LETTER

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Pervasive phosphorus limitation of tree species but not communities in tropical forests

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Phosphorus availability is widely assumed to limit primary productivity in tropical forests[1,2], but support for this paradigm is equivocal[3]. Although biogeochemical theory predicts that phosphorus limitation should be prevalent on old, strongly weathered soils[4,5], experimental manipulations have failed to detect a consistent response to phosphorus addition in species-rich lowland tropical forests[6–9]. Here we show, by quantifying the growth of 541 tropical tree species across a steep natural phosphorus gradient in Panama, that phosphorus limitation is widespread at the level of individual species and strengthens markedly below a threshold of two parts per million exchangeable soil phosphate. However, this pervasive species-specific phosphorus limitation does not translate into a community-wide response, because some species grow rapidly on infertile soils despite extremely low phosphorus availability. These results redefine our understanding of nutrient limitation in diverse plant communities and have important implications for attempts to predict the response of tropical forests to environmental change.

One of the longest-standing paradigms in ecology is that productivity in tropical forests is limited by phosphorus (P) availability[1,2]. The paradigm is supported by biogeochemical theory, which states that P depletion during long-term pedogenesis is sufficient to limit productivity on the old, strongly weathered soils that characterize much of the tropical biome[4,5]. There is also a wealth of indirect evidence for P limitation in tropical forests, including high nitrogen (N) availability[10], high N-to-P ratios in leaves[1] and correlations between forest properties and soil fertility at continental scale[11,12]. However, evidence from nutrient-addition experiments in tropical forests is scarce and contradictory. A community-wide growth response to P has been observed in a monodominant forest in Hawaii[13], but not in species-rich lowland tropical forests in Africa, Southeast Asia and the neotropics[6–9], and a recent meta-analysis found that the overall evidence for P limitation in the tropics is largely inconclusive[3].

Here we combine data on tree growth rates, species distributions and soil phosphatase activities to precisely quantify P limitation of individual species and whole communities in lowland tropical forests. We define P limitation as faster growth at greater P availability, which can manifest at the level of an individual species or an entire community. We measured the growth of 18,970 individual trees that were ≥10 mm in diameter at breast height (dbh; the trunk diameter at 1.3 m above the ground surface), comprising 541 species occurring in a network of 32 forest-dynamics plots across the Isthmus of Panama (Supplementary Table 1). The plots vary in size from 1 to 50 ha and were censused at least twice to provide growth rates for individual stems. The plot network spans a rainfall gradient (1,870–3,280 mm) with marked variation in lithology and soils, which generates a steep natural gradient in P availability that is unrelated to rainfall[14,15]. In particular, readily exchangeable phosphate extracted by anion-exchange membranes (resin phosphate)—a sensitive measure of the power of the soil to supply P for biological uptake—varies more than 300-fold[14], which represents a similar range to phosphate availability in lowland tropical forests globally[16–18].

We modelled species-specific growth rates using hierarchical models to disentangle the influence of environmental variables from the confounding effect of species turnover across the gradients of P and rainfall[14]. This approach isolates the influence of individual variables (that is, fixed effects) on the growth of the average species, given a hypothetical scenario in which other variables are held constant and the average species exists in all locations. Growth rates increased significantly with increasing resin phosphate (likelihood ratio test (LRT) for the fixed effect of resin phosphate, $P < 0.0001$; Fig. 1a, b, Extended Data Fig. 1 and Extended Data Table 1). Responses were independent of tree size (resin phosphate × dbh interaction, LRT $P = 0.72$), which indicates that both large and small trees grew faster in response to higher concentrations of resin phosphate (Fig. 1a, b). At intermediate soil moisture, the predicted growth of an average 100-mm-dbh tree increased from 0.77 mm y^{-1} at the lowest resin phosphate concentration to 1.03 mm y^{-1} at the highest, a growth increase of 34%. The growth of an average 10-mm-dbh tree across the same P gradient increased from 0.15 to 0.18 mm y^{-1}, an increase of 20%. The model indicated significant variation among species in their response to P (random effects for resin phosphate, LRT $P = 0.0015$; Extended Data Table 2), as demonstrated by the negative responses of some species to increasing concentrations of resin phosphate (Fig. 1 a, b). However, the significant fixed effect of resin phosphate demonstrates that most species respond positively to increasing P availability. Indeed, 90% of common species (that is, with >20 individuals in the dataset) responded positively to P as large trees, and 84% responded positively as small trees; only a small number of species did not respond positively to P in either life history stage (Extended Data Fig. 2a).

By contrast, increasing soil moisture increased growth rates only for smaller trees, consistent with smaller trees suffering greater water stress than adults owing to a less extensive root system (fixed effect of moisture, LRT $P = 0.003$; inclusion of a dbh × moisture interaction parameter, LRT $P = 0.002$; Fig. 1c, d and Extended Data Table 1). Therefore, across the range of soil moisture deficit in our study area, the predicted growth of a 10-mm-dbh tree at intermediate soil P increased from 0.15 mm y^{-1} at the driest site to 0.24 mm y^{-1} at the wettest site (LRT for a model using only trees of 10–100 mm dbh, $P = 0.001$). The growth of a 100-mm-dbh tree did not change significantly across the moisture gradient (0.86–0.89 mm y^{-1}; LRT for a model using only trees of ≥100 mm dbh, $P = 0.1$), reflecting the erratic responses of individual species to moisture (Fig. 1c, d).

Resin phosphate in our plots was not correlated with total inorganic N or soil properties, such as organic matter (total carbon (C) and total N) or texture (for example, clay concentration), but was correlated positively with base cations (Supplementary Table 2). To investigate the influence of other nutrients on tree growth, we performed separate model runs using N, calcium (Ca), potassium (K) and the micronutrient manganese (Mn) in place of resin phosphate (Extended Data Table 2). Neither Mn nor total inorganic N or K, the two most important plant nutrients other than P, were significant predictors of tree growth rates. Calcium was significant when it was the only nutrient

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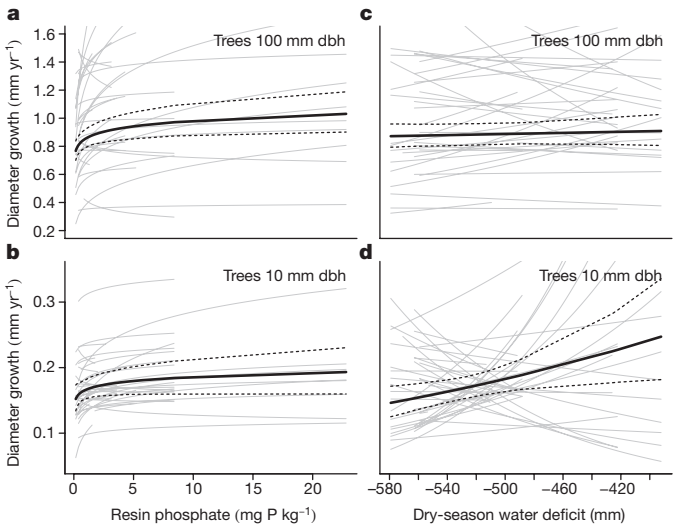

Figure 1 | Tree growth responses to phosphorus and moisture. **a**–**d**, Growth responses of the average species to resin phosphate (**a**, **b**) and dry-season soil-moisture deficit (**c**, **d**), predicted by the hierarchical model for an average large tree of 100 mm dbh (**a**, **c**) and an average small tree of 10 mm dbh (**b**, **d**). Phosphorus responses are predicted at average dry-season soil-moisture deficit, and moisture responses are predicted at average resin phosphate concentration. Dashed black lines show 95% credible intervals, calculated as the 2.5th and 97.5th quantiles of predictions from 1,000 random draws of model parameters. Grey lines represent the predicted responses of abundant species where they occur along the phosphorus gradient. For large trees (**a**, **c**), these are the 40 most-abundant species with dbh ≥ 100 mm. For small trees (**b**, **d**), these are the 40 most-abundant species with dbh between 10 and 50 mm. Some fast-growing species exceed the upper boundary of the *y* axis. $n = 18{,}970$ individual trees and 541 species were used in the models.

