

Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees

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Tropical forest vegetation is shaped by climate and by soil, but understanding how the distributions of individual tree species respond to specific resources has been hindered by high diversity and consequent rarity. To study species over an entire community, we surveyed trees and measured soil chemistry across climatic and geological gradients in central Panama and then used a unique hierarchical model of species occurrence as a function of rainfall and soil chemistry to circumvent analytical difficulties posed by rare species. The results are a quantitative assessment of the responses of 550 tree species to eight environmental factors, providing a measure of the importance of each factor across the entire tree community. Dry-season intensity and soil phosphorus were the strongest predictors, each affecting the distribution of more than half of the species. Although we anticipated clear-cut responses to dry-season intensity, the finding that many species have pronounced associations with either high or low phosphorus reveals a previously unquantified role for this nutrient in limiting tropical tree distributions. The results provide the data necessary for understanding distributional limits of tree species and predicting future changes in forest composition.

tropical soil resources | phosphorus limitation | climate response | environmental control | plant communities

Understanding how environmental factors govern the distribution, abundance, and coexistence of tropical tree species requires insight into the responses of individual species to individual resources across entire tree communities (1–5). However, the one feature of tropical forest ecosystems we find most appealing, high species diversity, is an impediment in species-specific studies, because data analysis is hindered by the many rare species comprising tropical communities. As a result, despite long recognition of the importance of rainfall and soil nutrients in regulating tropical forest structure and productivity (6–9), studies of the responses of individual species to individual environmental resources remain scarce. Most existing work is based on summary axes of species composition and broad classifications of soil type (10–15), demonstrating that communities vary with soil but offering little insight into responses of individual species.

Forests are highly variable across the geologically and climatically diverse Isthmus of Panama, providing an ideal setting for studying species responses to environmental variation. Tree species composition differs markedly from the wet Caribbean slope to the seasonally dry Pacific coast (16), and species distributions relative to rainfall can be predicted from experimental drought sensitivity (5). Moreover, the complex geology of the region provides a range of soil properties (17), and there are places where vegetation varies conspicuously across geological boundaries. Here, we combine observations on soil chemistry, dry-season intensity, and tree inventories (17, 18) to reveal how the distributions of 550 tree species vary with eight key environmental factors across the 65-km isthmus (Fig. S1).

Results

Soil chemistry was extremely variable among the 72 sampling sites. Phosphorus extractable by anion-exchange resin (resin phosphorus), which is the most biologically available form, varied 200-fold, a range close to that reported for the entire lowland tropics (6, 13, 19–21). Extractable calcium varied 400-fold (Table 1), and dry-season intensity also varied markedly across the sites, with the annual extreme moisture deficit averaging 580 mm at the driest site but only 370 mm at the wettest site (Table 1).

The strongest environmental predictors of species distributions were dry-season moisture and resin phosphorus, each having a substantial impact on more than half of the species (Fig. 1, Table 1, and Fig. S2). All combinations of joint responses were observed: species associated with high moisture and high phosphorus, low moisture and low phosphorus, or high of one and low of the other (Fig. 2 and Fig. S3). There were also generalists responding to neither resource, or to just one of the two resources (Fig. 3). The pronounced variability of species responses to moisture and phosphorus is reflected in the large SD of effect sizes across the community (Fig. 1). Additional species had modal responses to moisture, but responses to phosphorus were monotonic (Table 1 and Fig. S3). In separate models, we tested the impact of total phosphorus in place of resin phosphorus, and results were indistinguishable (SI Notes).

Calcium had a modest community-wide impact (Fig. 1, Table 1, and Fig. S4) but was highly correlated with magnesium and pH (Table S1); thus, we cannot separate their impacts. Species responses to phosphorus and calcium were positively correlated (SI Notes), suggesting that tree species may be responding to several nutrients in concert, with extreme variation in soil phosphorus and calcium the key to their importance in central Panama. Other soil nutrients, as well as the potential toxin aluminum, were unimportant. In particular, responses to inorganic nitrogen and iron were negligible, and a separate model with extractable organic nitrogen, which is available for uptake by plants (22) and serves as a surrogate for nitrogen mineralization (23), also showed a weak impact on tree distributions (SI Notes).

Distributions of genera were likewise predicted by moisture, phosphorus, and calcium, with community-wide results mirroring those for species but weaker (Figs. S5 and S6). Family responses to the same predictors were detectable but further attenuated

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Table 1. Summary statistics and tree species responses to soil and rainfall at 72 forest inventory sites

Environmental measure	Summary statistics				Species responses					
					Strong effect			Significant effects		
	Mean	SD	Minimum	Maximum	+	−	Total, %	Direct	Mode	Total, %
Dry-season moisture	−534.0	48.9	−579.4	−370.1	119	60	66.5	122	40	60.2
Resin phosphorus	3.0	4.3	0.1	22.8	62	93	57.6	77	9	32.0
Calcium	2,056.5	2,013.3	25.0	9,738.6	14	79	34.6	34	2	13.4
Potassium	73.3	72.7	12.3	351.9	26	1	10.0	11	0	4.1
Aluminum	940.9	259.1	323.3	1,463.0	7	8	5.6	10	1	4.1
Iron	172.9	79.6	78.0	727.9	0	4	1.5	6	2	3.0
Zinc	4.2	5.8	0.5	44.8	0	0	0.0	0	27	10.0
Inorganic nitrogen	3.7	1.3	0.6	7.4	0	0	0.0	0	0	0.0

Environmental measures are ordered from strongest to weakest impacts on tree distributions. Dry-season moisture is the extreme annual deficit of rainfall minus evapotranspiration in millimeters (*SI Materials and Methods*); soil nutrient concentrations are provided in milligrams per kilogram. Species responses are the number and percentage of the 271 species with ≥ 10 occurrences that were strongly or significantly associated with each measure. Strong associations were those in which the absolute value of the effect size was >0.5 . Direct significant effects were first-order logistic parameters whose Bayesian credible intervals did not include zero. Significant modes had Bayesian credible intervals that were fully within the observed environmental range but were not already counted as significant direct effects.

(Fig. S6). Strong associations of higher taxa reveal taxonomic conservatism: Nearly all *Pouteria* species, for example, occurred at the wet end of the climate gradient, and species in the family

Humiriaceae occurred exclusively in association with low phosphorus (*SI Notes*). Other taxa, however, encompassed divergent species responses, explaining the weakened community-wide responses at higher levels (Fig. S6 and *SI Notes*).

To evaluate the hierarchical method's effectiveness at detecting responses, we tested it against simulated data in which artificial species were assigned known environmental responses to one or more predictors. The model uncovered the assigned community-wide hyperdistributions accurately (Table S2). Moreover, we established that spatial autocorrelation did not bias results (Fig. S7). Additional results on moisture and calcium responses, as well as details on simulations and autocorrelations, are provided in *SI Text*.

