the global root trait
701 database (GRooT)³², which combines observations from the Fine-Root Ecology Database
702 (FRED)⁶³ with root data in TRY⁶⁴, as well as additional incorporated literature. This dataset has
703 strong representation of AM, EcM, and ErM mycorrhizal types but only a few non-mycorrhizal
704 species.

705 We computed species-level averages of the most commonly measured fine root traits by
706 first calculating the mean value of a species within a study and then averaging those values for a
707 species across studies. We cannot say anything about plasticity or intraspecific trait variation in
708 this study given that we were only able to analyze average trait values of species. RTD values
709 reported to be $> 1.0 \text{ mg mm}^{-3}$ were excluded from this study. This resulted in a dataset of 1,767
710 species with specific root length (SRL; m g^{-1}) and 1,426 species with root tissue density (RTD;
711 mg mm^{-3}), 1,283 species with root nitrogen concentration (root N, mg g^{-1}), and 1,623 species
712 with root diameter (RD; mm). Out of the 2,122 species in GRooT, 1,638 species were present in
713 sPlot for a total of 998,669 vegetation records. We discarded all plots that contained $< 80\%$ trait
714 coverage based on relative cover⁶⁵ for a total of 152,771 plots with SRL data, 154,192 plots with
715 RD data, 107,325 plots with RTD data, and 109,494 plots with root N data.

716 The majority of plots were located in Europe, Asia, North America, and Australia (Fig
717 S1A). Plots were found within all global biomes except tropical rainforests but were most
718 representative of temperate seasonal forest, boreal forest, woodland-shrubland, and temperate

719 grassland-desert biomes (Fig S1B). The paucity of root trait data in tropical forests prevented us
720 from including these biomes in our analysis, highlighting the importance of new data collection
721 in tropical ecosystems. We used the geographical coordinates of each plot to compile climate
722 data and ecoregion classification. The average minimum temperature in the coldest month was
723 downloaded from CHELSA (~1 km resolution)⁶⁶. The correlation between minimum
724 temperature and P:PET was weak and negative ($r = -0.12$) (Fig. S1D). Model results were
725 qualitatively similar if mean annual temperature was used instead of minimum temperature of
726 the coldest month. Water availability was expressed as the precipitation-to-potential
727 evapotranspiration ratio (P:PET) using the global Aridity index raster (~1 km resolution)⁶⁷.

728 Information on vegetation types was only available for a subset of plots in sPlot, and
729 most of these classified plots were located in Europe. To have all plots consistently assigned to
730 vegetation types, we ran one classification based on species' affinities to forest, grassland,
731 savanna, heathland, steppe, wetland, and other, as assigned based on expert opinion (available in
732 Supplementary Material). Based on the relative cover of each species within a given plot, we
733 summarized species based on their habitat affinities, and summed their relative cover. We then
734 assigned each plot to a habitat based on the following if-else conditions: if the pooled relative
735 cover of species with wetland affinities > 0.5 , then it was classified as "Wetland", if the relative
736 cover of species with forest affinities > 0.3 , then it was classified as "Forest", if the relative cover
737 of species with either grassland, savanna, heathland, or steppe > 0.7 , then we classified it as
738 "Grassland". These three if-else conditions were sequential, so that a plot assigned to "Wetland",
739 could not be also assigned to "Forest" or "Grassland". We selected the thresholds iteratively, in
740 order to maximize the overall accuracy of the classification based on species' habitat affinity,
741 when tested against sPlot's native habitat classification. Out of the 202,942 plots we considered,

742 23,885 were assigned to “Wetland”, 65,618 to “Forest” and 103,009 to “Grassland”. Another
743 10,420 remained unassigned and were removed from the analysis. The overall accuracy of the
744 classification was 0.67 and the Kappa statistic was 0.49. Compositional differences among the
745 three vegetation types are illustrated by a Principal Coordinates Analysis using Bray-Curtis
746 distances (Fig S1D). We included savanna species within grasslands and did not include a
747 ‘savanna’ category for two main reasons: 1) no plots in our dataset occurred in the savanna
748 regions of South America or Africa, and 2) the compositional data available to us could not be
749 used to reliably discern a savanna from a forest or grassland. This decision had no appreciable
750 affect on the results because the direction of the trait-environment interactions detected in this
751 study were relatively consistent between grassland and forest, so adding additional vegetation
752 types that are intermediary between the two would not have affected the results.