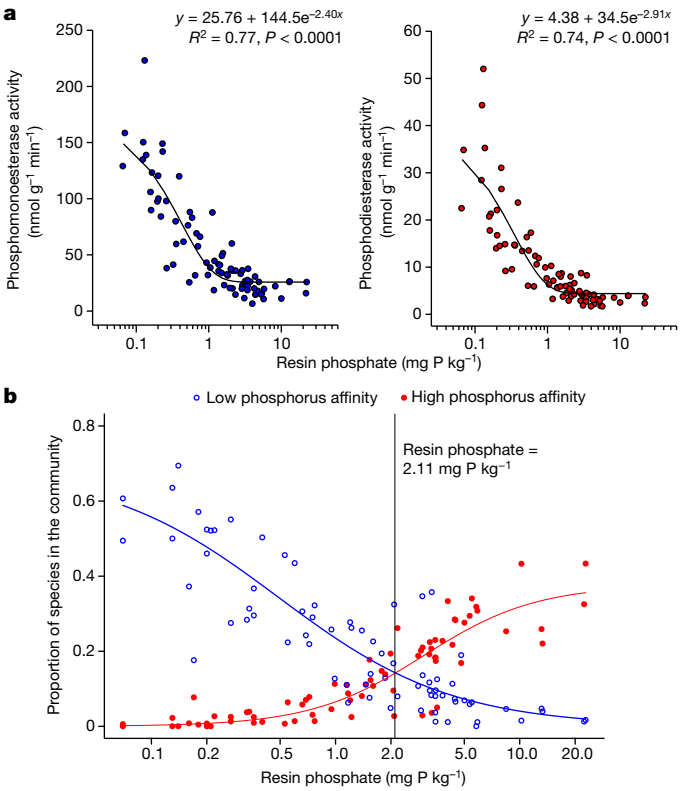

Figure 2 | A threshold for strong phosphorus limitation in lowland tropical forests. **a**, The relationship between resin phosphate (logarithmic scale) and phosphatase activities in soils from 83 sites under lowland tropical forest in Panama, showing marked increases in phosphomonoesterase activity (left, blue circles) and phosphodiesterase activity (right, red circles) at low concentrations of resin phosphate. The hydrolysis product is methylumbelliferone and the model fits are negative exponential functions determined by nonlinear regression. **b**, The relationship between resin phosphate and the proportion of tree species associated with low levels of soil phosphorus (effect sizes < −0.8, open blue circles and blue line) or high levels of soil phosphorus (effect sizes > 0.8, closed red circles and red line) in 72 lowland tropical forests in Panama. The proportion of species with low phosphorus affinity equals the proportion of species with high phosphorus affinity at 2.11 mg P kg^{-1} resin phosphate. The models are sigmoidal fits and were derived by nonlinear regression.

in the model, but was not significant in a model that included resin phosphate (Extended Data Table 3). Although we cannot rule out the possibility that Ca has an independent influence on growth rates in our plots, our model results therefore indicate that P is the primary nutrient determining tree growth rates in the lowland tropical forests of Panama. Indeed, there is little evidence that Ca limits productivity in forested ecosystems, including tropical forests[1], although we recognize that Ca limitation is possible in some tropical regions—including parts of Amazonia and Southeast Asia—that have soils with concentrations of exchangeable base cations at least an order of magnitude lower than in most of our plots[16,17].

Model predictions and piecewise linear regression demonstrate that growth responses to P increase markedly below approximately 2 mg P kg^{-1} resin phosphate (Fig. 1a, b and Extended Data Fig. 2b). Strong P limitation below this threshold is supported by changes in the activity of soil phosphatase enzymes, which release phosphate from organic compounds and are synthesized by plants and microbes in response to P demand[19]. For 83 soils across the P gradient (Supplementary Table 3), including the 32 plots analysed for tree growth, the activity of phosphomonoesterase and phosphodiesterase—the two enzymes involved in the hydrolysis of the majority of the organic P in tropical forest soils[15]—decreased exponentially with increasing resin phosphate (Fig. 2a and Extended Data Fig. 2c). Phosphatase activity increased markedly below 2 mg P kg^{-1} resin phosphate, which is almost identical to the concentration that triggers phosphatase genes and other phosphate starvation responses in bacteria[20] (0.16 μM P, equivalent to 2.15 mg P kg^{-1} resin phosphate). This supports previously published evidence that P availability can constrain the activity of soil microbes in lowland tropical forests[21,22] and, together with tree growth responses, demonstrates a coherent threshold for strong P limitation above- and belowground.

The resin phosphate threshold can be quantified precisely by changes in tree community composition along the P gradient. The distributions of individual tree species in lowland forests of Panama are determined primarily by P and moisture availability[14]. The strength of the association between a species and a resource can be described quantitatively by its effect size, the first-order parameter of the logistic model describing the relationship between the occurrence of a species and the resource[14]. A positive effect size for P indicates that a species occurs predominantly on high-P soils, whereas a negative effect size indicates that a species occurs predominately on low-P soils. The current study included 364 species with significant low-P associations (effect size < −0.8; 66% of the entire community) and 58 species with significant high-P associations (effect size > 0.8; 11% of the entire community) (Supplementary Table 4). Sites with low resin phosphate are dominated by species with low-P affinity, but these species are gradually replaced along the P gradient by species with high-P affinity. The resin phosphate concentration at which the tree community contains equal proportions of species with low- and high-P-affinity is 2.11 mg P kg^{-1} (Fig. 2b). This concentration is similar only for widespread species (Extended Data Fig. 2d), and varying the definition of significant P affinity (using effect sizes between ±0.5 and ±1.0) and the minimum number of occurrences of a species (between three and eight plots) yields resin phosphate threshold values between 1.96 and 2.37 mg P kg^{-1}.

Despite evidence for a coherent signature of strengthening P limitation below 2 mg P kg^{-1} resin phosphate, the growth rates for individual

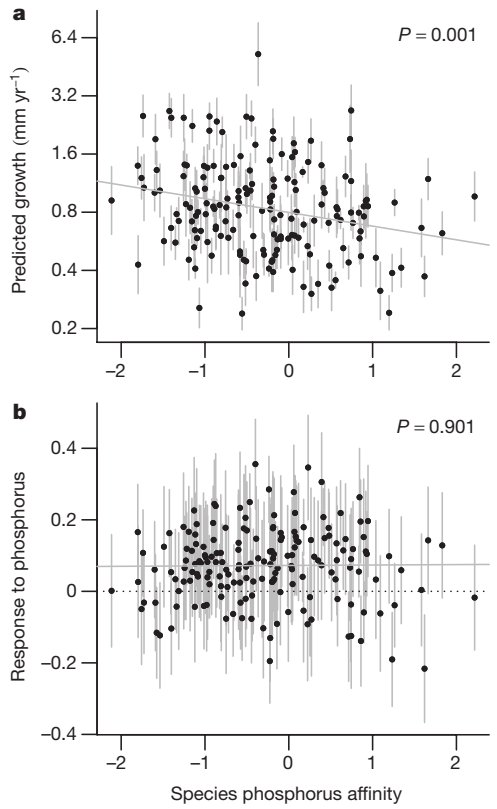

Figure 3 | Predicted growth rates and growth responses to increasing soil phosphorus for individual common species as a function of their phosphorus affinity. a, **b**, Growth rates (**a**) and phosphorus responses (**b**) were predicted by the hierarchical model. Common species are defined as those with growth data for >20 individuals. Each point represents the response ± standard error of a single species as estimated from the model, assuming a tree of 100 mm dbh. Growth rates in **a** are estimated at intermediate moisture and resin phosphate levels, although relative values were similar when estimated at low or high levels of phosphorus (Extended Data Fig. 3a). Responses in **b** were estimated at average soil moisture, and positive *y*-axis values indicate that the species grows faster at higher resin phosphate concentration. The *P* values indicate the significance of linear regressions of random effect size against species phosphorus affinity (grey solid line).

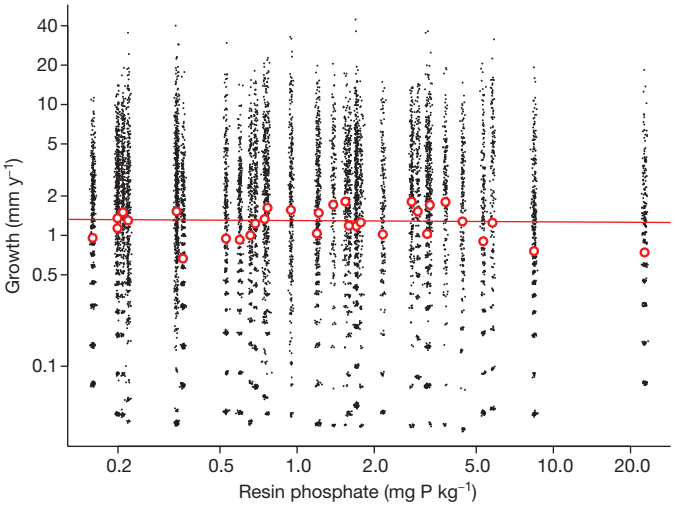

Figure 4 | Observed community-wide growth rates as a function of resin phosphate concentration. Plot-level growth rates (red circles) are for trees ≥ 100 mm dbh in 32 plots in lowland tropical forests in Panama. Growth rates of individual trees are shown as black points. Both axes are log-transformed. The line shows a standard linear regression between log-transformed growth and log-transformed resin phosphate; the slope is slightly negative (−0.022), but not significantly different from zero ($P = 0.06$).

species estimated by the hierarchical model at intermediate moisture and resin phosphate levels were on average greater for species associated with low-P soils (Fig. 3a). This pattern is consistent for modelled growth rates estimated at low or high resin phosphate concentrations, and for observed growth rates across the natural species ranges (Extended Data Fig. 3a, b). However, species P affinities were not related to their growth responses to P (Fig. 3b), demonstrating that individual species respond to P in a similar manner irrespective of where they occur on the P gradient.

