Functional traits determine trade-offs and niches in a tropical forest community

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How numerous tree species can coexist in diverse forest communities is a key question in community ecology. Whereas neutral theory assumes that species are adapted to common field conditions and coexist by chance, niche theory predicts that species are functionally different and coexist because they are specialized for different niches. We integrated biophysical principles into a mathematical plant model to determine whether and how functional plant traits and trade-offs may cause functional divergence and niche separation of tree species. We used this model to compare the carbon budget of saplings across 13 co-occurring dry-forest tree species along gradients of light and water availability. We found that species ranged in strategy, from acquisitive species with high carbon budgets at highest resource levels to more conservative species with high tolerances for both shade and drought. The crown leaf area index and nitrogen mass per leaf area drove the functional divergence along the simulated light gradient, which was consistent with observed species distributions along light gradients in the forest. Stomatal coordination to avoid low water potentials or hydraulic failure caused functional divergence along the simulated water gradient, but was not correlated to observed species distributions along the water gradient in the forest. The trait-based biophysical model thus explains how functional traits cause functional divergence across species and whether such divergence contributes to niche separation along resource gradients.

Niche theory predicts that functional trait differences across species govern the specialization of species for different fundamental niches (the abiotic conditions under which species can grow, survive, and reproduce) and realized niches (the abiotic and biotic conditions where species can thrive), thus allowing species to coexist in the same community (1–3). In this context, functional traits are considered measurable physiological and morphological characteristics that drive the performance of an organism (3). In contrast, neutral theory advocates that coexisting species tend to be selected for the most common environmental conditions and, therefore, that most coexisting species are functionally equivalent and share similar niches (4, 5). For diverse systems, such as tropical forest tree communities, many empirical studies have shown that functional traits of species are often distributed in ways that are consistent with mechanisms of community assembly, such as habitat filtering (6, 7), but lack depth to evaluate underlying mechanisms. More biophysical studies on mechanisms are often confined to small samples of species (8) or to theoretical simulations (9) and therefore fail to explain the community-level consequences of physiological differences among species. We lack studies that provide detailed trait-based biophysical models to understand the possible consequences of functional trait differences across species for niche separation, which in turn may act as one of the mechanisms contributing to species coexistence in species-rich communities (3, 10), such as tropical forests (11).

A classic hypothesis in plant ecology is that intraspecific trade-offs between biomass investments below vs. above ground provide a key mechanism for the acclimation of plants to different light and soil conditions (12). There is clear evidence in support of this hypothesis, both for woody plants (13) and for herbaceous plants (14). The same mechanism has been used to hypothesize about niche differentiation across plant species for light vs. nutrient gradients (15) or light vs. water gradients (16, 17). Plants with high investments in stem and leaves are predicted to be stronger competitors for light (18). Because aboveground investments come at the cost of investments below ground, the species that are strong competitors for light are predicted to be poor competitors for nutrients (15) and water (16). The hypothesis that such mechanisms result in a trade-off between species' ability to tolerate shade vs. their ability to tolerate drought and infertile soils (15, 16) has, however, been rejected for co-occurring species in different ecosystems by a multitude of empirical studies (e.g., refs. 19 and 20).

There is increasing support that trait trade-offs give rise to acquisitive species and conservative species. Acquisitive species are geared toward high resource acquisition rates and high growth and are successful in high resource habitats, whereas conservative species are geared toward high resource conservation, high stress tolerance, and high survival, and they are successful in low resource habitats (e.g., refs. 7 and 21–23). There is, however, a large gap in our understanding of the relationships between traits, mechanisms, growth, and survival (10, 24, 25) and maybe an even larger gap in our understanding of the evolutionary processes driving niche separation (2, 10, 25). For tropical forest, known as the most species-rich tree communities on earth, functional traits are correlated (26) and, moreover, such traits may correlate to distribution patterns of species at various spatial scales, suggesting that they contribute to functional divergence and niche separation (27, 28). In our study, we used a different approach: We present a unique study that uses biophysical principles to show how functional traits and trade-offs scale to carbon gain responses to light and water availability gradients that can be encountered by tree saplings in the forest and test whether such simulated responses explain the actually observed species distributions along light and water gradients in the forest. We considered the different carbon gain responses across species support for functional divergence and different distributions as evidence for niche separation. We applied this approach to a subsample of 13 species of a tree sapling community of a dry tropical forest, where saplings are expected to be limited by both shade and drought (29, 30).