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

764

765 *Data analysis*

766 We fit hierarchical models using Generalized Linear Mixed Effects Models to test
767 whether root traits explain species occurrences by their interactions with climatic gradients^{13,69},
768 which is the most appropriate method for evaluating how trait-environment interactions drive
769 species occurrences⁷⁰. We modeled binomial species presence-absence data using a logit link
770 function and binomial error structure. Given the size of the dataset, all models were fit in parallel
771 using an Intel compiled version of R on the high-performance computer cluster at the University
772 of Wyoming, where several days to four weeks were required to achieve model convergence. We
773 used the following packages in R version 3.6.1⁷¹ to conduct our analyses: stats⁷¹, ggplot2⁷²,
774 lme4⁷³, lmerTest⁷⁴, performance⁷⁵, plotbiomes⁷⁶, and labdsv⁷⁷.

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

782

$$783 \text{logit}(y) = \beta_0 + \gamma_{j0} + \delta_{k0} + (\beta_1 + \gamma_{j1}) \text{climate} + (\beta_2 + \gamma_{j2}) \text{climate}^2$$

784

785 where y was binomial presence and absence, β_0 was the global intercept, β_1 was the fixed effect
786 term describing the main effect of the climatic gradient, β_2 was the fixed effect term describing
787 the main effect of the squared-climatic term, which allowed to model optimum environments for

788 each species, γ_{j0} was a random intercept for each of j species drawn from a normal distribution
789 $N(0, \sigma^2_{\gamma_{j0}})$, δ_{k0} was a random intercept for each of k ecoregions drawn from a normal distribution
790 $N(0, \sigma^2_{\delta_{k0}})$, γ_{j1} was a random slope for each of j species drawn from a normal distribution
791 $N(0, \sigma^2_{\gamma_{j1}})$, and γ_{j2} was a random slope for each of j species drawn from a normal distribution
792 $N(0, \sigma^2_{\gamma_{j2}})$. We used the quadratic polynomial random effects from this model to compute the
793 optimum temperature and water availability for each species, *i.e.*, the value of the climatic
794 variables where the species attains its highest probability of occurrence. We regressed these on
795 the trait values of each species, where the relative abundance of each species in the dataset were
796 used as weights in the regression (see Fig. S2). The lme4 syntax for this model was
797 `glmer(occurrence ~ climate + climate2 + (climate + climate2|species) +`
798 `(1|ecoregion), family=binomial).`

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

803

$$804 \text{logit}(y) = \beta_0 + \gamma_{j0} + \delta_{k0} + (\beta_1 + \gamma_{j1})\text{climate} + (\beta_2 + \gamma_{j2})\text{climate}^2 + (\beta_3)\text{trait} + (\beta_4)\text{trait} \cdot \text{climate}$$

805

806 where β_3 was the fixed effect term describing the main effect of traits, and β_4 was the fixed effect
807 term describing the interaction between the trait and the climatic gradient. The lme4 syntax for
808 this model was `glmer(occurrence ~ climate + climate2 + trait + trait:climate`
809 `+ (climate + climate2|species) + (1|ecoregion), family=binomial).`

810 To evaluate the empirical support for the trait-environment interaction, we compared
811 model ‘ TxE ’ model to model ‘ E ’. Given the statistical power of the large dataset, we used three
812 criteria to assess the evidence of whether species occurrences can be explained by trait-
813 environment interactions: 1) differences in AIC between the two models (i.e., $AIC_{TxE} - AIC_E$) that
814 were < -4 (i.e., an absolute difference > 4)⁷⁸, 2) significant likelihood ratio tests using a chi-
815 square statistic, and 3) a significant fixed effect interaction term in the linear predictor. All three
816 criteria needed to be met to consider these to be important interactions. We used a threshold of
817 AIC differences more negative than -4 following suggested rules of thumb for model comparison
818 ⁷⁸.