Discussion

Dry-season intensity and plant-available phosphorus are the main drivers of tree distributions across environmental gradients in Panama. The importance of moisture in limiting species ranges is established, but a dominant role for phosphorus as a limit to tree species occurrence in the tropics has not been demonstrated. Many previous studies have inferred effects of soil on tree communities based on summary axes of species composition and soil properties (10–15), but these do not provide evidence of species-specific responses to individual nutrients. Other studies have concluded that phosphorus constrains productivity of lowland tropical forests (9, 24, 25), based predominantly on evidence that phosphorus limits productivity on old landscapes with strongly weathered soils (26–28) and that tropical forest leaves have high nitrogen-to-phosphorus ratios (9). Limiting productivity, however, is not the same as limiting species distributions. Our key finding is that both rainfall patterns and soil phosphorus partition the community and that some species showed a preference for high phosphorus and others for low phosphorus. This parallels results from outside the tropics, for example, in Western Australia, where many *Proteaceae* specialize on low-phosphorus soil and avoid high phosphorus (29).

Nitrogen, as we measured it, did not have an impact on species distributions, and we considered both inorganic forms, which are the most available biologically, and extractable organic forms, which serve as a surrogate for mineralization rate (23). The absence of strong species responses to nitrogen is not surprising, given abundant evidence for the high availability of nitrogen in lowland tropical forests (30) and recent increases in atmospheric nitrogen deposition in Panama (31).

The newly discovered importance of phosphorus expands our understanding of tree natural history in Panama, which has long

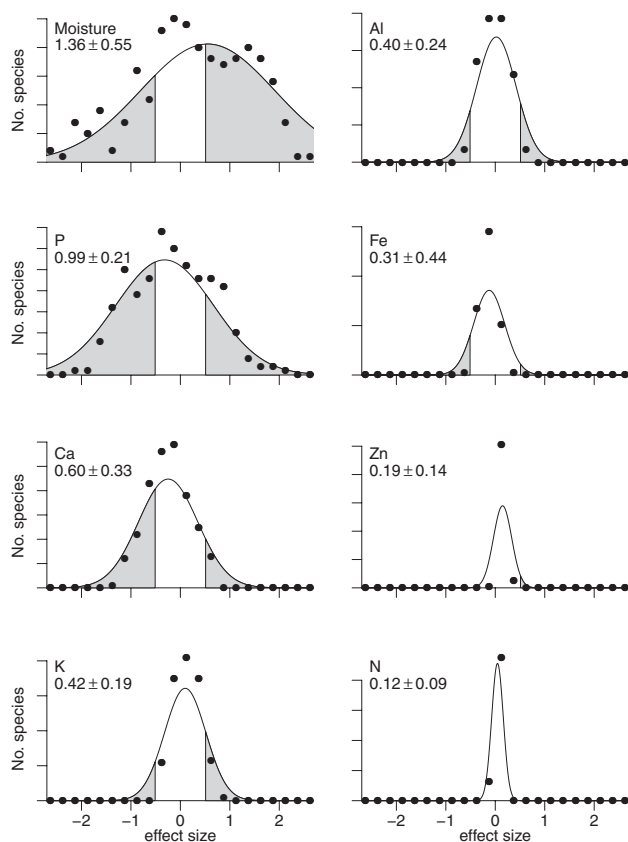


Fig. 1. Histograms of individual species responses to eight environmental factors. The horizontal axis is the effect size, b , defined as the first-order parameter of the logistic model. The shaded portions of each curve highlight species with strong responses ($|b| > 0.5$; Table 1). The curves are fitted hyperdistributions of b ; the fitted SD (hyper-SD) of b with its credible interval is noted. Points give the observed number of species within bins of width 0.25 (i.e., the observed hyperdistribution), including just the 271 species with ≥ 10 occurrences. Moisture, dry-season moisture; P, plant-available (resin) phosphorus; N, inorganic nitrogen (Table S1 and *SI Materials and Methods*).

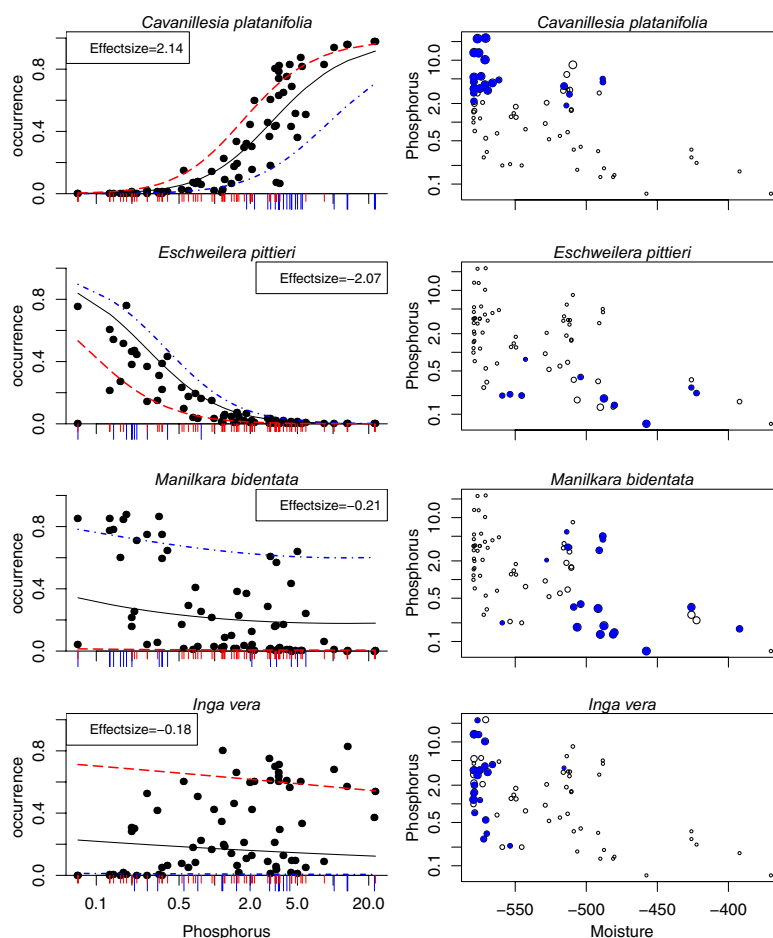


Fig. 2. Responses of four species to plant-available (resin) phosphorus and dry-season moisture. (*Left*) Graphs show occurrence probability per site (*y* axis) as a function of phosphorus concentration (*x* axis) (milligrams per kilogram, log scale). The solid curve is the logistic model's prediction of the species response to phosphorus (the modeled occurrence when phosphorus is varied), whereas the other seven predictors are held constant at their means. The dashed curve (red) is the response to phosphorus under dry conditions (1 SD below mean moisture), whereas the remaining factors are held at their means. The dotted-dashed curve (blue) is the response to phosphorus under wet conditions (1 SD above mean moisture), whereas the remaining factors are held at their means. The black points are the modeled response when all eight factors were varied, the model's best prediction at each site. Below the *x* axis, blue bars show where a species was observed and red bars shown where it was absent. The four species were chosen to illustrate a range of joint moisture-phosphorus responses: *C. platanifolia* had a strong positive response to phosphorus and to drier conditions; *E. pittieri* was associated with low phosphorus and high moisture; *Manilkara bidentata* and *Inga vera* were indifferent to phosphorus but had opposing moisture responses, with the former occurring with high moisture and the latter with low moisture. The effect size noted for each species is the first-order logistic parameter for phosphorus, b_P , with $b_P > 0$ meaning a species associated with high phosphorus. (*Right*) Graphs show phosphorus concentration (milligrams per kilogram, log scale) plotted against dry-season moisture (millimeters) at all 72 sites, with filled circles (blue) showing where each species was observed. A more negative dry season had less moisture (*SI Materials and Methods*). The size of the points indicates the model prediction for each species, based on all eight factors, with larger circles having a higher predicted occurrence. *C. platanifolia* and *E. pittieri* were perfectly segregated by phosphorus but overlapped considerably on the moisture gradient. *M. bidentata* and *I. vera* were segregated by moisture but not phosphorus.

focused on the dry season and moisture deficit (2, 5, 16, 32). Two species contrasting in phosphorus response serve to illustrate these issues. One is the giant canopy emergent, *Cavanillesia platanifolia*, whose conspicuous deciduous crowns are easy to spot on the dry Pacific slope, where deciduous species generally are most numerous (33). However, *C. platanifolia* occurs patchily and is absent on some hillsides while abundant on others, and our soil analysis reveals that this is a result of phosphorus limitation: High phosphorus is a better predictor of its presence than low moisture (Fig. 2). Conversely, although more subtly, *Eschweilera pittieri*, which we previously considered a wet-forest specialist (34), is, in fact, better predicted by low phosphorus than by high precipitation (Fig. 2).