Even though most individual species are P limited and grow faster as P availability increases, community-wide growth rates (at the plot level) did not vary significantly across the P gradient (Fig. 4). Similarly, neither plot-level aboveground biomass nor relative biomass increment varied significantly with resin phosphate (Extended Data Fig. 3c). It therefore appears that overall growth is maintained on infertile soils by a subset of species that grow rapidly despite extremely low P availability (Fig. 3a). These species gradually disappear from the community as soil P increases (Fig. 1a, b), replaced by species that are better adapted to higher P availability but that have slightly slower growth on average. The net result is consistent community-wide growth across the entire P gradient despite widespread species-specific P limitation.

These results redefine our concept of nutrient limitation in species-rich plant communities by demonstrating that P limitation occurs at the level of the individual species rather than the entire community. Where diversity is high, variation in fertility drives species turnover and differences in community composition, rather than variation in growth rates of the same species assemblage. This pattern is common along fertility gradients in species-rich plant communities[23,24] and supports the suggestion that retrogression—the process by which low P availability causes a decline in biomass and productivity on old soils[5]—is unlikely to occur in diverse tropical forests because they contain species that can be productive on low-P soils[25].

Although we cannot explain how some species maintain high growth rates on low-P soils, it presumably involves mechanisms that promote efficient use of P, including exhaustive re-translocation of foliar P, synthesis of sulfolipids or galactolipids instead of phospholipids, low ribosomal RNA concentrations or efficient exploitation of soil organic P compounds[1,26,27]. These low-P-specialist species are therefore potential targets for efforts to develop crops that can maintain growth on infertile soils. Although some species might be particularly sensitive to high P availability[23,26], as suggested by the negative response to P of some species in our plots, most low-P specialists respond positively to small increases in resin phosphate within their natural ranges. Their exclusion from high-P sites is therefore presumably driven by physiological or ecological factors such as responses to herbivory or pathogens[28], or trade-offs between growth and nutrient acquisition[29], which paradoxically cause them to be outcompeted by slower-growing species that are better-adapted to survive and reproduce on more fertile soils.

Our results have implications for efforts to incorporate P into coupled climate–carbon cycle models to improve predictions for the tropical biome under future atmospheric chemistry and climate scenarios[30]. For example, P constraints on growth responses to increasing atmospheric carbon dioxide concentrations are likely to be species specific, confounding the simple inclusion of P limitation in earth system models. However, in addition to revealing the nature of P limitation in tropical forests, we show a quantitative resin phosphate threshold below which P limitation strengthens markedly above- and belowground. Although resin phosphate data are not widely available for lowland tropical forest soils, the values correspond closely to 'plant-available' P concentrations measured by routine soil P tests and are correlated strongly with total and organic P concentrations

(Extended Data Figs 4, 5), making it possible to predict the pan-tropical extent of P limitation in lowland tropical forests. Given that extractable P concentrations below 2 mg P kg^{-1} occur widely in Asia, Africa and South America[16–18], it seems likely that species-specific P limitation is pervasive in tropical forests worldwide.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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METHODS

Tree growth rates. We measured the growth of 18,970 stems comprising 541 species (excluding palms and lianas) in a network of 32 plots across the Isthmus of Panama[14,31–33]. Annual precipitation across the plots varied between 1,870 and 3,280 mm y^{-1}, and elevation ranged between 20 and 643 m above sea level, although most plots were below 200 m above sea level. Details of the floristic composition of the plots were previously published[14,31,32] and locations are detailed in Supplementary Table 1. In each plot, all trees larger than 100 mm dbh were tagged, measured and identified to species. Twenty-six of the plots also included stems between 10 and 100 mm dbh, typically inside a central 40 × 40 m quadrat. Lianas were not included in the census. Most plots were 1 ha in area, but two plots were larger (6 ha at Sherman and 50 ha on Barro Colorado Island, BCI). To prevent these two larger plots from dominating the results with their much larger sample size, we subsampled two 1-ha plots from each larger plot with all trees to 100 mm dbh, and a 40 × 40 m quadrat within each plot to 10 mm dbh.

Tree growth was measured between 1996 and 2011. Twenty-five plots were established between 1996 and 1999, six plots were established after 1999 and one plot (BCI) is older (the first census was completed in 1983). Most plots were re-censused only once after their establishment. We included only census intervals greater than three years and ignored intermediate re-censuses (Supplementary Table 1). For consistency, for the BCI plot we included only data from between 2000 and 2010. For five of the plots that had multiple census intervals greater than three years, we calculated the growth in each census interval independently and averaged growth over the whole period to yield a single measure for each individual stem. All tree census data, including every tree measurement in every census through to the middle of 2012, is available online without restriction in permanent archives at the Smithsonian Institution Library[34,35].

We calculated growth as diameter increment per year (mm y^{-1}) for the main stem of each individual tree, as long as the stem survived and the dbh was taken at an identical position in both censuses. Extreme errors were excluded on the basis of an independent assessment of measurement error: trees were eliminated if dbh in the second census was more than four times the measurement error lower than dbh in the first census, and when growth was >75 mm y^{-1}. We also eliminated palms, for which diameter growth has little meaning for most species. Growth data was log-transformed for analysis. Modest negative growth rates (that is, those not excluded as extreme errors) were included by converting all growth rates ≤ 0 to half the minimum measurable growth (0.5 mm divided by the census time interval). Because census intervals were large for some of the plots, we calculated the mean dbh of each individual tree over the whole census interval. For the analysis, we log-transformed dbh and centred it at 100 mm. We included a quadratic term for dbh in the model.

Soil analysis. Soils in the plots include several taxonomic orders (oxisols, ultisols, alfisols and inceptisols)[15] and vary considerably in chemical properties, including pH (3.3–7.0), organic C (2–10%) and resin phosphate (0.16–22.8 mg P kg^{-1}) (Supplementary Table 1). A number of soil parameters have been measured in the plots and previously reported in detail[14,15,33]. For each site, soil data represent the average of five cores (inventory transects and 40 × 40 m plots), 13 cores (1-ha forest-dynamics plots) or 25 cores (the 6-ha plot at Sherman and the 50-ha plot on BCI), where each core was analysed individually. Cores were taken from the surface soil (0–10 cm in depth), which integrates the nutrient cycle and contains the majority of the extractable nutrients and fine roots. Additional samples were taken up to a depth of 1 m in the soil profile, but extractable nutrient concentrations, especially of resin phosphate, were much lower at depth and are not discussed further. The 32 plots studied in the hierarchical analysis are a subset of the broader plot network, and a number of additional plots were studied for phosphatase activities and to calculate P and moisture effect sizes (see later; Supplementary Table 3).

Our primary measure of available P was readily-exchangeable phosphate determined by extraction with anion-exchange membranes (that is, resin phosphate)[36]. This is a sensitive measure of the capacity of the soil to supply phosphate that reflects the distribution of approximately 60% of the species in the region[14]. The detection limit of the method is approximately two orders of magnitude lower than other procedures for estimating plant-available phosphate, such as Mehlich-III[37] or Bray-1[38], and extraction is conducted in deionized water, which avoids soil-specific chemical interactions that occur with acidic or chelating extractants. For the hierarchical analysis, resin phosphate concentrations were log-transformed and standardized to a mean of zero.

Extractable base cations (including Ca, K and magnesium (Mg)), and micronutrients (including iron (Fe), Mn and zinc (Zn)) were determined by Mehlich-III extraction[37] and inductively-coupled plasma optical-emission spectrometry on an Optima 7300DV (Perkin Elmer). Phosphate was determined in the Mehlich extracts by automated molybdate colorimetry. Extractable phosphate was also determined by Bray-1 extraction and molybdate colorimetry[38]. Inorganic N (including ammonium and nitrate) and dissolved organic N (DON) were determined by extraction in 2 M KCl with colorimetric detection[39]. Total P was determined by ignition (550 °C × 1 h) and extraction (1 M H_2SO_4, 1:50 soil-to-solution ratio, 16 h extraction), with phosphate detection by automated molybdate colorimetry[15,40]. This procedure provides a simple and rapid estimate of total P for most soils, although it can underestimate the true values in strongly weathered soils such as many of those in the current study. On average, resin phosphate represented only a small fraction of the total P (0.5 ± 0.05%), although with considerable variation (range 0.04–1.95%). Organic P was determined by alkaline extraction[15] in a solution containing 0.25 M NaOH and 0.05 M EDTA. Phosphatase activities were determined using methylumbelliferyl-linked substrates as previously described[41]. Assays were conducted at pH 5.0 in 50 mM acetate buffer for phosphomonoesterase and phosphodiesterase, the two enzymes involved in the hydrolysis of the majority of the organic P in tropical forest soils[15]. Activity was expressed on the basis of dry soil, microbial biomass C and total organic C (determined as total C; no soil contained carbonate). Microbial C was determined by fumigation–extraction[42] and total C by dry combustion on a Flash 1112 elemental analyser (Thermo Fisher Scientific).