819 We further classified these significant interactions into two general types: 1) “trade-offs”
820 and 2) “unidirectional benefits”. Trade-offs occur where certain trait values confer adaptive
821 advantage at one end of an environmental gradient and other trait values confer benefits at the
822 opposite end of the gradient (Fig. 1A). Unidirectional benefits occur when a trait confers an
823 adaptive advantage at only one end of an environmental gradient (Fig. 1B). In order to be
824 considered a ‘trade-off’, the effect of traits on probability of occurrence had to switch signs
825 between each end of the environmental gradient¹². To test this, we illustrate the first partial
826 derivative of the model with respect to the trait ($\partial y / \partial T$) to demonstrate how the effect of the
827 trait on probability of occurrence changes along the climatic gradient. A significant positive
828 interaction would be illustrated as a line with positive slope that passes through $\partial y / \partial T = 0$ (Fig.
829 1A). In contrast, ‘unidirectional benefits’ were interactions where a trait exhibits an effect on
830 probability of occurrence at one end of the gradient but has no effect on probability of
831 occurrence at the other end of the gradient (Fig. 1B). To operationalize this distinction, we
832 plotted model-predicted probabilities as a function of each trait at the low end (1st percentile) and

833 high end (99th percentile) of each climatic gradient. Given the size of the datasets, these
834 percentiles include thousands of observations. If the probability of occurrence at one end of the
835 gradient did not exceed 5% whereas the probability of occurrence at the other end of the gradient
836 exceeded 5%, then we considered this to be a ‘unidirectional benefit’. Given the large number of
837 absences that is typical with sparse community datasets, the average probability of species
838 detection was approximately 0.01, thus a 5% probability would be a five-fold increase from the
839 average. Using these criteria, the nature of each trade-off is listed in Table 1 and Figs. 2 and 3.

840 We limited our analyses to models with one trait and one climate gradient rather than
841 fitting more complex models with multiple traits and multiple climate gradients. We took this
842 choice to make our work more comparable to other recent work⁵⁸ and to achieve a more
843 straightforward interpretation of interactions. We also limited our models to one climate gradient
844 because model convergence was problematic even for the environment-only models (model *E*).
845 These models included hundreds of random slopes and intercepts with respect to climate
846 variables and squared variables to fit quadratic polynomials to account for each species’
847 nonlinear response to climate (Fig. S2). Adding a second climate variable would add hundreds
848 more coefficients to account for each species’ nonlinear response to that gradient, and we would
849 need to include their interaction. Finally, we limited models to only one trait because including
850 two traits reduced the number of species with data for both traits that could be included in the
851 model. The occurrence of species-level average trait values are plotted along each climate
852 gradient in Figs. S3 and S4.

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856 **Data Availability**

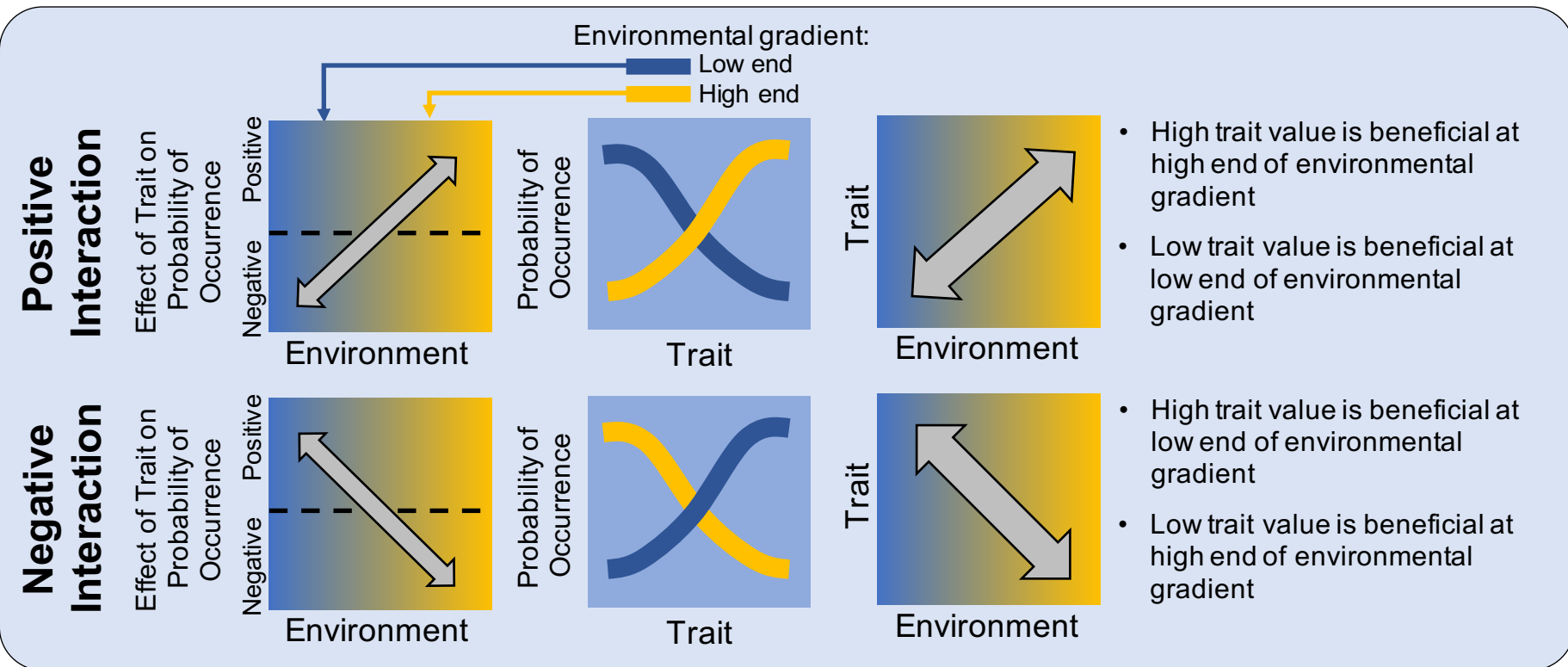
857 All code and data needed to reproduce the model results can be accessed at