Species traits that might govern the observed ranges of responses to soil phosphorus and drought are poorly understood in tropical trees. Deciduous species may require high phosphorus

due to the frequent turnover of leaves (35), whereas low-phosphorus specialists might acquire organic or recalcitrant inorganic forms by synthesizing specialized phosphatases, secreting organic acids, or associating with mycorrhizas efficient at phosphorus acquisition (29, 36, 37). There are traits known to affect species performance under drought conditions (38), but the extent to which these determine species distributions remains unknown. Ranges might also be restricted by competition, such that species demanding high phosphorus or ample moisture outgrow low-resource specialists where the resources are plentiful. Now that we have quantitative measures of species responses to individual resources, we can begin experimental studies on mechanisms underpinning resource specialization using species with known distributions (5, 39–42). Physiological, genetic, and phylogenetic understanding of traits linked to species distributions could then become the basis for predictive models about how

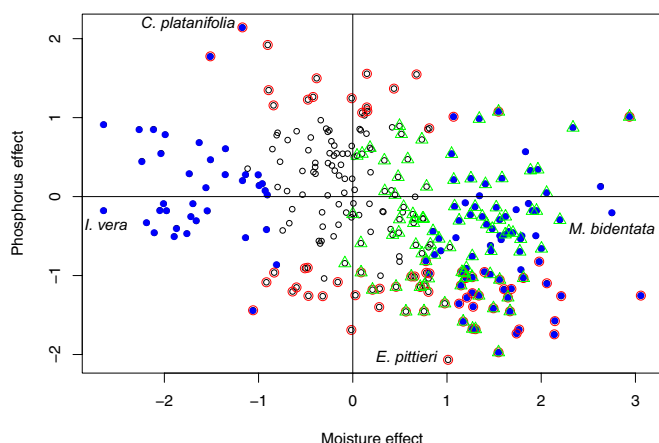


Fig. 3. Quantitative responses to dry-season moisture and plant-available (resin) phosphorus for individual species. Response is measured by the effect size, b (Fig. 1); $b > 0$ means a species associated with high moisture or high phosphorus. Solid blue points are statistically significant effects relative to moisture; open red circles are significant relative to phosphorus. The green triangles indicate species with a significant modal response to moisture. Only species with ≥ 10 occurrences are included. Species identified are those whose individual responses are shown in Fig. 2. There is a weak but significant negative correlation between the two responses ($r^2 = 0.10$).

community dynamics and ecosystem functions are responding to human perturbations.

Materials and Methods

Tree Occurrence. Tree species were surveyed in plots or inventories at 72 forested locations near the Panama Canal, each $<0.5 \text{ km}^2$ in area (Fig. S1 and SI Materials and Methods). Our analysis is based on the presence and absence of the 550 fully identified, naturally occurring species with three or more records at those sites.

Climatic Predictors. Dry-season rainfall is the climatic variable most clearly affecting forests in Panama (43). To estimate dry-season moisture, rainfall data from 47 gauges maintained by the Panama Canal Authority were used to calculate the cumulative moisture deficit (precipitation minus potential evapotranspiration) at its most extreme every year. An optimized spatial kernel was fitted to the results at 47 gauges and used to interpolate mean dry-season moisture at the 72 sample sites (SI Materials and Methods). Total annual rainfall estimated by the same kerneling method was closely correlated with dry-season moisture; elevation and temperature were not included in the model due to limited variation.

Soil Predictors. We collected samples of surface soil at all 72 sites and returned them immediately to the laboratory for standard analyses of organic, inorganic, and total nitrogen; readily exchangeable phosphorus (extracted with anion-exchange resin); pH; and extractable aluminum, calcium, potassium, magnesium, manganese, iron, and zinc (SI Materials and Methods). Total phosphorus was later determined on a dried subsample. Soil texture was not included in the model due to limited variation (most soils were clays). Nutrient concentration to a depth of 1 m was analyzed but not

included in species modeling because most nutrients and fine roots were in the surface horizon.

Modeling. A set of eight environmental predictors was used in the model of tree distributions (Table 1), chosen as the largest set among which correlations were weak (Table S1). Soil concentrations were log-transformed; each predictor was then standardized to mean = 0 and SD = 1, such that model parameters were comparable across species and resources. We modeled species occurrences against the eight factors simultaneously using Gaussian logistic regression, a method that allows monotonic or unimodal responses to some or all predictors (44). All species were included at once using a hierarchical Bayesian approach [a multilevel regression (45)]. The hierarchy consists of a lower level of species-level response parameters beneath an overarching community-wide distribution of those responses (4, 45, 46). The upper level, the hyperdistribution and particularly its SD, measures the variability of responses across a community and thus reveals whether a resource differentiates species. The lower level provides a separate measure for the response of every species to each environmental factor. The hierarchical aspect was critical, preventing overfitting in rare species but weighting all species according to frequency. Parameters were fitted with a Gibbs sampler based on Metropolis updates, producing credible intervals for all statistics.

The first-order logistic parameter estimates the change in occurrence probability of a species (relative to its mean occurrence) over the main part of the gradient of one resource, assuming other resources were held constant (Fig. 1 and Fig. S2). The most extreme response is ≈ 2 , where a species has high occurrence at one end of the gradient and ≈ 0 at the other (45). The second-order parameter defines the mode of responses. Further details on the model and parameters are presented in SI Materials and Methods.

Genera and Families. The same model was also fitted to the distributions of genera and families. The occurrence of a genus was the pooled occurrences of all its species (i.e., if any of its species occurred at a site, the genus did as well). All 867 species identified to the genus level were used, but only genera with >1 species were entered in the model, because genera with 1 species only repeat the species results. This left 145 genera with three or more occurrences. Similarly, we estimated responses of 66 families with >1 species and three or more occurrences.

Spatial Autocorrelation. Semivariograms were calculated from observed occurrences and from residuals around the model's predicted occurrences to test whether unexplained spatial autocorrelation could bias parameter estimates (SI Materials and Methods and SI Notes).

Simulations. Tree communities with no environmental responses were simulated by placing 500 species randomly at 72 sample sites, matching occurrence probabilities of real species. Tree communities with responses were simulated using observed soil and climate data, along with randomly assigned logistic response parameters for eight predictors (SI Materials and Methods and SI Notes).