We hypothesize that two coupled trade-offs explain the distribution of tree species along gradients in light and water availability. First, we expect that acquisitive species are characterized by higher levels of photosynthetic proteins (such as Rubisco) than conservative species. Acquisitive species will thus have higher carbon gain rates than conservative species when light is not limiting, but carbon gain may not compensate for the protein-driven high respiration rate at low light levels (7, 31). Hence, we expect that the interspecific differences in the photosynthetic protein

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concentrations result in a trade-off between high carbon gain at high light levels and carbon starvation at low light levels.

Second, to maintain their high photosynthetic rates at high resource levels, acquisitive tree species require high stomatal conductance and, in turn, a high hydraulic conductivity of the water-transporting wood to sustain a high transpiration rate (9, 32). Highly conductive wood, however, involves a higher risk of hydraulic failure, i.e., the cavitation of xylem water columns, under dry conditions (30, 33). Under increasingly dry conditions, acquisitive species are therefore expected to close stomata and reduce transpiration to avoid hydraulic failure, which creates a risk to starve from carbon deficiency when photosynthesis goes too far down (34, 35). When conservative species are indeed less vulnerable to hydraulic failure, they may keep stomata open and maintain positive carbon budgets under similar dry conditions (34, 35). Hence, this mechanism means that acquisitive species are expected to achieve high carbon gain at high light levels and high water availability because their higher photosynthetic leaf protein concentrations are coupled with higher stem conductance and stomatal conductance than those of conservative species and that conservative species have higher tolerances to both shade and drought because their lower respiration costs are coupled with lower risks for hydraulic failure or stomatal closure under dry conditions. To test these hypotheses, a process-based plant model was parameterized with functional trait data (Table 1) from 13 co-occurring tree species in a Bolivian tropical dry forest. The model calculates the daily carbon gain on the basis of the hydraulic structure, stomatal coordination, and photosynthesis of plants (see *Methods*, Fig. S1, and *SI Text S1* for computational details and *SI Text S2* and Tables S1–S4 for parameterization). The predicted specific carbon gain responses to light and water availability gradients were compared with observed species distributions along these gradients in the forest.

Results and Discussion

Isocline Patterns. The simulations predicted curved, and not rectangular, zero carbon gain isoclines for all species (e.g., Fig. 1 and Fig. S2). This curved pattern results from a coupling in transpiration and photosynthesis through the stomata: When plants have zero carbon gain because the stomata are partially closed, increasing water availability allows for more open stomata and thus for higher gas exchange rates and carbon gain at the same light level, and increasing light allows for higher carbon gain at the same

water availability level. In that sense, light and water partially act as complementary resources for carbon gain (Fig. 1 *A* and *B*).

A Gradient from Acquisitive to Conservative Species. The model predicted that all species achieved higher carbon gain with increasing light or water availability (Fig. 1 *A*, *C*, and *D* and Fig. S2). The species with higher carbon gain at maximum resource availability ran more rapidly into lower carbon gain or even net carbon loss with decreasing light or water availability (Figs. 1 *A*, *C*, and *D* and 2*A*) and, in most cases, had higher light and water compensation points (Fig. 2 *B* and *C*) than species with lower carbon gain at maximum resource levels. The zero carbon gain lines, demarcating the fundamental niche where a species is expected to survive, show only few crossovers across species (Fig. 1*B*). This observation confirms the existence of a gradient from acquisitive species to more conservative species in this tropical forest community, where the more acquisitive species have higher resource requirements, have higher resource compensation points, and grow potentially faster than more conservative species.

Functional Traits and Trade-Offs in Response to Light. We expected that the higher leaf nitrogen concentration of acquisitive species would cause higher carbon gain at high light availability and higher light compensation points and thus lower tolerance to low light availability. A sensitivity analysis (Table 1) showed that more acquisitive species traded off their high maximum carbon gain with a higher light compensation point because they had a larger leaf area index and indeed because they had a higher leaf nitrogen concentration (Fig. 2*B*). Moreover, leaf area index and leaf nitrogen concentration drove a trade-off between maximum carbon gain and negative minimum carbon gain at the lowest light levels (Fig. 2*A*). We suspect that acquisitive species are selected for producing leaves more rapidly and thus maintaining a larger leaf area index and total leaf area to drive high growth rates under favorable conditions. This, however, comes at the cost of self-shading and higher respiration rates under less favorable conditions (22). Hence, our hypothesis that high carbon gain of acquisitive species at high light levels traded off with high respiration rates at low light levels is confirmed (36), but with an unexpected role of their higher leaf area index and more self-shading.