All analyses, other than total C and total P, were determined on fresh soils within 4 h (KCl extraction) or 24 h (resin phosphate and phosphatase activity) of sampling, to avoid the rapid changes that can occur during storage or pretreatment[36]. All soil chemical properties are expressed on the basis of oven-dry equivalent soil (determined by drying at 105 °C for 24 h).

Dry-season water deficit. To characterize site moisture status we calculated dry-season water deficit (in mm) as previously described[14,33]. Dry-season water deficit measures the intensity of the dry season (between December and April) as the net moisture deficit: cumulative daily precipitation minus evapotranspiration at its most extreme at the end of the dry season. A more negative water deficit indicates a stronger (that is, longer) dry season. For the analysis, water deficit was standardized and centred on a median of −525 mm; positive values represent more humid sites and negative values represent drier sites.

Data analysis. All data manipulation and analysis was done using R statistical software (R Development Core Team; https://www.r-project.org/). We investigated whether dry-season soil water deficit and resin phosphate levels influenced forest growth at the community and at the species level using hierarchical linear mixed-effect models ('lmer' function in the package 'lme4')[43]. The hierarchical modelling approach is a multiple regression analysis that differentiates between fixed effects (the overall response to a parameter) and random effects (the random variation in responses among individuals). In our models we evaluated the fixed effects of moisture, tree size and nutrients, and random variation in responses among species and among plots.

Model selection and evaluation of parameter probability values was performed using LRTs and the Akaike information criterion (AIC). LRTs evaluate whether the likelihood of a model fit changes significantly as each individual parameter is added (or dropped) from the model. If the LRT is significant, and the AIC is smaller when a parameter is added to the model, that parameter is considered a significant improvement to the model. Therefore, probability values represent the probability that the parameter improves model fit relative to the same model without that parameter. A significant fixed effect in the hierarchical model indicates an overall response to a parameter (for example, resin phosphate), whereas a significant random effect indicates that the response to the fixed effect varies across species or plots. The variance and standard deviation values for the random effects terms indicate the extent to which species vary in response to the fixed effect, and are not an estimate of the variation explained by the term.

Data entered the model as the log-transformed growth of each individual tree. In the final model, each species was allowed to vary randomly in its response to all model parameters, and random parameters were allowed to co-vary with one another. All analysis and figures were conducted based on the following form (in R notation): log growth ~ log dbh + log dbh squared + moisture deficit + log resin P + moisture deficit:log dbh + (log dbh +log dbh squared + moisture deficit + log resin P + moisture deficit:log dbh | species).

We evaluated the model using the complete tree community data, including 541 species and 32 plots. All species-specific model outputs, including estimated growth and responses to moisture and P, are shown in Supplementary Table 5. However, as in many tropical forests, most species were rare and appeared as singletons or at a very low sample size. These rare species contribute to the overall model, but the species-specific estimates have reduced significance because the hierarchical model 'shrinks' them towards the community mean. Therefore, to look at species-specific trends we evaluated 175 species that had growth data for at least 20 individuals in the study sites (Supplementary Table 6).

Diameter growth is highly correlated with basal area growth, but we checked whether basal area growth responded differently than dbh growth to P in simplified models that included P, moisture deficit and dbh as predictors of growth. In these

models, the fixed effect of P and the responses of individual species using the two growth estimates were essentially identical ($R^2 = 0.86$), and in fact showed a slightly stronger effect of P on basal area growth than on dbh growth.

We also tested a model with plot as a random effect, to account for factors such as stem density or canopy structure that were not included in the model, but which could contribute to differences in growth among plots. Adding the plot random effect significantly improved the model, but the overall results were essentially unchanged, confirming that for most species growth increases with increasing P even after accounting for random unexplained variation among plots (Extended Data Table 4a). Compared to the main model, the growth response to P was slightly stronger in the model with a plot random effect, and the fixed effect of P was significantly improved ($P = 0.02$). However, the model output was noisier, as expected from the inclusion of an additional plot-level parameter, with the lower t-value suggesting greater variability in the responses among species (Extended Data Table 4a). We therefore did not include a random plot-effect in the final model to avoid over-parameterization.

Stem density in our plots is greater at wetter sites (Supplementary Table 1), as is common elsewhere in the tropics[11,44], and plot-wide growth rates are negatively correlated with the density of trees ≥ 10 cm dbh owing to greater shade in sites with many large stems. After controlling for moisture, stem density is not correlated significantly with resin phosphate or any other soil nutrient. However, to confirm whether stem density affects the relationship between growth and P, we ran a separate model that included stem density as a fixed effect (Extended Data Table 4b). Stem density slightly improved the original model, but the effect of P on growth remained highly significant (LRT $P < 0.0001$). Furthermore, stem density did not improve the model containing a plot random effect (described earlier), presumably because the plot effect includes variation in stem density as well as other unidentified differences among plots. Variation in stem density therefore does not affect our conclusions regarding the relationship between P and growth.

Variation in growth within species was considerably larger than variation among species or due to environmental factors, so the model explained only about 35% of the variance in growth. Of this, the largest effect was the change in growth rate due to tree size. For example, at average dry-season soil water deficit and resin phosphate concentration, a tree of 10 mm dbh grew 0.17 mm y^{-1}, compared to 0.87 and 1.25 mm y^{-1} for trees of 100 and 200 mm dbh, respectively. Nonetheless, we were able to detect significant community-wide trends in tree growth as a function of the environment.

Although P and rainfall are not correlated in our plot network, P is correlated with base cations. We therefore conducted separate linear mixed effects models evaluating the effect of different parameters on tree growth, evaluated as log(growth). These models included resin phosphate, total inorganic N (ammonium plus nitrate) and the base cations Ca and K. The linear models were run using the function lmer (from the lme4 R package) and probability (P) values were calculated using LogLik model comparisons after dropping or adding one parameter at a time (Extended Data Tables 2, 3).

Classification of P and moisture affinities. The majority of species in our plots have restricted distribution across the study area, with many showing affinity towards the wetter or the drier side of the gradient, or for high or low concentrations of resin phosphate. Moisture and P affinities were quantified by logistic regression, involving the assessment of species-by-species occurrence probability with respect to dry-season moisture deficit (moisture affinity) and resin phosphate (P affinity)[14]. The presence or absence of each species in 72 locations across the Isthmus of Panama was fitted in a hierarchical model as a function of dry-season water deficit and soil parameters. The strength of the affinity of each species to moisture or P is defined by the 'effect size', which is the first-order parameter of the logistic model. Species with strong negative P associations (that is, negative effect sizes) occur predominantly in sites with low resin phosphate concentrations, whereas species with strong positive P associations (that is, positive effect sizes) occur predominantly in sites with high resin phosphate concentrations. Species moisture and P affinities (effect sizes) are listed in Supplementary Table 4.

Because P affinity is a quantitative response, dividing species into groups is arbitrary. We classed low-P specialists as species with logistic coefficients (effect sizes) < -0.8 and high-P specialists as species with coefficients > 0.8. Species with P association scores between -0.8 and 0.8 occur across the entire range of resin phosphate concentrations and were classified as generalists. Relaxing or strengthening the definition of significant effect size to values between ± 0.5 and ± 1.0 did not influence the principal results. Similarly, moisture affinity is the first-order slope of the effect of dry-season water deficit in this function and represents the probability of occurrence in wetter or drier sites. Effect sizes greater than zero represent species that are found mostly in wetter sites (that is, sites with shorter dry seasons) and values less than zero represent species that are more frequently found in drier sites (that is, sites with longer dry seasons).

To assess the influence of resin phosphate on species distributions, we summed the total number of species at every inventory site that had significant responses to soil P. Both specialist groups essentially disappear at one end of the P gradient: at low resin phosphate concentrations there are no high-P-specialist species, whereas at high resin phosphate concentrations there are no low-P-specialist species. Fitting sigmoidal models to the data yielded a value at which the two models intersect—the point at which the tree community consists of equal proportions of species with high-P affinities and species with low-P affinities (Fig. 2b).

