

# Foliar Stoichiometry is Marginally Sensitive to Soil Phosphorus Across a Lowland Tropical Rainforest

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## ABSTRACT

The distribution of nutrients, both vertically and horizontally in a forest, has long been theorized to influence primary productivity. Working at La Selva Biological Station, Costa Rica, we gathered the most comprehensive foliar samples to date for a lowland tropical rainforest to measure horizontal and vertical trends in foliar nutrients. The mean traits of foliage from forest floor to top-of-canopy were determined at 45 plots placed across the landscape in a stratified random design. Area-basis foliar N and P for these vertically integrated columns varied by a factor of 3, while foliar N:P and mass-basis foliar N and P varied by a factor of 2. The variance in plot-level foliar N:P and P was best explained by total soil P, while variance in foliar N was best explained by soil pH (regression trees:  $r^2 \geq 0.20$ ,  $p \leq 0.01$ ). Other soil, topographic, and forest structure factors offered no additional explanatory power for variation of foliar

nutrients from plot to plot. To explore vertical trends, we aggregated the data across the landscape into 2 m vertical segments. We found that foliar N:P was unrelated to height in the canopy, and that area-basis foliar N and P increased with height in the canopy (linear regression:  $r^2 = 0.82$  and  $r^2 = 0.65$  respectively,  $p < 0.0001$  for both). We compared these vertical trends to those of the eight other elements quantified in the leaves, and the only other element enriched with height was potassium (K). Vertical nutrient enrichment was driven by increases in leaf mass per area (LMA), not mass-basis concentrations. Altogether, these findings suggest that, even in diverse tropical rainforests, foliar chemistry may reflect environmental constraints.

**Key words:** foliar N:P; leaf Mass per Area; la Selva; landscape; foliar Micronutrients.

## HIGHLIGHTS

- 45 vertical transects reveal tropical forest landscape foliar N:P of  $21.8 \pm 0.5$ .
- Soil P explains 23% of horizontal variance in plot-level foliar N:P.
- Foliar N, P, and K increase with height on an area-basis but not on a mass-basis.

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## INTRODUCTION

Variation in the nitrogen to phosphorus (N:P) stoichiometry of live photosynthetic tissue may reflect nutrient limitation to net primary productivity (NPP) in some ecosystems (Redfield 1958; Koerselman and Meuleman 1996; Falkowski and others 1998; Sterner and Elser 2002). In lowland tropical rainforests, which represent less than a tenth of the land surface yet nearly a third of terrestrial NPP, it has been difficult to interpret the relationship between foliar chemistry and nutrient availability (Bonan 2008; Cleveland and others 2011). Adjacent tropical plants vary substantially in foliar stoichiometry (Townsend and others 2007; Sullivan and others 2014; Asner and Martin 2016), and this variation demands a more comprehensive foliar sampling. In particular, the vertical distribution of leaves can be highly related to the NPP of a lowland tropical rainforest (Cushman and Kellner 2019), and tropical forest trees partition foliar nutrients vertically (Leuning and others 1991; Lloyd and others 2010). Yet, to our knowledge, the vertical distribution of foliar nutrients has never been sampled systematically to capture the topographic and substrate variability of a lowland tropical rainforest landscape. Thus, the degree to which foliar nutrients are indicative of other ecosystem properties in lowland tropical rainforests remains an open question.

Despite very limited sampling relative to other biomes, some authors have interpreted high N:P in tropical foliage as an indication of P limitation to NPP, low levels of available P in tropical soils, or both (McGroddy and others 2004; Reich and Oleksyn 2004). Highly weathered, acidic, and P-poor soils are indeed relatively abundant in tropical rainforests (Sanchez 2019). Resorption of P is also higher relative to N during foliar senescence in tropical rainforests (Vitousek 1984; Reed and others 2012). Further evidence of the importance of P comes from recent MODIS-derived aboveground NPP estimates in the neotropics, which were positively correlated with the foliar P concentrations of the region's woody plants, but not with their foliar N content (Šímová and others 2019). On the other hand, the few fertilization experiments in mature lowland tropical rainforests do not demonstrate P limitation to NPP (Townsend and others 2011; Alvarez-Clare and others 2013; Wright and others 2018). Even a lowland Amazonian site with a high tree foliar N:P of 25 (55 molar) was found to be co-limited by N and P in a fertilization study, rather than limited by P alone (Fisher and others 2013).