More details on all methods are provided in SI Materials and Methods.

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Supporting Information

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SI Materials and Methods

Tree Species Occurrence. We surveyed woody species with free-standing stems ≥ 1 cm in diameter at 72 locations near the Panama Canal (Fig. S1), each with an area < 0.5 km². Sites were arranged to span geological formations (1) and the rainfall gradient (2), but all were within 65 km of one another. Most were at low elevation, with just two sites > 600 m above sea level, with the highest at 888 m. All were in closed-canopy forest, including undisturbed old growth and secondary stands 60–100 y old (2). Forty surveys were permanent census plots in which every individual tree was located, measured, and identified (3): the 50-ha plot at Barro Colorado (4, 5), a 5.96-ha plot at Fort Sherman (6), and 38 1-ha plots (2, 7). At 32 other sites, surveys were 1-d inventories in which all tree species were noted until we could find no more without counting individuals. Additional tree surveys have been used in other reports (2, 8); the 72 described here are those including soil analyses.

We identified nearly every tree, either on the spot or later, after comparison against keys or guides (9–13) and herbarium specimens (Smithsonian Tropical Research Institute and the University of Panama), producing a total of 890 species at the 72 sites. Of these, 779 were fully identified and 88 others were identified to genus level; another 23 were rare individuals we could not recognize. In the analyses of climate and soil responses, we included the 550 species that were fully identified, native to the region, never cultivated, and had three or more occurrences at the 72 sites.

Plots were complete censuses and included every tree species in the defined area and diameter range. Inventories were intended to capture every species, and the mean (\pm SD) of species encountered in inventories was close to that in plots (102.6 ± 41.4 vs. 113.9 ± 42.7), suggesting we were reasonably successful. Although the area sampled at each site varied, most sites covered 1–10 ha, and the increase of species number with an area over that range is modest (14). We thus assume a detection probability of ~ 1 for each species and model species occurrence probability per location.

Rainfall and Dry-Season Duration. We used 47 Panama Canal Authority rainfall stations with 3–47 y of uninterrupted data since 1960 (daily records are available for download at <http://dx.doi.org/10.5479/data.bci.20130204>) to calculate dry-season moisture availability, defined as the cumulative deficit of precipitation minus potential evapotranspiration (PET) at its most extreme every year (8). Evaporation data were taken from the station at Barro Colorado Island, because none other were available; to apply those data to other sites, we corrected for elevation, assuming that a 100-m increase reduced PET by $0.1 \text{ mm} \cdot \text{d}^{-1}$ (15).

Define the cumulative moisture deficit D_{ij} between days i and j as

$$D_{ij} = \sum_{t=i}^j (P_t - E_t), \quad [\text{S1}]$$

where P_t and E_t are precipitation and PET on day t . D_{ij} was calculated for every pair of days with $i \geq 1$ Sept and $j \leq 1$ July (the following year), thus spanning one December-to-March dry season. The minimum during one season, $D_m = \min(D_{ij})$, is a measure of the severity of that dry season, and the mean \bar{D}_m was calculated across all available years at each station. The driest rainfall gauge by this measure was at Hodges' Hill near

the Pacific coast, with $\bar{D}_m = -606$ mm. The wettest was at Esperanza in steep hills near the Caribbean, with $\bar{D}_m = -106$ mm. We used \bar{D}_m at the 47 rainfall stations to fit a spatial kernel, optimizing the distance and elevation windows (16), and applied the kernel to the 72 sample sites. Because \bar{D}_m is a negative number, it measures moistness (the higher, the wetter); thus, we refer to it as dry-season moisture, or just moisture for brevity. As an independent check, we estimated soil water content gravimetrically throughout the dry season at 17 sites, and the minimum gravimetric water correlated well with \bar{D}_m ($r^2 = 0.54$).

Soil Chemistry. Soil was collected and analyzed from 72 tree survey sites. In each of the large plots (Barro Colorado and Fort Sherman), 26 individual cores were collected; at each 1-ha plot, 13 were collected; and at inventory sites, 5 were collected. All sampling was done during the wet season. Cores were taken to a depth of 10 cm, and the soil was returned immediately to the laboratory, where roots and small stones were removed by hand. Nitrogen was extracted within 6 h of collection, and phosphate, cations, and pH were determined within 24 h; prompt analysis is critical due to rapid changes in nutrient concentrations during storage (17). Each core was analyzed separately, and the average of all cores at a single site was used in modeling. Deeper soils were also sampled, but below the surface horizon, there were few fine roots ($< 10\%$ of the total) and much lower nutrient concentrations.

Nitrogen fractions (ammonium, nitrate, dissolved organic) were determined by extraction in 0.5 M K_2SO_4 for 1 h; inorganic fractions were determined by automated colorimetry on a Lachat Quikchem 8500 (Hach Ltd.), and total dissolved nitrogen was determined by automated combustion and gas chromatography (TOC-V^{CSH} organic carbon analyzer; Shimadzu). Organic nitrogen was calculated as the difference between total dissolved nitrogen and total inorganic nitrogen. Soil pH was determined with a glass electrode (Hach Ltd.) in a solution with a 1:2 ratio of soil to water. Readily exchangeable phosphate was determined by extraction with anion-exchange membranes (17); we refer to this measure as plant-available or resin phosphorus. All other inorganic nutrients were extracted in Mehlich-3 solution (0.2 M NH_4OAc , 0.25 M NH_4NO_3 , 13 mM HNO_3 , 15 mM NH_4F , 1.0 mM EDTA) (18): 5 g of soil on a dry-weight basis was shaken for 5 min in 50 mL of Mehlich-3 solution, centrifuged ($8,000 \times g$ for 10 min), and then analyzed for cations (aluminum, calcium, potassium, magnesium, manganese, iron, zinc) and phosphorus using inductively coupled plasma-optical emission spectrometry on an Optima 2100 (PerkinElmer). Total phosphorus was determined by ignition ($550^\circ \text{C} \times 1 \text{ h}$) and acid extraction (1 M $\text{H}_2\text{SO}_4 \times 16 \text{ h}$), with phosphate detected by molybdate colorimetry (19). This procedure gave 100% recovery of phosphorus from reference soils, and at 19 sites, it produced estimates indistinguishable from an H_2O_2 - H_2SO_4 digest (20).

Data Processing. Data from all tree plots and inventories were condensed to the presence and absence of each species, producing a 550×72 occurrence matrix I . For environmental predictors, we selected the largest set of measures from which all pairs were weakly correlated ($r^2 < 0.40$): dry-season moisture, along with soil aluminum, calcium, iron, potassium, phosphorus, zinc, and inorganic nitrogen. Magnesium, manganese, pH, and organic nitrogen were excluded because they were highly correlated with calcium. Three phosphorus measures (Mehlich-3 solution, resin, and total) were highly correlated with one another (Table S1); thus, we used just the resin method, which best

matches what should be readily available to trees. Soil texture was omitted because most sites were clays; elevation was omitted because nearly all sites (70 of 72) were <600 m above sea level, with the cutoff separating lowland from midelevation forests; and total annual rainfall was omitted because it correlated closely with dry-season moisture.

Predictors other than pH and dry-season moisture were log-transformed, and all were then standardized by subtracting their means and dividing by their SDs. The standardized environmental predictors form a 72×8 habitat matrix X .