Biomass and biomass growth. Aboveground dry biomass (AGB) was estimated for each of the plots using allometric equations relating volume to stem diameter, combined with species-specific wood density. Details and examination of errors were previously published[45]. A caveat is that several early censuses omitted measurements of very large buttressed trunks owing to the difficulty of transporting long ladders to remote sites. Omitting large trees can cause a substantial error in the calculation of standing biomass, but we used later censuses to avoid this bias. In the end, only two large trees were omitted, from two different plots, accounting for no more than 1.5% of total forest mass. Biomass growth posed a greater concern, because this requires two censuses in which every tree is measured at precisely the same position on the stem. To avoid this bias, we measured relative biomass growth on the sample of trees measured twice at the same position (that is, total biomass increment of all those surviving trees divided by initial biomass of those same trees). This enabled all plots to be included. Growth and standing stock of biomass were regressed against the estimated intensity of the dry season and the logarithm of resin phosphate across the 32 plots.

Some of the forest surrounding the Panama Canal is successional, and has been re-growing since the United States took over the region in the early part of the 20th century. However, we do not have precise information on successional status of individual plots other than those on BCI (over 500 years since disturbance). Based on the presence of individuals of gap-demanding or edge species, four of the thirty-two plots support forest that appears to be relatively young (less than 60 years of regrowth), and all the rest are at least 120 years old. However, the four plots were included in biomass calculations because they did not have lower biomass than mature secondary or primary forest on BCI. This is consistent with growth rates and aboveground biomass of secondary forests in the region approaching those of undisturbed forest after a few decades of regrowth[46].

Piecewise linear regression. We used piecewise linear regression to investigate whether the forest as a whole showed a nonlinear growth response to soil P (that is, that growth rates increase (or decrease) faster at one end of the P gradient than the other). To confirm that the decreasing slope indicated by model predictions is real (that is, not an artefact of log-transformation), we employed a piecewise regression model, using the response variable log(growth) and the predictor resin phosphate (untransformed). Piecewise regression fits a standard linear response in two separate sections of the x axis and determines whether the slope of y (the response variable) differs between the sections. The key notion is that the break point, b_x, defining the two sections, $x < b_x$ and $x > b_x$, is estimated along with the two separate slopes. The null hypothesis is that the response of y to x is linear across the entire range of x, with no change in slope. That hypothesis is rejected if there is any b_x that allows the slopes on either side to differ significantly. The piecewise model includes the constraint that separate linear regressions in the two sections meet at the break point, so the two regressions are not fully independent. However, there is no direct constraint on the position of the break or the two slopes. If the underlying response y on x is not linear, the piecewise method should demonstrate the manner in which it differs.

Application of the piecewise model applied to the growth of many tree species in response to P involved a substantial number of species that spanned only narrow ranges of P, especially those restricted to low P. Because we were interested in whether there was a universal P concentration at which the response of growth changes, we were forced to pose the question about only generalist (occuring across a reasonably wide range of P levels) species. We thus restricted the analysis to those species occurring over at least a tenfold variation in P. Because two different regressions are needed for each species, the model is data-demanding, so we added the further restriction that species have at least 20 individuals at five or more sites. Furthermore, the piecewise model employed only P (and not moisture) as the predictor of growth.

The piecewise model with two sections requires four parameters: b_x, the two slopes s_1 and s_2, and a single intercept, y_0, defined as the estimated response at b_x. As in all the models we employed, species were incorporated as a random effect. A full model thus included these four parameters for every species, plus a set of hyper-parameters (the fixed effect) describing the mean response across species. A likelihood function describing the probability of observations given all the parameters, assuming Gaussian error functions, is required. Parameters were fitted using a previously described Bayesian hierarchical method[14]. We were interested

in the fixed effect, b_x, s_1, and s_2, and whether the slopes differ significantly, as established if 95% intervals of posterior distributions did not overlap.

Data availability. Tree census data are available online from the Smithsonian Library at http://dx.doi.org/10.5479/data.bci.20130603 and http://dx.doi.org/10.5479/data.stri.2016.0622. Site and soils data and species responses generated during hierarchical modelling are available in the Supplementary Information. All other data are available from the corresponding authors upon reasonable request.