858 <https://idata.idiv.de/ddm/Data/ShowData/3475>

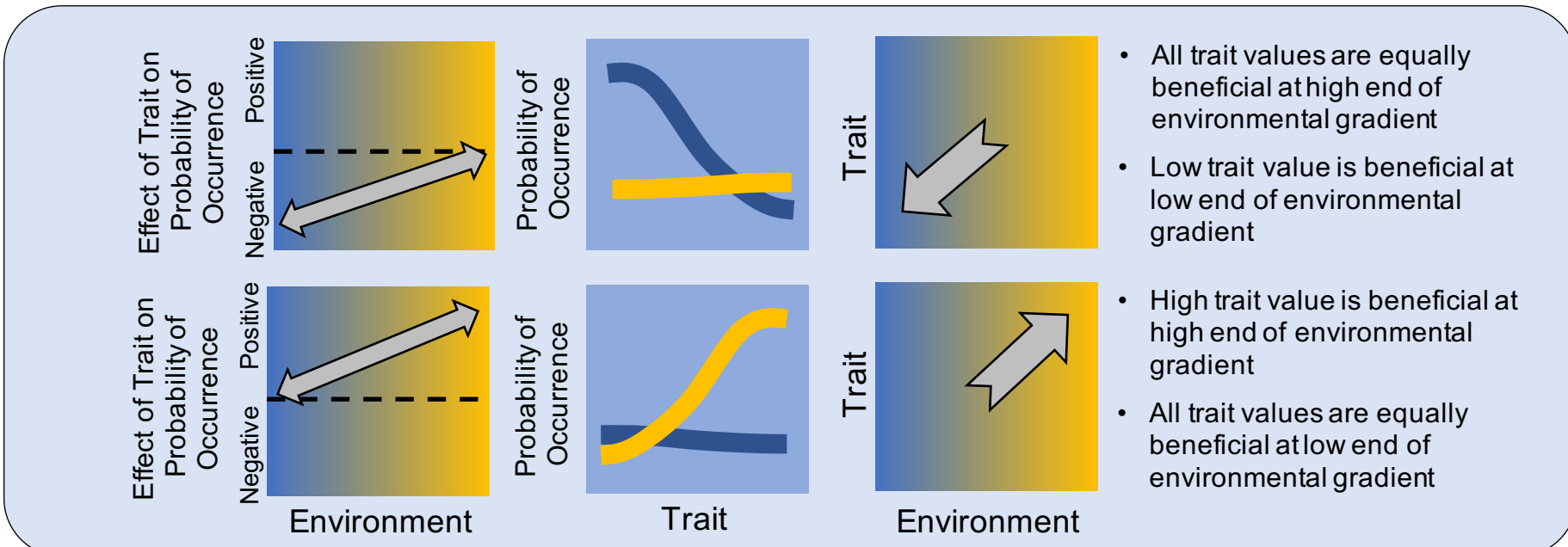
859

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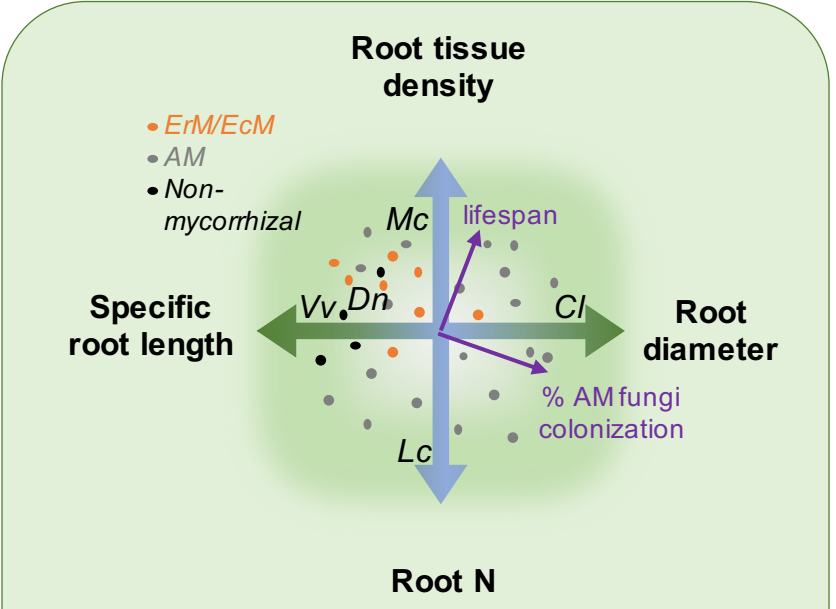
(A) Trade-off



(B) Unidirectional Benefit (illustrated for a positive trait-environment interaction)

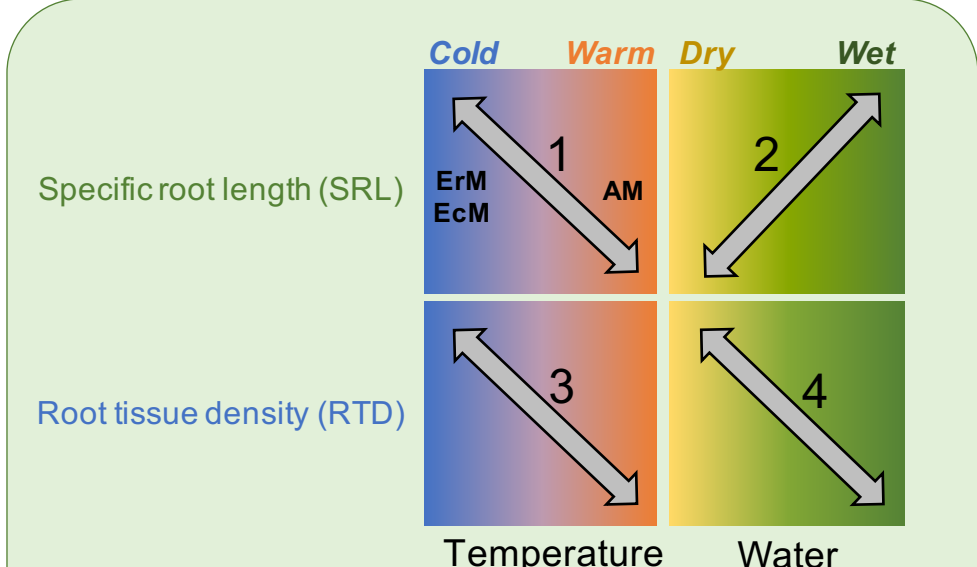


(C) The root economics space



- 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
- Bergmann et al. (2020)

(D) Hypotheses for root trait-climate relationships



- High SRL/thin diameter in cold climates where AM fungi are rare, and where EcM and ErM fungi that inhabit thin roots are abundant. Low SRL/thick diameter in warm climates where AM fungi are abundant.
- 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.
- High RTD/low root N in cold climates to construct dense, long-lived tissue that resists freezing. Low RTD/high root N in warm climates that favor high metabolic rates.
- 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.