Functional Traits and Trade-Offs in Response to Water. We hypothesized that stomatal response and cavitation result in a trade-off between high carbon gain at high water availability and carbon

Table 1. Functional plant trait values and their effects on performance estimates for the studied sapling community

Traits, units	LAI, $m^2 \cdot m^{-2}$	A_s, cm^2	LMA, $kg \cdot m^2$	N_{mass}, $mg \cdot g^{-1}$	ψ_{min}, MPa	ρ_s, $kg \cdot m^3$	K_s, $kg \cdot m^{-1} \cdot s^{-1} \cdot MPa^{-1}$
Mean	1.120	0.17	0.091	25	−1.77	435	5.0
Min	0.460	0.06	0.051	18	−3.42	211	0.7
Max	2.390	0.31	0.167	34	−0.17	629	16.0
Sensitivities							
Max C gain	59.2	−0.29	−1.5	19.3	−1.6	−0.2	0.3
LCP	29.0	0.9	4.1	35.5	0.3	−0.6	0.0
WCP	0	0	2.0	−2.0	62.0	0.0	−2.0

Minimum, maximum, and average trait values are given for the studied species (for values of individual species, see Table S4). The sensitivities (%) in maximum carbon gain, light compensation point (LCP), and water compensation point (WCP) to the observed variation in functional traits were calculated. These sensitivities show the responses in these performance traits to the variation in each functional trait, with this variation calculated as the difference between max/min values of a functional trait relative to the mean value of the trait. The considered functional traits include leaf area index (LAI), the stem sapwood cross-section area (A_s), the leaf mass per area (LMA), the nitrogen mass per leaf mass (N_{mass}), the minimum leaf water potential (ψ_{min}) at the end of the dry season, the wood density (ρ_s), and the sapwood-specific hydraulic conductivity (K_s). We calculated the sensitivities S (%) (carbon gain, LCP, or WCP) in response to a functional trait X: $S = 100\% \times 1/2 \times \{[|Y(X_{min}) − Y(X_{mean})|]/Y(X_{mean}) + [|Y(X_{max}) − Y(X_{mean})|]/Y(X_{mean})\}$. A minus sign was added to Y when X had a negative effect on Y.
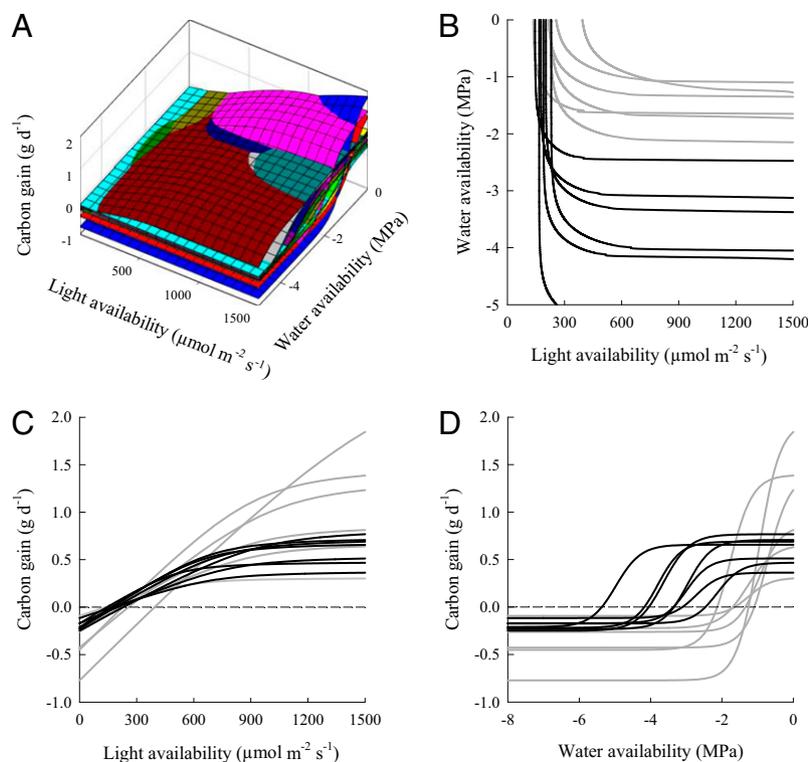
Fig. 1. Carbon gain landscapes for 13 co-occurring tree species of a Bolivian forest. Carbon gain was calculated as the difference between diurnal gross photosynthesis rate minus diurnal maintenance respiration rate. (*A*) Carbon gain landscapes along gradients of light availability as the average vertical light intensity in (μmol·m^{-2}·s^{-1}) units, and water availability as the soil water potential in (Pa) units. Different plane colors represent different species ([Fig. S2](#)). (*B*) Zero carbon gain isoclines along the light and water availability gradient, indicating the border of the fundamental niche. (*C*) Carbon gain at saturated soil water availability (soil water potential = 0 Pa) along a light availability gradient. The cross-points with the dashed line (carbon gain = 0) represent the estimated light compensation points of the species. (*D*) Carbon gain at saturating light availability (light intensity = 1,500 μmol·m^{-2}·s^{-1}) along a water availability gradient. Cross-points with the dashed line (carbon gain = 0) represent the estimated water compensation points of the species. In *B*–*D*, gray lines represent species known as pioneers and black lines show species known as shade tolerant. These two species groups are shown for illustration purposes only, because no formal tests among species groups were performed.