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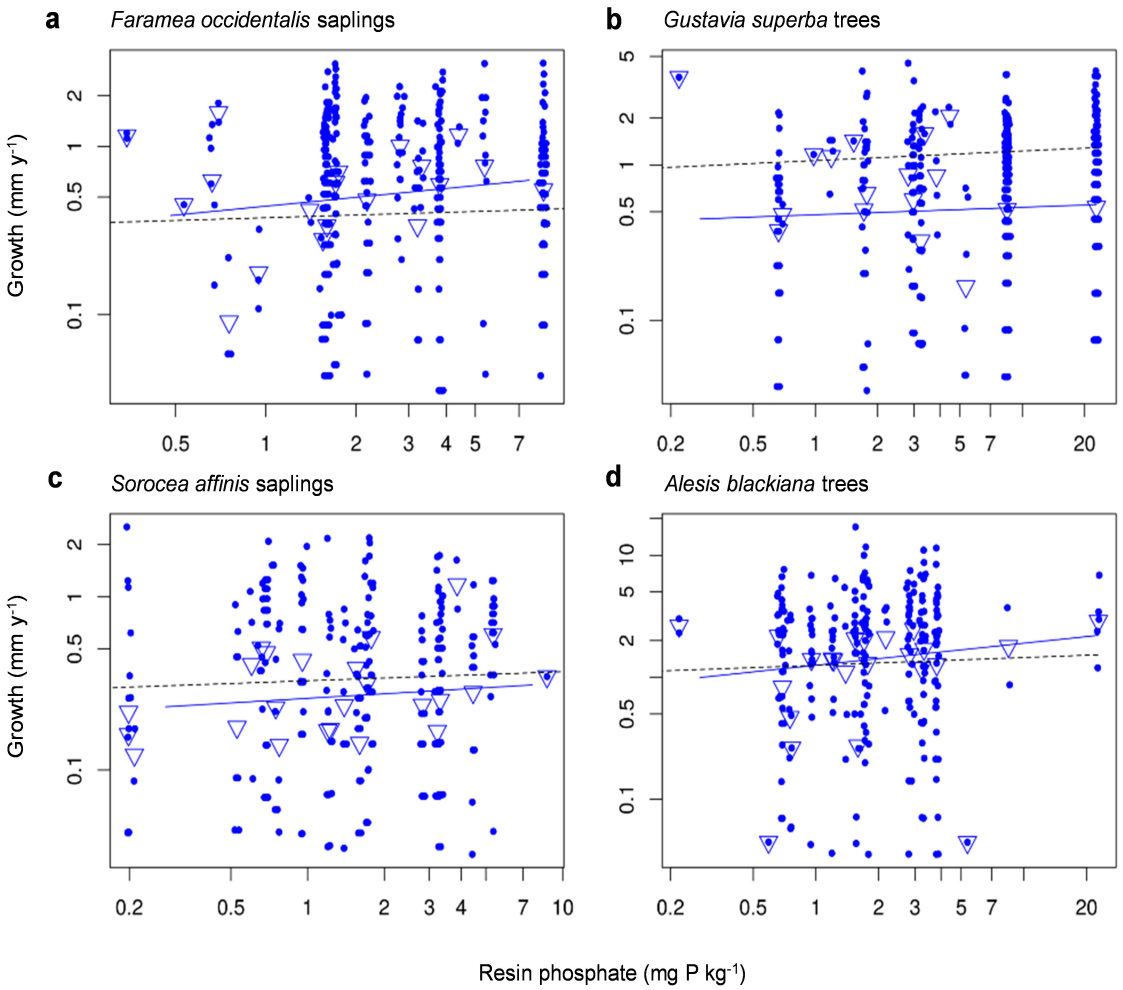
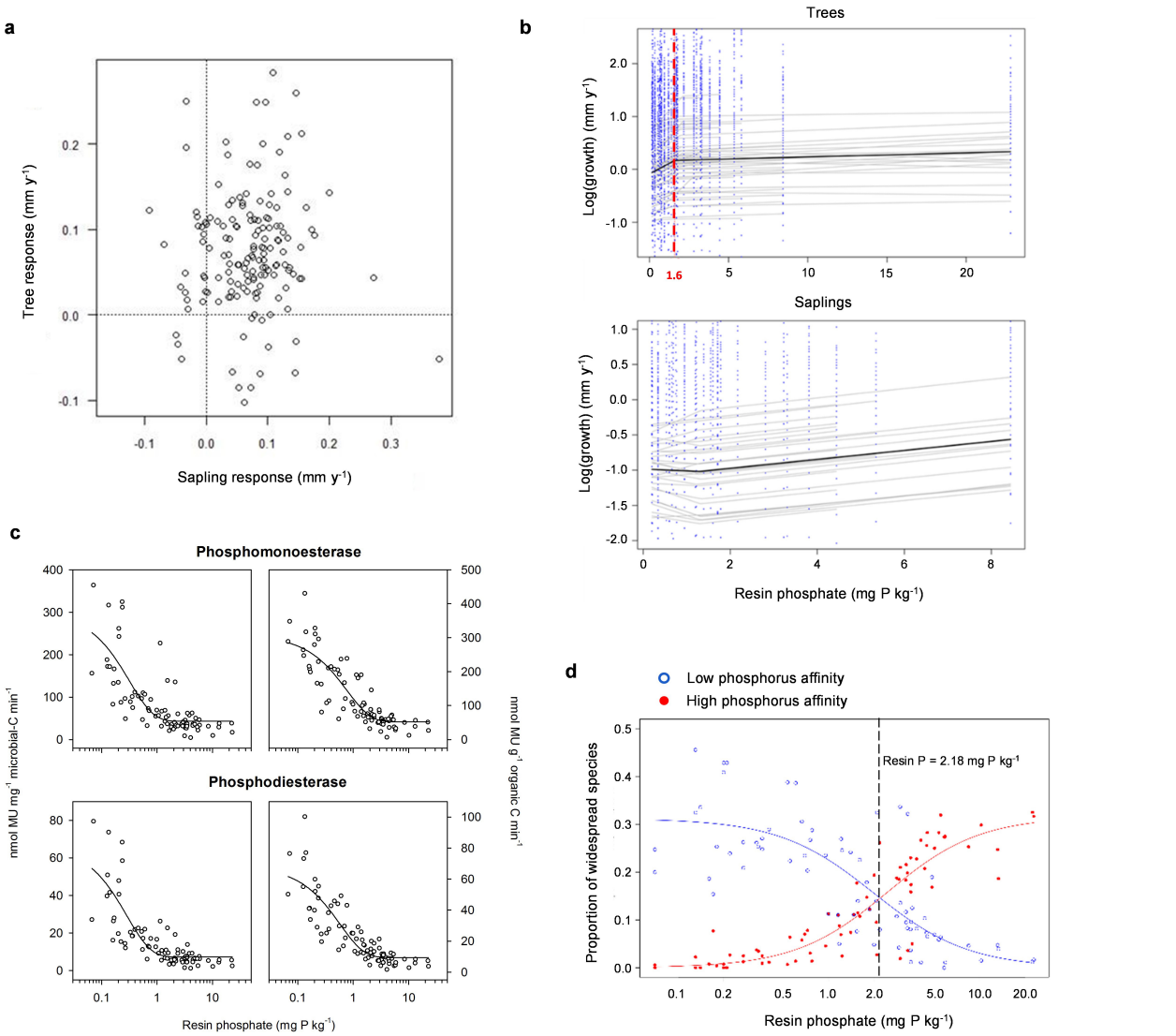
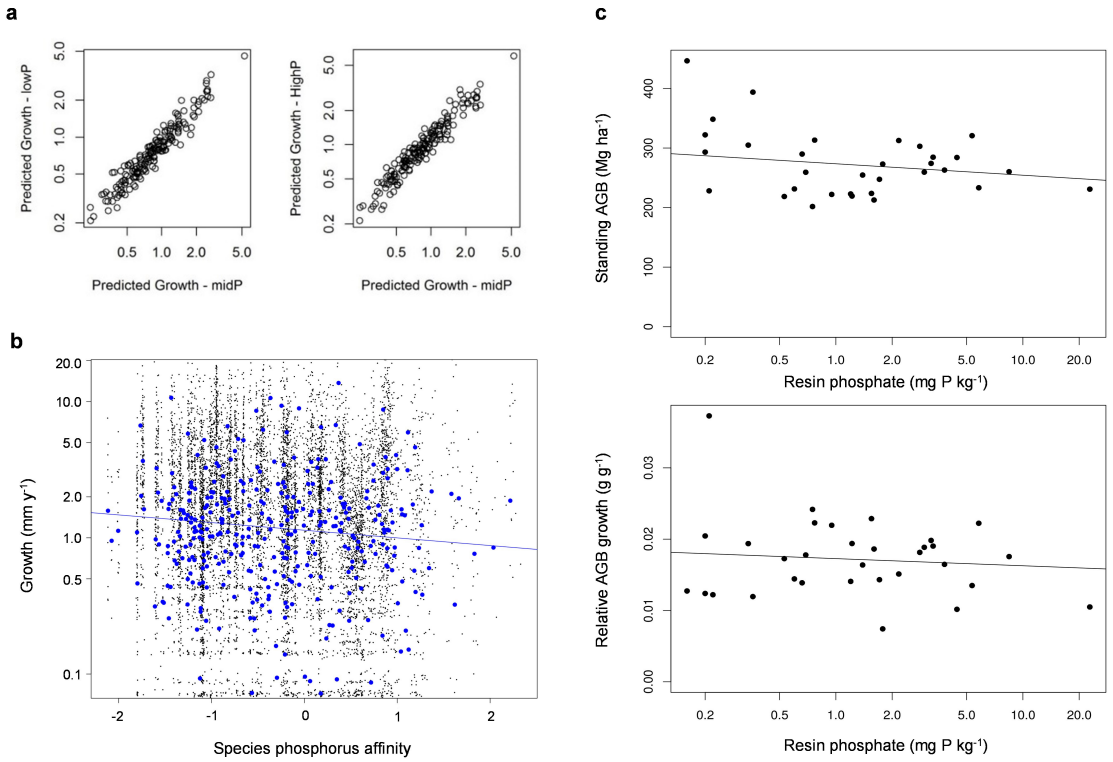


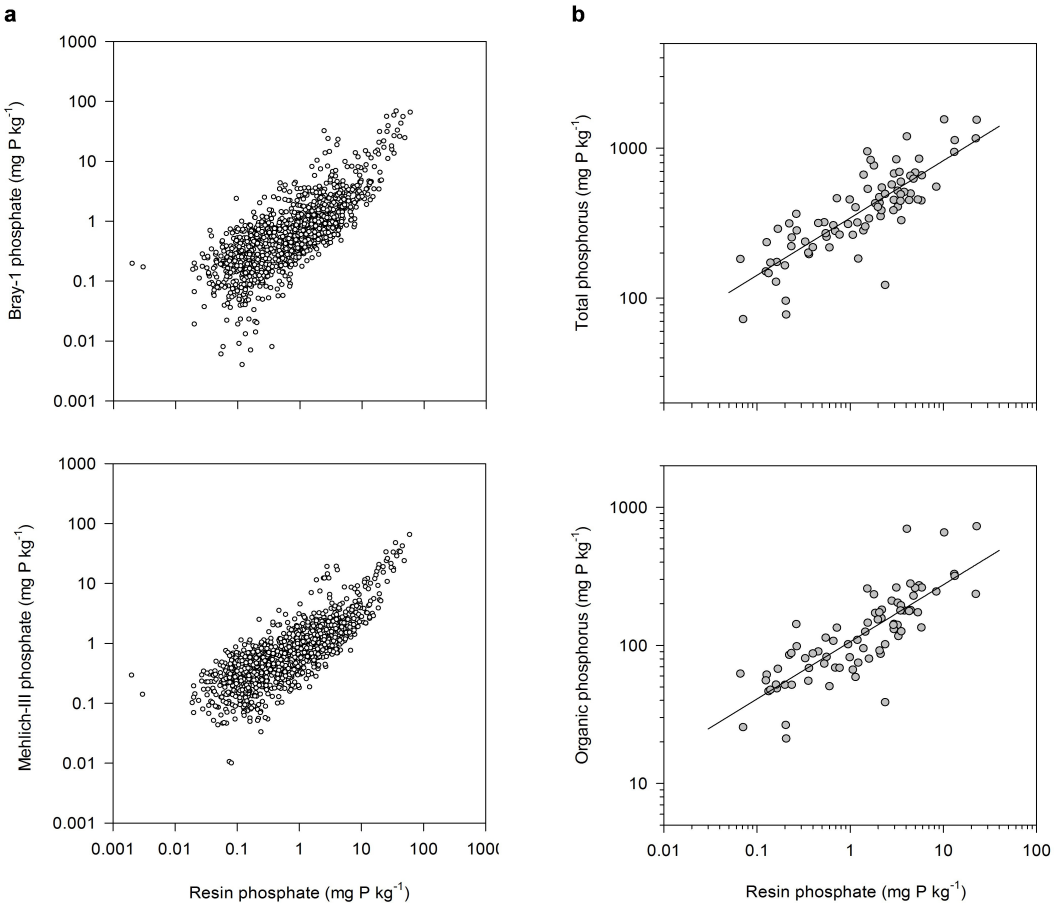
Extended Data Figure 1 | Growth responses of individual species to resin phosphate. a–d, Blue points represent the observed growth of individual trees, and blue triangles the species mean growth in a plot. The solid blue line is the modelled species response to resin phosphate, and the dashed black line is the fixed response of the entire community (as in Fig. 1). The four species are among the most abundant and widespread in the two size classes: *Faramea occidentalis* (Rubiaceae), an understory evergreen tree/shrub (**a**); *Sorocea affinis* (Moraceae), an understory deciduous tree (**b**); *Gustavia superba* (Lecythidaceae), an understory tree (**c**); and *Alseis blackiana* (Rubiaceae), a canopy tree (**d**). Saplings (**a**, **c**) include all individuals $\geq$ 10 mm and <50 mm dbh; the dashed black line is the community-wide estimate at 30 mm dbh. Trees (**b**, **d**) include all individuals $\geq$ 100 mm dbh; the dashed black line is the community-wide estimate at the mean dbh of all trees $\geq$ 100 mm dbh. Both the *y* axes (growth in mm y^{-1}) and *x* axes (resin phosphate in mg P kg^{-1}) are plotted on logarithmic scales. The number of individuals were: 398 saplings (*F. occidentalis*), 328 saplings (*S. affinis*), 620 trees (*G. superba*) and 253 trees (*A. blackiana*).