Model. The probability of occurrence of each tree species at each survey was fitted with Gaussian logistic regression (21, 22) against the eight standardized environmental measures, X . This model requires 17 parameters per species: a single intercept a , eight first-order parameters \vec{B} , and eight more second-order parameters, \vec{C} (the arrows indicate \vec{B} and \vec{C} are vectors). The occurrence probabilities \vec{P} for a single species are then modeled as

$$\vec{P} = \gamma(a + X\vec{B} + X^2\vec{C}), \quad [\text{S2}]$$

where γ is the inverse-logit function, $\gamma(y) = \frac{e^y}{1+e^y}$. Because there were 72 sites, \vec{P} is a vector of length 72 and X is the 72×8 matrix of predictors. Call the parameters for one species $\vec{\theta} = (a, \vec{B}, \vec{C})$, with a vector of length 17.

Because predictors X were standardized to mean = 0 and SD = 1, first-order parameters \vec{B} are directly comparable across different resources, and each b_{sr} reveals how species s responded to resource r . Indeed, the first-order logistic parameter, b_{sr} , is close to the change in the predicted occurrence of species s between $r = -1$ (1 SD below the mean) and $r = +1$ (1 SD above the mean) relative to mean occurrence, when all other resources are held at their means. This can be shown with the partial derivative $\frac{\partial \vec{P}}{\partial b_{sr}}$, or empirically with fitted results (Fig. S2). We thus define \vec{B} as effect sizes: the effect of resources on species occurrences (Fig. 1).

Likewise, the second-order parameters \vec{C} are comparable across species and resources, revealing tendencies toward a modal response. Estimated \vec{C} were nearly always <0, meaning local maxima, as expected for response curves (21). The location of fitted maxima, however, often fell outside the observed resource gradients, and our test for significance of a mode was based on its location (more information is provided in the section on fitting the model).

Hierarchical Component and Hyperdistributions. We added a hierarchical or multilevel component (23) to the model by defining species as a group effect (24). Define θ as the 550×17 matrix of parameters for all species; one row holds the parameters $\vec{\theta} = (a, \vec{B}, \vec{C})$ for one species. The group level is defined by assuming that θ follows a community-wide Gaussian hyperdistribution, $\theta \sim \mathcal{N}(\vec{\mu}, \mathbf{v})$, where $\vec{\mu}$ is the vector of means and \mathbf{v} is the covariance matrix. In Bayesian terms, \mathcal{N} is a prior for the parameter θ , and $\vec{\mu}$ and \mathbf{v} are hyperparameters.

We assumed, however, that \mathbf{v} had zeroes off-diagonal, and is thus a vector of variances, equivalent to independent Gaussian hyperdistributions for each parameter. Use σ_r for the associated SDs (the diagonal of $\sqrt{\mathbf{v}}$). Each σ_r , the SD of species responses to resource r , is a measure of how differently species behaved relative to r , and thus indicates whether a resource is important in differentiating tree species (Fig. 1). The hypermeans, $\vec{\mu}$, define the average response of the entire community to each resource and are outside our focus in this study.

Model Fitting. There were two stages to fitting the model's parameters. The first stage was for individual species parameters. Consider species s and its observed occurrences \vec{I}_s , logistic parameters $\vec{\theta}_s = (a, \vec{B}, \vec{C})$, and predicted occurrences $\vec{P}_s(\vec{\theta}_s)$. The

likelihood of \vec{I}_s depends on $\vec{\theta}_s$ as well as on the hyperdistribution and its hyperparameters, $\mathcal{N}(\vec{\mu}, \mathbf{v})$, as follows:

$$L\{\vec{I}_s | (\vec{\theta}_s, \vec{\mu}, \mathbf{v})\} = L\{\vec{I}_s | P_s(\vec{\theta}_s)\} \cdot L\{(\vec{\theta}_s) | \mathcal{N}(\vec{\mu}, \mathbf{v})\}. \quad [\text{S3}]$$

The first likelihood to the right of the equal sign is standard occurrence modeling: the probability of observations of species s given the logistic model's predictions. The second likelihood on the right is the probability of observing the logistic parameters, given the hyperdistribution. Other than the hyperdistribution, no prior probabilities were used for species parameters. The parameters for each species were fitted one at a time with the likelihood of Eq. S3, with one species independent of the remaining species (the interdependence of species comes from the hyperparameters).

The second stage in the model was the hierarchical aspect, fitting the hyperparameters using the likelihood of observing the entire matrix of species parameters θ ,

$$L(\theta | \vec{\mu}, \mathbf{v}) = \mathcal{N}(\vec{\mu}, \mathbf{v}). \quad [\text{S4}]$$

No prior probabilities were assumed on the hypermeans $\vec{\mu}$. For \mathbf{v} , models were run, including an inverse- γ prior (24), or a flat prior >0, and results were indistinguishable.

Parameter fitting was accomplished with a Gibbs sampler using a Metropolis update algorithm (25, 26) written in the programming language R (27). The sampler works by updating each of the parameters in sequence, holding other parameters fixed while the relevant likelihood (Eq. S3 or Eq. S4) is used to locate the target parameter's next value. The step size used in the updates was adjusted adaptively through the runs, allowing more rapid convergence (26). To diagnose convergence of parameter estimates, we completed four independent model runs, each starting with different parameter values for every species and run for 4,000 steps, where each step means one update for every parameter (28). Parameter values from independent runs became indistinguishable after step 2,000 (based on correlations of species parameters, or hyperparameters, across separate runs); thus, the first 2,000 steps of each chain were discarded and postburn-in chains were combined (8,000 parameter values in total) as estimates of Bayesian posterior distributions. The mean of a chain was taken as the best estimate for a parameter, and 2.5th and 97.5th percentiles were taken as 95% credible intervals. The first-order effect for every species and every resource, b_{sr} , was considered statistically significant if its credible intervals did not overlap zero. The position of the local maximum (or minimum) for each response was considered significant if 95% credible intervals of $b_{sr}/2c_{sr}$ (the mode's position) were inside the observed range of resource r .

Alternative Models. Robustness of results from the main model was assessed by running alternative models using different combinations of environmental predictors or different methods. Results from models with one to seven predictors were compared, and regardless of which predictors were included, dry-season moisture always had the strongest impact and provided the best model fit, and phosphorus and calcium were the predictors with the next strongest impact [based on hyper-SDs, Akaike Information Criteria, or Deviance Information Criteria (29)]. Moisture-response parameters for individual species from different models were highly correlated ($r^2 > 0.96$), as were phosphorus responses ($r^2 > 0.83$), regardless of what other predictors were included. Parameters for calcium were altered more when moisture or phosphorus was added to a model ($r^2 \sim 0.65$), and parameters for other factors were less consistent across models.

The R package *lme4*, whose function *lmer* fits hierarchical models using a different method (30), produced results indistinguishable from those of our Bayesian model. We also tested models with a full covariance matrix, using Bayesian fitting or *lmer*, and found results to be less reliable. Off-diagonal elements of the matrix were poorly fitted, with very slow convergence. The overall results, with moisture, phosphorus, and calcium being the best predictors, still appeared, however.

We also ran models in the absence of the hierarchic framework, with each species tested independently. The full 17-parameter model failed to converge in more than half of the species. Species with <10 records nearly always failed, and those with up to 25 records had 20% failure rates. Some of the species that could be fitted had absurdly high positive responses ($>10^8$) to some resources offset by similarly low negative responses to others.