starvation at low water availability. However, the water compensation point was only moderately, and not significantly, correlated with maximum carbon gain [Fig. 2*C*, Pearson's $R = 0.40$, $n = 13$, $P = 0.09$ (one-tailed)]. The expectation is most obviously confirmed for the three most acquisitive species, which had higher water compensation points than most other species (Fig. 2*C*) because their stomata closed at higher (less negative) leaf water potentials, to avoid cavitation (37, 38). The stomatal coordination thus shaped the fundamental niches of species in response to soil water availability. A moderate positive correlation between light compensation points and water compensation points across species [Pearson's $R = 0.42$, $n = 13$, $P = 0.08$ (one-tailed)] supports our prediction that conservative species tolerate both shade and drought. The explained variation was, however, relatively low, because the correlation was mainly driven by the three most acquisitive species, which tolerate neither shade nor drought.

The specific hydraulic conductivity and stem sapwood area explained only little variation in carbon gain or water compensation point (Table 1). This insensitivity to hydraulic conductivity and sapwood area suggests that sapling stems were hydraulically overbuilt: The sapwood seems larger and more conductive than needed for effective water supply from roots to leaves. The stems are thus probably not overbuilt for hydraulic safety reasons, but for biomechanical reasons, as biomechanical safety determines minimum stem investments in tropical forest saplings (39). Possibly, leaves and roots pose stronger bottlenecks for water flow than sapwood in saplings (40), whereas sapwood poses a bottleneck for water flow in large trees (41, 42).

Consequences of Species Performance for Species Distribution. Are the simulated tolerances to water and light reflected in the observed species distributions in the forest? To tackle this question we related the simulated maximum carbon gain, light compensation point, and water compensation point to observed species distributions along the light and water availability gradient, as independently measured in the forest (*Methods* and *SI Text S3*). The more acquisitive species are indeed found at higher light levels in the field as indicated by the positive relation between species simulated maximum carbon gain and light index (Fig. 3*A*) as well as between light compensation point and light index (linear regression: $R^2 = 0.68$, intercept $= 0.672$, slope $= 0.0059$, $P < 0.001$, $n = 13$, where the light index is the average crown light exposure of saplings as observed in the field) (43) (*Methods* and *SI Text S3*). In contrast to our prediction, the acquisitive species were not found at higher water levels in the field. Instead, acquisitive species had a lower water index (Fig. 3*B*), indicating that they are associated with dry crests where soil water availability is low (29, 30). Because acquisitive species do not have deeper roots (27), they probably do not have access to deeper water sources than conservative species (44). They may have a higher fine root density (as shown for seedlings) (27), facilitating water acquisition. Possibly, the acquisitive species gain sufficient carbon during the wet periods, so that they survive the low carbon gain by stomatal closure during dry periods. Moreover, they probably benefit from crests, which provide more high-light canopy gap sites than valleys. Additionally, in those canopy gaps the loss of a large transpiring canopy may locally create higher levels of water availability (44), although this