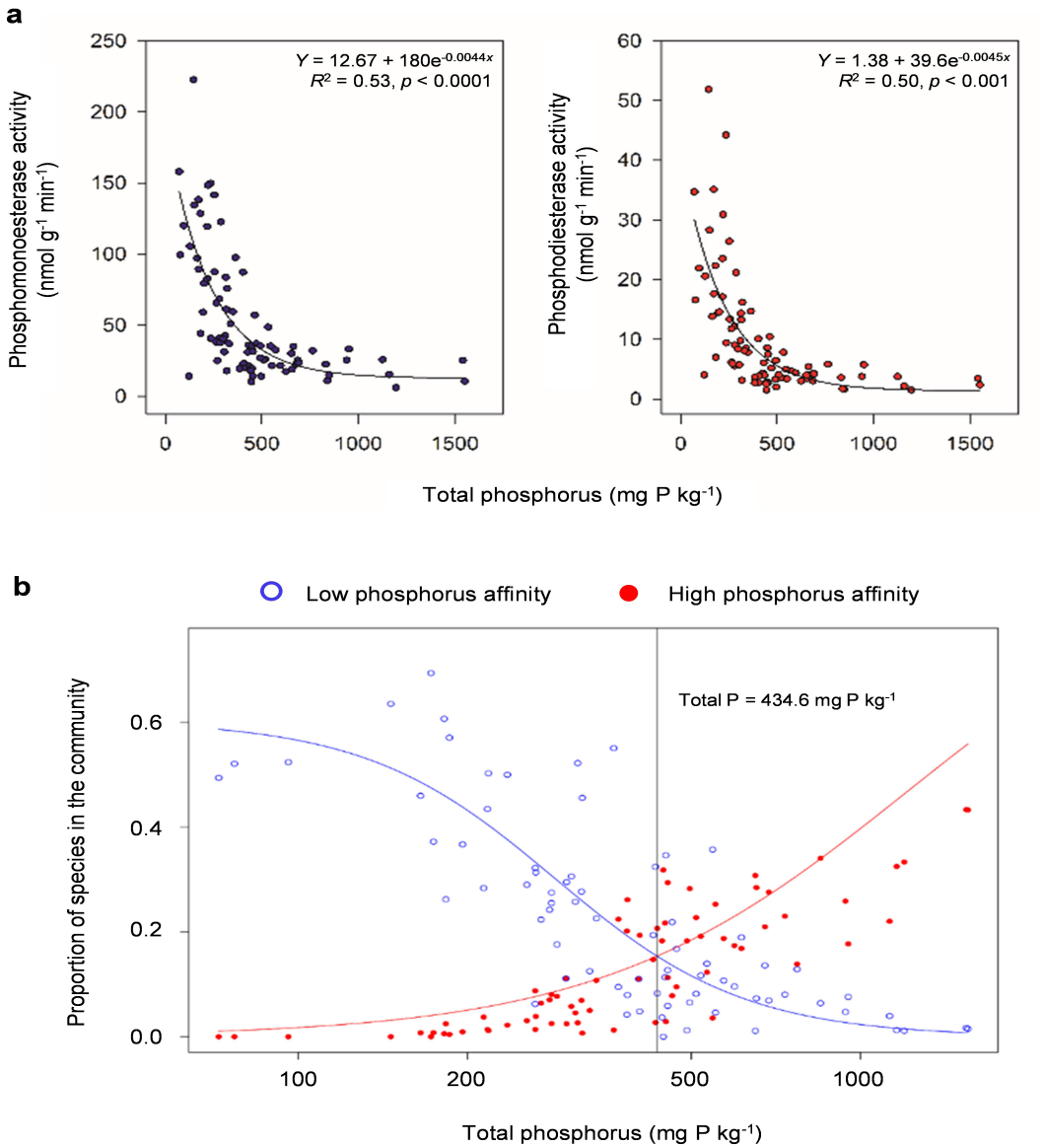
Extended Data Figure 2 | Responses to resin phosphate above and below ground. a, Modelled responses of common species to resin phosphate as adult trees and saplings. Trees were defined as being 100 mm dbh and saplings were defined as being 10 mm dbh. The responses of trees and saplings are unrelated by simple linear regression ($R^2 = 0.006$; $P = 0.74$). As trees 90% of species have a positive response to increasing resin phosphate concentrations (points above the horizontal dotted line), and as saplings 84% of species have a positive response to increasing resin phosphate concentrations (points to the right of the vertical dotted line). Only three common species responded negatively as both small and large trees. **b**, Piecewise linear regression model using common widespread species, showing the relationship fitted to the response of growth (log-transformed) to resin phosphate concentration for trees >100 mm dbh (top) and saplings <100 mm dbh (bottom). The black line is the community-wide mean, or fixed response. Each grey line is the fit for one species and blue dots are the growth rates of individual trees. For trees, the break point between large and small responses to phosphorus is at 1.6 mg P kg^{-1} resin phosphate (red dashed vertical line; 95% credible interval 1.3–2.0). To the left of this break, $s_1 = 0.16$ (95% credible interval 0.06–0.28) and to the right, $s_2 = 0.01$ (−0.01–0.03). For saplings, s_2 was significantly positive. However, the two slopes had widely overlapping credible intervals, forcing us to accept the null hypothesis of no change in slope. **c**, Specific phosphatase activity and resin phosphate for 83 sites under lowland tropical forest in Panama, showing phosphomonoesterase activity and phosphodiesterase activity expressed on the basis of the soil microbial biomass carbon (left) and total soil organic carbon (right). For both transformations, the relationships are almost identical to those for non-standardized activities, but the models explain a slightly smaller proportion of the variance. The hydrolysis product is methylumbelliferone and model fits are exponential functions determined by nonlinear regression. **d**, The proportion of the widespread species at a site that have negative or positive associations with soil phosphorus, against the resin phosphate concentration for 72 lowland tropical forests in Panama. Species with negative associations with soil phosphorus (low-phosphorus affinity), open blue circles and blue line; species with positive associations with soil phosphorus (high-phosphorus affinity), red circles and red line. The point at which the proportion of low-affinity species equals the proportion of high-affinity species corresponds to a resin phosphate concentration of 2.18 mg P kg^{-1}.



Extended Data Figure 3 | Growth responses to phosphorus at the species and community levels. a, Similarity in the growth rates of individual common species as predicted by the hierarchical model at three different resin phosphate concentrations. Each point represents the growth rate of a single species as estimated from the model, assuming intermediate moisture and a tree of 100 mm dbh. The graphs show the predicted species responses at intermediate resin phosphate (*x* axis, predicted growth − midP; as shown in Fig. 2a) against the predicted responses at low resin phosphate (predicted growth – lowP; left) and high resin phosphate (predicted growth – highP; right) concentrations. Only species that are common in the dataset (growth data available for >20 individuals) are plotted. The relative estimated responses are virtually identical across the entire phosphorus gradient. **b**, Observed growth rates as a function of species phosphorus affinities, with growth rates of individual trees ≥ 100 mm dbh shown in black and species-level median growth for the 362 species with estimated phosphorus affinities in blue. The *y* axis (growth) is log-transformed. The blue line shows a standard linear regression between log-transformed growth and phosphorus affinity (effect size), using median species growth ($n = 362$), weighted by species abundance. The slope (−0.13) is significantly different from zero ($P = 0.00014$), demonstrating that growth rates were greater for species with low-phosphorus affinity. **c**, Standing above-ground biomass (AGB) (top) and annual relative AGB growth (that is, standardized by the total AGB) (bottom) as a function of resin phosphate concentration. Data are from 32 plots across the phosphorus gradient in Panama. The resin phosphate scale is logarithmic. The linear regression relating standing AGB to log(resin phosphate), dry-season intensity and successional state revealed a slight negative but non-significant effect of phosphorus on biomass (slope = −7.9, $P = 0.37$). The same regression for relative AGB growth was likewise negative but not significant (slope = −0.002, $P = 0.09$). Biomass was significantly and negatively related to dry-season intensity (that is, more biomass at wetter sites) ($P = 0.003$), but relative biomass growth was not correlated with dry season intensity ($P = 0.07$).



