

# Supporting Information

Condit et al. 10.1073/pnas.1218042110

## SI Materials and Methods

**Tree Species Occurrence.** We surveyed woody species with free-standing stems  $\geq 1$  cm in diameter at 72 locations near the Panama Canal (Fig. S1), each with an area  $< 0.5$  km<sup>2</sup>. 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 ( $102.6 \pm 41.4$  vs.  $113.9 \pm 42.7$ ), 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  $\sim 1$  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

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

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  $\hat{D}_m$  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  $\hat{D}_m = -606$  mm. The wettest was at Esperanza in steep hills near the Caribbean, with  $\hat{D}_m = -106$  mm. We used  $\hat{D}_m$  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  $\hat{D}_m$  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  $\hat{D}_m$  ( $r^2 = 0.54$ ).

**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  $\text{K}_2\text{SO}_4$  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<sup>CSH</sup> 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  $\text{NH}_4\text{OAc}$ , 0.25 M  $\text{NH}_4\text{NO}_3$ , 13 mM  $\text{HNO}_3$ , 15 mM  $\text{NH}_4\text{F}$ , 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  $\text{H}_2\text{O}_2$ - $\text{H}_2\text{SO}_4$  digest (20).

**Data Processing.** Data from all tree plots and inventories were condensed to the presence and absence of each species, producing a  $550 \times 72$  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  $72 \times 8$  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  $\gamma$  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  $72 \times 8$  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  $\theta$  as the  $550 \times 17$  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  $\theta$  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  $\theta$ , 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  $\vec{\sigma}$  for the associated SDs (the diagonal of  $\sqrt{\mathbf{v}}$ ). Each  $\sigma_r$ , 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  $\theta$ ,

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

No prior probabilities were assumed on the hypermeans  $\vec{\mu}$ . For  $\mathbf{v}$ , models were run, including an inverse- $\gamma$  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  $b_{sr}/2\sigma_r$  (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 *sgeostat* (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  $\vec{\theta} = (a, \vec{B}, \vec{C})$  (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 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  $\approx 0$  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  $\geq 10$  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  $\sigma$  (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  $\sigma$  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-

sponse ( $\sigma < 0.3$ ) estimated to be strong, and in no case was a strong response ( $\sigma > 0.5$ ) estimated to be weak. Negligible resource effects ( $\sigma = 0.10$ ) were overestimated, however, up to  $\sigma \approx 0.3$  (Table S2). Covariance among species response parameters did not affect these results. Individual species parameters were recovered well when the simulated community response was strong and species had  $\geq 10$  occurrences ( $r^2$  in Table S2); in all cases in which individual species had weak responses ( $b < 0.5$ ), the model recovered the species parameters poorly. Model estimates for real tree responses to potassium and aluminum,  $\sigma \approx 0.4$ , were close to false-positive results

in simulations, but real responses to moisture, phosphorus, and calcium were well outside the range of false-positive results.

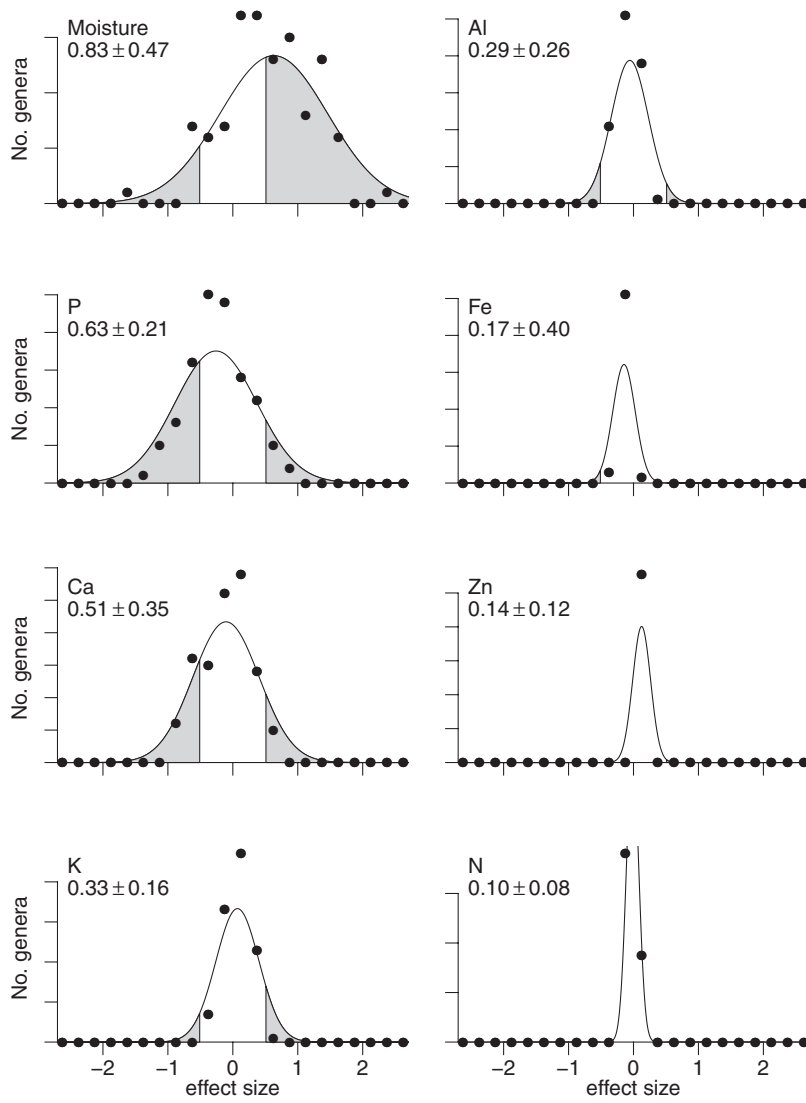
**Complete Results.** Location, elevation, and rainfall at the 72 sampling sites are available for download (<http://dx.doi.org/10.5479/data.bci.20130204>), along with a list of the 550 species in the study, with family names and occurrences at those 72 sampling sites (<http://dx.doi.org/10.5479/data.bci.20130204>). The species response parameters and soil chemistry results will be made available as digital tables on request.

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







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

Parameter	Simulation 1			Simulation 2		
	True $\sigma$	Fitted $\sigma$	$r^2$	True $\sigma$	Fitted $\sigma$	$r^2$
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  $\geq 10$  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 ( $r^2 = 0.22$ ).