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Fig. 2. Possible trade-offs across performance traits. (*A*) Minimum vs. maximum carbon gain; (*B*) maximum carbon gain vs. light compensation points; (*C*) maximum carbon gain vs. water compensation points. Actual trade-offs are suggested by a negative relationship for *A* and positive relationships for *B* and *C*. Increasing trends were fitted with a linear model ($y = A + B \times x$), a quadratic model ($y = A + B \times x + C \times x^2$), and a sigmoidal model ($y = e^{(A+B/x)}$), and only the most significant model fit is shown (if $P < 0.05$).

outcome was less clear for our site (29). Hence, even for the studied dry forest, acquisitive species might be more limited by light than by water and be confined to the brighter light conditions of the crests.

From Functional Trait to Niche Separation. Our study confirms that species with alternative functional designs can achieve similar net carbon gains at given resource levels (i.e., at the crossover points in Fig. 1), which is in line with another modeling study (9). Our study, however, does show that such species become functionally divergent, when traits and biophysical principles are scaled to carbon gain responses to resource gradients. Different functional designs thus create a spectrum from acquisitive species that achieve rapid carbon gain in high resource habitats to conservative species that occupy larger fundamental niches because they tolerate low availability of different resources, i.e., both shade and drought (Fig. 1 and Fig. S2). Moreover, most species encountered fundamental niche spaces where they achieved higher carbon gain and thus had a competitive advantage compared with other species (Fig. 1*A*), which in turn may contribute to differentiation in the realized niches (11).

We found support for the idea that the saplings of the 13 tree species are functionally divergent for light and therefore occupied different light niches within the forest. We show that species were also functionally divergent for water, but this divergence was not related to the observed species distributions along a water availability gradient in the forest. Possibly, species with divergent designs of water acquisition differ in their responses to seasonal

Fig. 3. Actual species distributions in relation to maximum carbon gain. Distributions were defined by indexes for light and water availability. For the light index we took the average population-level crown exposure of saplings 2 m tall (43), which is a strong predictor of incident radiation (48) (*Methods* and *SI Text S3*). For the water index, we quantified the relative position of saplings of each species along slopes, which is a strong predictor of the soil water availability in this forest (29) (*Methods* and *SI Text S3*). As such, species with a high light index are mainly found in high light habitats and species with a high water index are mainly found in wet valleys. See Fig. 2 for the procedure of fitting lines.

dynamics in water availability, but become functionally equivalent species in terms of annual carbon gain and survival for the spatial (topographic) gradient in water availability. This interpretation is consistent with some co-occurring species in Mediterranean areas, which differ in their designs for water acquisition but achieve similar carbon gain over longer time spans (34, 35). It could also be that the species differences in water acquisition lead to partitioning of gradients at larger scale, such as gradients in precipitation (27, 45). We thus showed how a trait-based biophysical model can explain functional divergence in response to resource gradients and whether this divergence contributes to niche separation across species. How such mechanisms contribute to species coexistence in the community assembly, or to niche partitioning at larger spatial scales, still remains to be tested (45).

Methods

To test our hypotheses, we parameterized a process-based plant model with functional trait data from 13 co-occurring tree species in a Bolivian tropical dry forest. In the plant model a 3D plant structure is specified and a biochemical photosynthesis model is coupled with a biophysical stomatal conductance model (Fig. S1 and *SI Text S1*) (42). The modeled plant structure consists of a cylindrical crown, with a given top height, crown bottom height, crown radius, sapwood area, and total leaf area, where the leaves are assumed to be uniformly distributed within the crown (Fig. S1 and *SI Text S1*). The crown is assumed to have an average nitrogen concentration per unit leaf area, and this nitrogen is distributed optimally over the crown following the predictions made by big-leaf models (46). The modeled trees were simulated for an environment characterized by irradiance, air temperature, air vapor pressure, and soil water potential. For any combination of environmental conditions, the model can predict the water flow, photosynthesis, and respiration on the basis of the assumptions that transpiration equals stem water flow and that nitrogen levels of proteins are optimally partitioned between two major photosynthesis processes, i.e., carboxylation and electron transport (*SI Text S1*).