Extended Data Figure 4 | Relationships between resin phosphate and other measures of soil phosphorus. a, Comparison of resin phosphate concentration and two common extraction procedures for plant-available phosphorus, showing values for 1,184 fresh (field-moist) soil samples at depths of up to 100 cm in lowland tropical forests of Panama. Relationships are shown for Bray-1 phosphate (top) and Mehlich-III phosphate (bottom). For both extractions, phosphate was determined in the extracts by automated molybdate colorimetry. Resin phosphate is strongly correlated to Bray-1 phosphate (Pearson product–moment correlation 0.81, $P < 0.0001$) and Mehlich-III phosphate (Pearson product–moment correlation 0.87, $P < 0.0001$). **b**, Relationship between resin phosphate concentration and total phosphorus (top) and organic phosphorus (bottom). Data are from soils from 83 sites in central Panama, with each value being the mean of multiple individual soil samples at a single site. The relationships are described by the following equations, derived from linear regression of log-transformed data: total phosphorus: $y = 342.43 \times (x^{0.3821})$, $R^2 = 0.68$, $P < 0.001$; organic phosphorus: $y = 106.01 \times (x^{0.4136})$, $R^2 = 0.66$, $P < 0.001$.



Extended Data Figure 5 | Phosphorus limitation threshold for total phosphorus. a, Relationships between phosphatase activities and total phosphorus concentrations in soils from 83 sites under lowland tropical forest in Panama. The figure shows phosphomonoesterase activity (blue circles, left) and phosphodiesterase activity (red circles, right). The hydrolysis product is methylumbelliferone and the model fits are negative exponential functions determined by nonlinear regression. The activity of both phosphatases decreases markedly at total phosphorus concentrations >400 mg P kg^{-1}. **b**, The proportion of species at a site that has a negative association with soil phosphorus (low-phosphorus affinity, blue circles and blue line) or positive association with soil phosphorus (high-phosphorus affinity, red circles and red line) against total soil phosphorus for 72 lowland tropical forests in Panama. The models are sigmoidal fits and phosphorus associations are defined as effect sizes >0.8 (positive affinity) or <-0.8 (negative affinity). The point at which the proportion of low-affinity species exceeds the proportion of high-affinity species corresponds to a total phosphorus concentration of 435 mg P kg^{-1}.

Extended Data Table 1 | Results of the full model used for analysis of the effect of resin on tree growth

Fixed effects	Estimate	Std. Error	*t* value	Probability (*P*)
Intercept	–0.1459	0.0414	–3.52	
Log(dbh)	0.5719	0.0246	23.23	< 0.0001
Log(dbh)^2	–0.0667	0.0153	–4.36	< 0.0001
Moisture deficit	0.0100	0.0177	0.57	0.003
Log(dbh) × moisture deficit	–0.0505	0.0197	–2.57	0.002
Log(Resin P)	0.0716	0.0203	3.52	< 0.0001
Log(dbh) × Log(Resin P)	0.0059	0.0150	0.40	0.72

Random effects	Parameter	Variance	Std. Dev.	Probability (*P*)
Species	Intercept	0.410	0.640	
	Log(dbh)	0.077	0.277	< 0.0001
	Moisture deficit	0.015	0.123	0.002
	Log(dbh)^2	0.027	0.164	< 0.0001
	Log(dbh) × deficit	0.023	0.151	< 0.0001
	Log(Resin P)	0.031	0.176	0.0015
	Log(dbh) × Log(Resin P)	0.007	0.085	0.72
Residual		1.397	1.182	

P values indicate significant improvements in the model when each individual parameter was included; they were calculated using LogLik model comparisons after dropping one fixed effect parameter at a time (relative to a model in which only the intercept varied randomly per species). Species random effects show the variance among species in the response to each fixed effect value. *P* values for random effects were generated from separate model runs shown in Extended Data Table 2. Response variable = log(growth); number of observations = 18,970; number of species = 541. dbh, diameter at breast height.

Extended Data Table 2 | Models evaluating the effects of moisture and nutrients on tree growth

(a) Moisture model

Fixed effects	Estimate	Std. Error	*t* value	Probability (*P*)
Intercept	–0.1535	0.0404	–3.80	
Log(dbh)	0.5804	0.0243	23.93	< 0.0001
Log(dbh)^2	–0.0647	0.0152	–4.26	< 0.0001
Moisture deficit	–0.0084	0.0177	–0.47	0.003
Log(dbh) × moisture deficit	–0.0606	0.0189	–3.21	0.001

Random effects	Name	Variance	Std. Dev.	Probability (*P*)
Species	Intercept	0.409	0.640	
	Log(dbh)	0.078	0.279	< 0.0001
	Moisture deficit	0.019	0.137	0.002
	Log(dbh)^2	0.027	0.165	< 0.0001
	Log(dbh) × deficit	0.019	0.137	< 0.0001
Residual		1.408	1.187	

(b) Effects of adding individual nutrients to the model

	Estimate	Std. Error	*t* value	Fixed effects *P* value	Random effects *P* value
Log(Resin P)	0.0707	0.0181	3.91	< 0.0001	0.0015
Log(Total Inorganic N)	0.0152	0.0096	1.59	0.11	ns
Log(Mehlich Ca)	0.0522	0.0169	3.09	< 0.0001	< 0.0001
Log(Mehlich K)	0.0044	0.0115	0.38	0.77	ns
Log(Mehlich Mn)	0.0046	0.015	0.49	0.63	ns

a, Model evaluating the effect of moisture deficit and dbh on growth, with no nutrients included. All fixed and random-effect parameters included in the moisture model significantly improved the model based on AIC model comparisons. **b**, Parameters and *P* values obtained from adding a single nutrient parameter at a time to the moisture model. *P* values evaluate the improvement in the model based on LogLik model comparisons after adding each nutrient parameter, one at a time, first as a fixed effect and then to the species random effect. Response variable = log(growth); number of observations = 18,970; number of species = 541. ns, not significant ($P > 0.1$).

Extended Data Table 3 | Model evaluating the effect on tree growth of resin phosphate and Mehlich calcium

Fixed effects	Estimate	Std. Error	*t* value	Probability (*P*)
Intercept	–0.134	0.041	–3.27	
Log(dbh)	0.574	0.024	23.74	*
Log(dbh)^2	–0.067	0.015	–4.43	*
Moisture deficit	–0.005	0.019	–0.25	*
Log(dbh) × moisture deficit	–0.049	0.019	–2.60	*
Log(Resin P)	0.052	0.020	2.65	0.008 †
Log(Mehlich Ca)	0.027	0.017	1.63	0.11 ‡

P values were calculated using LogLik model comparisons after adding the nutrient parameters, one at a time, to the moisture model in Extended Data Table 2. Response variable = log(growth); number of observations = 18,970; number of species = 541.
*See Extended Data Table 2 for *P* values.
†Also significant (*P* = 0.02) when log(resin P) was added to the Mehlich Ca model in Extended Data Table 2.
‡Also non-significant (*P* = 1.0) when log(Mehlich Ca) was added to the resin P model in Extended Data Table 2.

Extended Data Table 4 | Additional model runs to examine the influence of plot-level parameters on tree growth response to phosphorus

(a) Model including a plot random effect

Fixed effects	Estimate	Std. Error	*t* value
Intercept	–0.1330	0.0531	–2.51
Log(dbh)	0.5698	0.0244	23.39
Log(dbh)^2	–0.0716	0.0152	–4.73
Moisture deficit	–0.0100	0.0403	–0.25
Log(Resin P)	0.0942	0.0409	2.30
Log(dbh) × moisture deficit	–0.0290	0.0198	–1.47
Log(dbh) × log(Resin P)	0.0091	0.0154	0.59

(b) Model including stem density

Fixed effects	Estimate	Std. Error	*t* value
Intercept	–0.1413	0.0412	–3.43
Log(dbh)	0.5826	0.0243	24.00
Log(dbh)^2	–0.0710	0.0154	–4.62
Moisture deficit	0.0356	0.0181	1.96
Log(Resin P)	0.0514	0.0189	2.72
Log(dbh) × moisture deficit	–0.0517	0.0191	–2.71
Log(dbh) × log(Resin P)	0.0125	0.0135	0.93
Stem density	–0.0803	0.0143	–5.63

a, Model including a plot random effect. **b**, Model including the effect of stem density. Both models are for trees $\geq$ 10 mm dbh. Stem density was calculated as the number of stems $\geq$ 100 mm diameter. *P* values were not calculated, but *t*-values < -2 or >2 are generally significant at $P > 0.05$ for sample sizes >60. Response variable = log(growth); number of observations = 18,970; number of species = 541.