Spatial Autocorrelation. We measured spatial autocorrelation (31) using semivariograms in species composition (2), calculated as the classic measure from the R package *sgstat* (32). Semivariograms were estimated first for species occurrences and then for residuals of occurrence around the model's predictions ($1 - P_k$ where species k occurred, $-P_k$ where it did not). In both cases, we calculated the mean semivariance across species.

Simulations. Tree occurrences were simulated at 72 sample sites using observed climate and soil measures. Two kinds of simulations were performed: (i) random placement at the 72 sites, such that species had no resource responses, and (ii) placement based on simulated response curves using random Gaussian logistic parameters assigned to every species.

In random placement, 500 species were each assigned an occurrence probability drawn from a logit-normal distribution (mean = -3.2 and SD = 1.5 , matching observed occurrences) and then placed at 72 sites using random binomial draws around the occurrence probabilities. To simulate resource responses, species were assigned logistic parameters $\bar{\theta} = (a, \bar{b}, \bar{c})$ (Eq. S2) using random draws from multivariate Gaussian hyperdistributions. A small Gaussian error was added at random to the logistic occurrence probability at each site (mean = 0 , SD = 0.03) and binomial random draws then determined occurrences. The hyper-SD for each resource was varied arbitrarily from 0.1 to 1.1 to simulate weak to strong environmental effects; strong covariances among some parameters were also simulated. The R functions *morm*, *rbinom*, and *rmvnorm* provided random draws (27, 33).

SI Notes

Responses to Moisture. A sample of the responses of four species to moisture jointly with plant-available (resin) phosphorus is shown in Fig. S3, selected to show a range of behavior (parallel to Fig. 2). *Triplaris cumingiana* had a negative response to moisture but a positive response to phosphorus; *Socratea exorrhiza* was exactly the opposite. *Randia armata* and *Hieronyma alchorneoides* offer examples of modal responses to moisture: *R. armata* had a positive effect size, increasing in occurrence over the main part of the moisture gradient but then decreasing; *H. alchorneoides* had an effect size ≈ 0 because it showed little change in the main part of the moisture gradient, with a mode close to mean moisture (-534 mm). *H. alchorneoides* was counted in Table S2 as a species with a significant modal effect, but *R. armata* was not because it was already counted as having a significant positive effect.

Responses to Calcium. A sample of the responses of four species to calcium jointly with resin phosphorus is shown in Fig. S4, repeating two species whose phosphorus-moisture responses appear in the main text (Fig. 2). *Cavanillesia platanifolia* was always absent where $\ln(P) < 0.5$ and where $\ln(Ca) < 6$; the model fitted negative effects to both, although the effects were stronger for phosphorus. In *Eschweilera pittieri* and *Tetrathylacium johansenii*,

phosphorus was the better predictor, and in *Ghoshispora foliacea*, calcium was better. Responses to phosphorus and calcium were positively correlated across species ($r^2 = 0.33$ among species with ≥ 10 occurrences).

Responses to Other Resources. A model with Mehlich-3 phosphorus substituted for resin phosphorus (never together due to their high correlation) produced similar results to our main model. Indeed, Mehlich-3 phosphorus was the stronger predictor; calcium remained next in importance, regardless. Omitting calcium to test other correlated nutrients revealed that organic nitrogen and manganese were weaker predictors than calcium, whereas magnesium and pH were similar to calcium.

Response of Genera and Families. The community-wide response hyperdistributions for genera closely matched those for species, although hyperstandard distributions were reduced by about one-third for all predictors (Fig. S5 compared with Fig. 2). Results were similar for families, although reduced again. There were many genera, and fewer families, having strong associations with wet conditions and low phosphorus but few with the opposite associations (Fig. S6).

The weakening of responses from species to genera to families means that at least some genera were composed of species with varying responses to the environment, and likewise for families. A few examples illustrate the range of species mixes found within higher taxa.

Pouteria had 12 species that were remarkably homogeneous in moisture response: 10 of 12 shared very strong associations with high moisture. Their phosphorus responses were mixed however, varying from strongly negative to weakly positive. The genus as a whole thus had a strong moisture but negligible phosphorus response (Fig. S6). The family Humiriaceae had consistent phosphorus responses: its four species, in three genera, shared a strong association with low phosphorus but varied in moisture responses (Fig. S6).

Examples of mixed associations include *Matayba* (Sapindaceae) and *Trichilia* (Meliaceae). *Matayba* had three species partitioning the phosphorus-moisture gradients: *Matayba apetala*, associated with wet sites and low phosphorus; *Matayba glaberrima*, associated with dry sites and high phosphorus; and *Matayba scrobiculata*, associated with dry sites and low phosphorus. *Trichilia* had six divergent species: Four occurred preferentially at dry sites with high phosphorus, and one was exactly the opposite. The last, *Trichilia tuberculata*, was associated with high phosphorus but was moisture-neutral. Both genera appeared to be generalists (Fig. S6).

Spatial Autocorrelation. The semivariogram in species occurrence increased from 0 to 18 km (Fig. S7). Residuals around the full model, however, showed no increase in the semivariance beyond 0.5 km (Fig. S7). Few of the 72 sample sites were <0.5 km apart, but as a check of the importance of spatial autocorrelation on estimates, we repeated the model after omitting 15 sites so that no two were within 500 m of each other. Hyperparameters from this reduced model were indistinguishable from those of the model with 72 sites.

Simulations. In simulated distributions with no habitat response (random placement), community-wide SDs σ (the hyper-SDs) as fitted by the hierarchical logistic model were <0.17 for all 16 response parameters. For individual species, the highest magnitude for a fitted first-order parameter was $|b| = 0.19$. The model did not report a single significant response for individual species (of $16 \times 550 = 8,800$ tests).

When confronted with simulated habitat responses, the model always accurately estimated σ whenever the response was strong, defined as $\sigma > 0.5$ (Table S2 shows results for two simulations; three others had similar results). In no case was a weak simulated re-

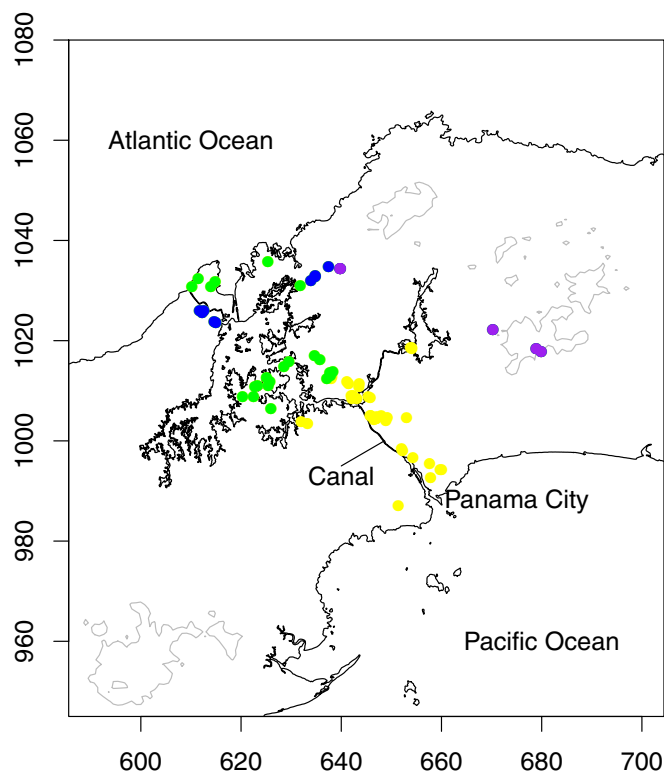


Fig. S1. Map of tree survey sites in the Panama Canal area. The Pacific Ocean is to the south, and the Atlantic (Caribbean) is to the north. Units on the axes are UTM (Universal Transverse Mercator) coordinates (zone 17) in kilometers, and the 600-m elevation contour is shown in gray. Estimated dry-season moisture is color-coded: with yellow being the driest ($\leq 550 \text{ mm} \cdot \text{y}^{-1}$) through green to blue, with purple ($\geq 400 \text{ mm} \cdot \text{y}^{-1}$) being the wettest.

