# 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**

| | | | | | Species responses | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Summary statistics | | | | Strong effect | | | Significant effects | | |
| Environmental measure | 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*).

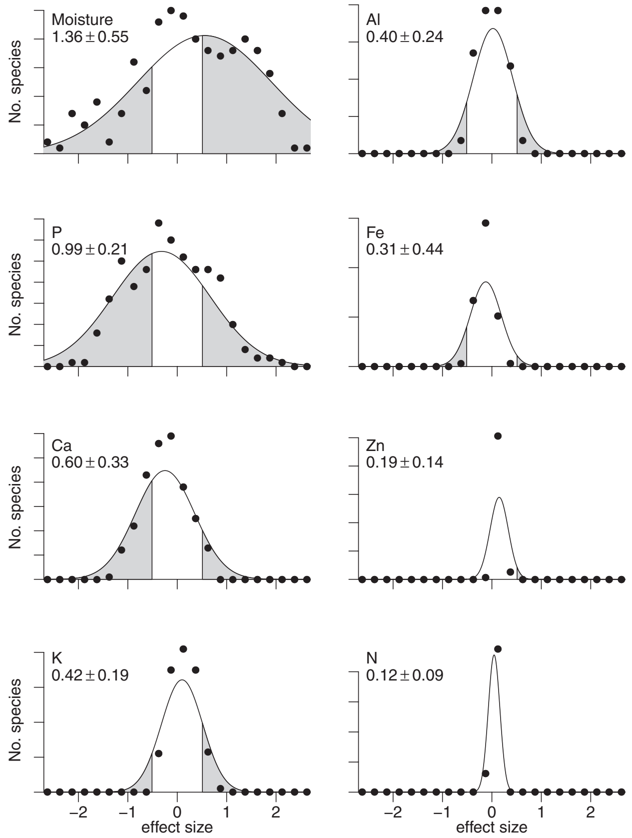

**Fig. 1.** Histograms of individual species responses to eight environmental factors. The horizontal axis is the effect size, *b*, defined as the first-order parameter of the logistic model. The shaded portions of each curve highlight species with strong responses ($|b| > 0.5$; Table 1). The curves 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*).

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

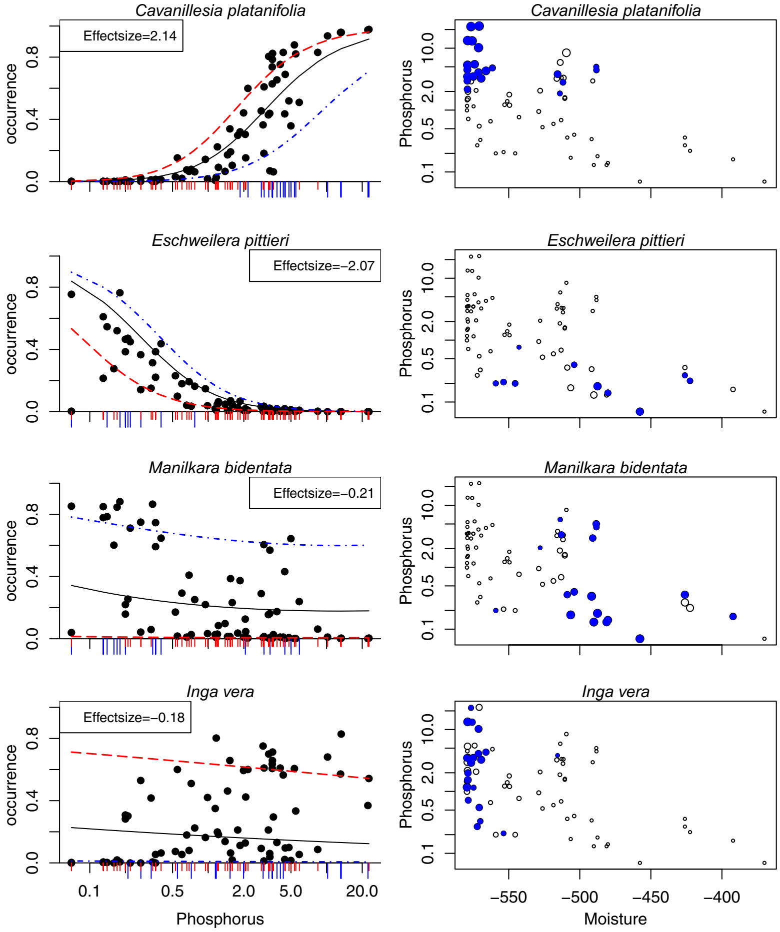

**Fig. 2.** Responses of four species to plant-available (resin) phosphorus and dry-season moisture. (*Left*) Graphs show occurrence probability per site (*y* axis) as a function of phosphorus concentration (*x* axis) (milligrams per kilogram, log scale). The solid curve is the logistic model's prediction 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

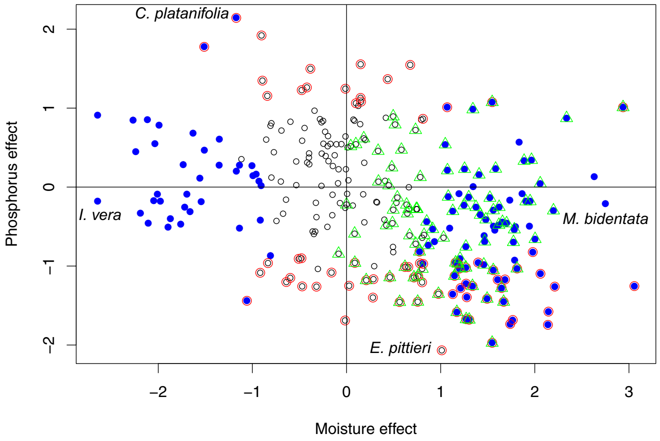

**Fig. 3.** Quantitative responses to dry-season moisture and plant-available (resin) phosphorus for individual species. Response is measured by the effect size, *b* (Fig. 1); $b > 0$ means a species associated with high moisture or high phosphorus. Solid blue points are statistically significant effects 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 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 Materals 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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