For each species, we parameterized the model with the same values for photosynthetic traits of C$_3$ plants at 25 °C (*SI Text S2*, Table S1, and, for derived calculated traits, Table S2). We measured functional trait values for five 1.5- to 2-m tall saplings per species in the field (Tables S3 and S4) (30). Because pioneer and shade-tolerant species co-occurred only at relatively exposed conditions, we sampled all saplings with partial or full overhead exposure in forest borders along logging roads. We thus reduced the confounding effects of plastic responses to variation in light or associated environmental conditions. The focus of this study is thus on inherent across-species differences, which are relatively large compared with plastic differences within species in the studied sapling community (31).

We used the average functional trait values of the five saplings per species to parameterize the 3D plant structure, photosynthetic traits, and hydraulic traits that drive the carbon gain in the plant model (Fig. S1 and *SI Text S1*). On the basis of the measurement of crown width and total leaf area, we calculated the leaf area index (LAI) as the total leaf area per crown surface area. We also included the measured stem sapwood area (A_s), wood density (ρ_s), leaf mass per leaf area (LMA), sapwood-specific hydraulic conductivity (K_s), and the leaf water potential after a period of dry 2 mo hence referred to as minimum leaf water potential (ψ_{min}). The leaf nitrogen mass per leaf mass (N_{mass}) was not estimated from an average but based on a pooled leaf sample of five individuals (Tables S3 and S4) (see ref. 30 for measurement procedures).

We used the model to simulate the carbon gain of each species in response to gradients in light and water availability. The simulated light gradient ranged from 0 to 1,500 μmol·m^{-2}·s^{-1}, which covers the light heterogeneity encountered in tropical forests (47). The water gradient was characterized by the soil water potential running from −6 to 0 MPa, which covers most soil water variation in this forest (29). Carbon gain was calculated as the gross photosynthesis minus the maintenance respiration costs. Leaf or sapwood turnover costs were not included, but vary less and are probably less important than for sapling communities in wetter tropical forests. The simulations provide predictions for the fundamental niche where species achieve positive carbon gain and, more specifically, for the maximum carbon gain, the light compensation point (light level at zero carbon gain at saturated water conditions), and the water compensation point (water potential at zero carbon gain at saturated light conditions). We used the simulated maximum carbon gain and compensation points as predictors for the estimates of the realized light and water niches (the indexes in Fig. 3), as derived from independent field observations of species distributions.

For the light index, we used the average population-level crown exposure of 2-m tall saplings, on the basis of an inventory of the 13 study species and other species in 80 ha of forest (*SI Text S3*). On average 1,253 individuals per species (range: 48–9,064) were measured over their full size range for their height and crown exposure (43). Crown exposure was scored by two independent observers (mean difference 0.1 ± 0.01 SE) on an ordinal scale: 1 if the tree does not receive any direct light, 2 if it receives lateral light, 3 if it receives overhead light on 10–90% of the crown, 4 if it receives full overhead light on >90% of the crown, and 5 if it has an emergent crown (43). There is a good relation between the crown exposure and both canopy openness and incident radiation (48). For each species the crown exposure was related to tree height using a multinomial logistic regression analysis (43). Using the regression equation, the population average crown exposure at a standardized height of 2 m was calculated and used as the light index in our study.

For the water index (a proxy for water availability), we used the relative position of saplings along a topographic gradient from relatively dry crests to moist slopes and wet valley bottoms (29) (*SI Text S3*). Topographic position is a good indicator of soil water availability in the studied forest (29), as well as in other tropical forests (48, 49). Crest, slope, and valley areas were distinguished on a topographic map of 80 ha of forest (the same forest area was used for the light index). Sixty 10 × 10-m plots were established in a stratified random way at each slope position (valley bottom, slope, and crest; n = 20 plots per slope position) (*SI Text S3*), and tree saplings of all species were inventoried in all plots. On average, 78 individuals (range 12–401) were found per species (10). From this, we calculated for each species the proportion of individuals found at each of the three slope positions. To weight for differences in water availability, we multiplied these proportions by 1 for crest, 2 for slope, and 3 for the valley bottom. We used the average of the three resulting values as our water index, which potentially can vary from 0.33 to 1.0 (*SI Text S3*).

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