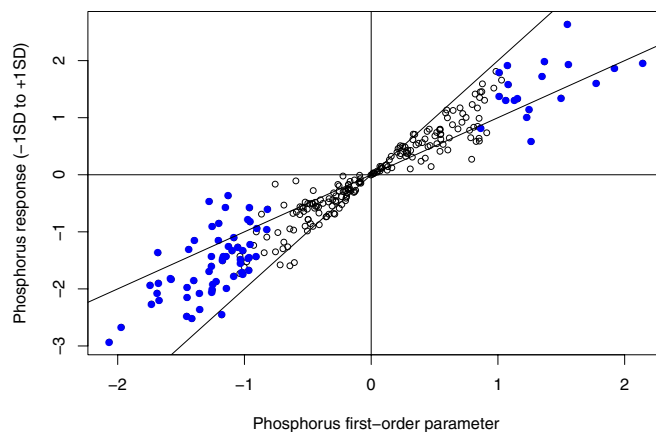


Fig. S2. Relationship between the first-order logistic parameter for plant-available (resin) phosphorus and the estimated change in tree species occurrence across the phosphorus gradient. Each point is one species, including only those with ≥ 10 occurrences. The x axis is the first-order parameter, b_p , in the Gaussian logistic model; the y axis is the difference in the fitted response between 1 SD below mean phosphorus and 1 SD above mean phosphorus, divided by the mean occurrence of each species (with other resources held at their mean). The two lines are at $y = x$ and $y = 2x$; filled points indicate statistically significant phosphorus responses.

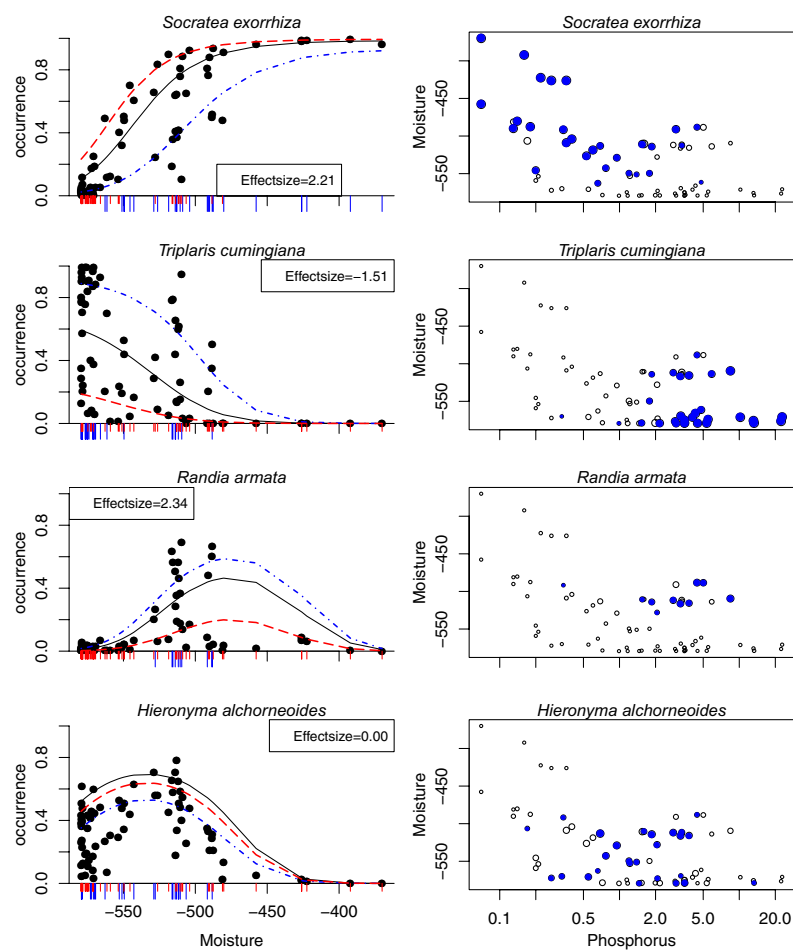


Fig. S3. Occurrence of four species in response to moisture and resin phosphorus (complete description is provided in legend for Fig. 2).

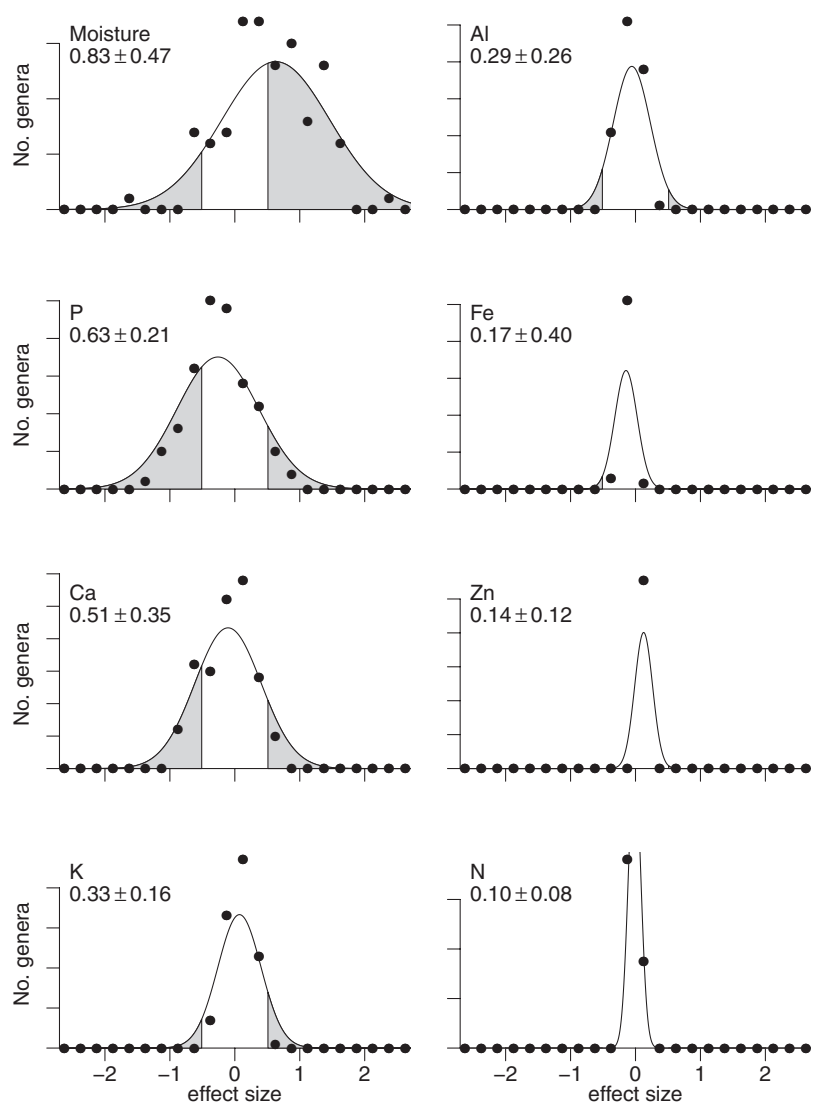


Fig. S5. Histograms of generic responses to eight environmental factors (Fig. 1). Moisture, dry-season moisture; P, plant-available (resin) phosphorus; N, inorganic nitrogen.

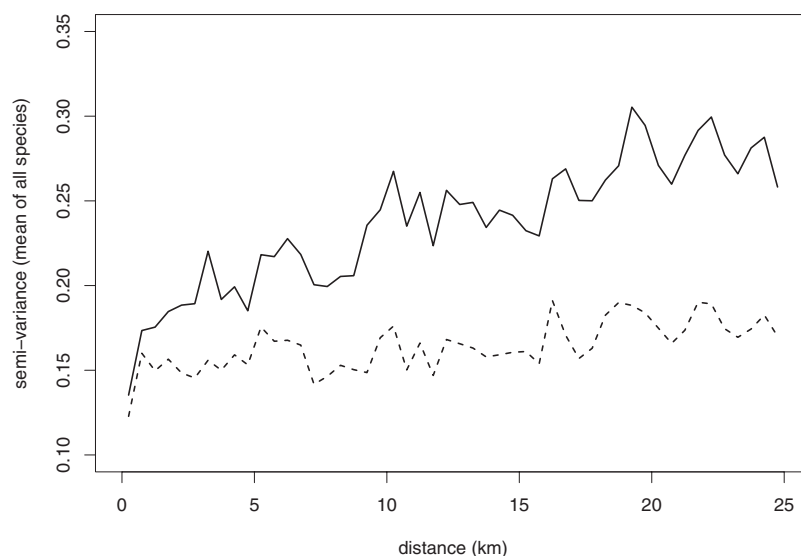


Fig. S7. Semivariograms of species occurrence (solid line) and of model residuals of species occurrence (dashed line). Each estimate is the average semivariance for all 550 species in 1-km distance bins (the first two bins are 0–500 m and 500–1,000 m).

Table S1. Correlations among concentrations of soil factors and dry-season moisture at 72 sites where tree species were surveyed, given as r^2 , with a sign included to indicate direction

Environmental measure	P							P							N		
	Moisture	Al	Ca	Fe	K	Mg	Mn	(resin)	(Mehlich)	Total P	Zn	pH	NH ₄	NO ₃	(Inorg)	DON	
Moisture		0.039	-0.016	0.036	-0.043	-0.044	-0.003	-0.304	-0.271	-0.187	-0.046	-0.041	0.012	-0.035	-0.018	0.140	
Al	0.039		-0.168	0.027	-0.187	-0.115	-0.102	-0.194	-0.054	-0.060	-0.027	-0.163	0.060	-0.139	-0.038	0.170	
Ca	-0.016	-0.168		-0.145	0.383	0.753	0.465	0.385	0.222	0.420	0.296	0.811	0.011	0.108	0.107	-0.462	
Fe	0.036	0.027	-0.145		-0.045	-0.138	-0.145	-0.091	-0.276	-0.118	-0.105	-0.107	0.061	-0.009	0.005	0.003	
K	-0.043	-0.187	0.383	-0.045		0.450	0.240	0.329	0.214	0.241	0.155	0.363	0.007	0.079	0.063	-0.296	
Mg	-0.044	-0.115	0.753	-0.138	0.450		0.462	0.258	0.159	0.240	0.395	0.603	0.008	0.015	0.025	-0.394	
Mn	-0.003	-0.102	0.465	-0.145	0.240	0.462		0.069	0.033	0.097	0.214	0.402	0.031	0.075	0.101	-0.096	
P(resin)	-0.304	-0.194	0.385	-0.091	0.329	0.258	0.069		0.638	0.730	0.209	0.401	-0.030	0.135	0.057	-0.070	
P(Mehlich)	-0.271	-0.054	0.222	-0.276	0.214	0.159	0.033	0.638		0.615	0.138	0.204	-0.052	0.089	0.018	-0.208	
Total P	-0.187	-0.060	0.420	-0.118	0.241	0.240	0.097	0.730	0.615		0.193	0.391	-0.002	0.101	0.076	-0.295	
Zn	-0.046	-0.027	0.296	-0.105	0.155	0.395	0.214	0.209	0.138	0.193		0.294	-0.001	0.010	0.005	-0.179	
pH	-0.041	-0.163	0.811	-0.107	0.363	0.603	0.402	0.401	0.204	0.391	0.294		0.006	0.092	0.073	-0.543	
NH ₄	0.012	0.060	0.011	0.061	0.007	0.008	0.031	-0.030	-0.052	-0.002	-0.001	0.006		0.004	0.347	-0.001	
NO ₃	-0.035	-0.139	0.108	-0.009	0.079	0.015	0.075	0.135	0.089	0.101	0.010	0.092	0.004		0.654	-0.087	
N(Inorg)	-0.018	-0.038	0.107	0.005	0.063	0.025	0.101	0.057	0.018	0.076	0.005	0.073	0.347	0.654		-0.076	
DON	0.140	0.170	-0.462	0.003	-0.296	-0.394	-0.096	-0.470	-0.208	-0.295	-0.179	-0.543	-0.001	-0.087	-0.076		

Statistically significant correlations are in boldface. DON, dissolved organic nitrogen; Mehlich, Mehlich-3 solution.

Table S2. Hyper-SDs assigned for each resource to simulate species' responses (true σ) compared with the hyper-SDs returned by the model (fitted σ)

Parameter	Simulation 1			Simulation 2		
	True σ	Fitted σ	r^2	True σ	Fitted σ	r^2
Dry-season moisture	1.38	1.353	0.89	1.38	1.343	0.84
Aluminum	0.10	0.227	0.00	0.20	0.200	0.15
Calcium	0.66	0.608	0.59	0.40	0.408	0.30
Iron	0.10	0.195	0.08	0.30	0.316	0.31
Potassium	0.10	0.251	0.01	0.10	0.217	0.18
Resin phosphorus	0.97	0.952	0.74	0.85	0.830	0.68
Zinc	0.10	0.208	0.01	0.20	0.318	0.22
Inorganic nitrogen	0.10	0.260	0.00	0.10	0.270	0.01

Also given is the r^2 between the assigned species' responses (their first-order logistic parameters) and the responses returned by the model, calculated using species with ≥ 10 occurrences. For $\sigma \geq 0.8$, r^2 remained >0.7 , including species down to 6 occurrences. In the first simulation, there was no covariance among species' responses to different predictors; in the second simulation, species' responses to calcium and phosphorus were positively correlated ($r^2 = 0.83$) and moisture and Fe were negatively correlated ($r^2 = 0.22$).