Tropical foliar stoichiometry interpretation is also complicated by the controls of different foliar nutrients. Much of the variance across individuals in foliar N results from phylogenetic variation, whereas much of the variance in foliar P (and other rock-derived nutrients) is best explained by location, and thus in part by local soil conditions (Fyllas and others 2009; Asner and others 2015a; Asner and Martin 2016). Chemical variation among individuals in a single tropical rainforest site is often as large as the variation among sites (Townsend and others 2007; Sullivan and others 2014; Asner and Martin 2016; Balzotti and others 2016). Thus, without comprehensive sampling of the entire photosynthetic community, it remains unclear whether and how foliar nutrients yield meaningful information about lowland tropical forest nutrient status.

The distribution of foliar nutrients within a canopy also contributes to the relationship between productivity and nutrient resources. The photosynthetic benefit of redistributing N to upper, well-lit leaves has long been thought to exceed the cost of amino acid transport (Field 1983). However, among the leaves of tropical and subtropical woody plants, no vertical trend of mass-basis enrichment of N, P, K, calcium (Ca), or magnesium (Mg) has been observed vertically (Lloyd and others 2010; Niinemets and others 2015), nor do mass-basis foliar N or P increase with light intensity (Poorter and others 2019). In North American mixed spruce and fir stands, mass-basis foliar Ca was significantly higher in sun leaves than shade leaves, but this was not observed for N, P, K, Zinc (Zn), or Mg (Richardson 2004). Thus, despite a theoretical benefit to photosynthetic optimization, mass-basis vertical nutrient enrichment does not seem to be common (Hirose and Werger 1987; Hikosaka and others 2016).

Nonetheless, an increase in the leaf mass supporting each square centimeter of leaf surface (leaf mass per area, LMA) can enrich the nutrient resources of the photosynthetic surface without changing stoichiometry (Lloyd and others 2013; Osnas and others 2013). LMA increases with height in every forest where it has been studied, including at our study location in northeastern Costa Rica (Cavaleri and others 2010), but whether there is mass-basis vertical nutrient enrichment remains an open question for the complex canopies characteristic of tropical rainforests. Plants with better light access are better situated to acquire nutrients via improved mycorrhizal relations (Konvalinková and Jansa 2016), symbiotic N-fixation (Taylor and Menge 2018), and investment in root biomass

(Poorter and others 2019). Competition for full-sun positions between trees and lianas could alter vertical trends in foliar chemistry (Asner and Martin 2012), as could the sensitivity of palms' canopy position to soil nutrient conditions (Cámara-Leret and others 2017). Sampling foliage of all major plant functional groups, and accounting for the relative abundance of their foliage, is therefore necessary to rigorously test for mass-basis foliar nutrient enrichment with height.

In tropical forests, investigators rarely harvest whole plots because the effort involved is substantial (but see Golley 1975; Delitti and Burger 2000). Instead, investigators select mature, undamaged leaves for chemical analysis. However, the exclusion of old leaves from analyses can lead to overestimates of mass-basis foliar N (Albert and others 2018), the exclusion of senescing leaves results in a foliar stoichiometry that is less sensitive to soil nutrient availability (Vitousek 1984; Reed and others 2012; Tully and others 2013), and the exclusion of herbivory-damaged leaves likely results in oversampling of foliage with reduced N concentrations (Tao and Hunter 2011) and perhaps reduces the detected value for foliar N:P as well (Awmack and Leather 2002). Scaling from foliar samples to the landscape is also a challenge. At larger spatial scales, it becomes intractable to collect leaves from each plant in a plot and estimate the abundance of leaves on each plant (*sensu* Grubb and Edwards 1982). A recent innovation is to regress average foliar nutrition on visible to short-wave infrared spectra detected for calibration plots, and then scale that relationship to the landscape by using the spectra detected via airborne remote sensing (Asner and others 2015b). This method shows promise for resolving the environmental factors associated with foliar trait heterogeneity across a landscape (Asner and others 2015a), but only assesses the traits of the uppermost sunlit canopy.

In this context, we sought to comprehensively characterize horizontal and vertical heterogeneity in foliar chemistry across a continental lowland tropical rainforest, and probe whether that heterogeneity reflects the biotic and abiotic differences that have been proposed as important for plant nutrient status. We designed a method analogous to dragging a plankton net from the bottom to the top of the photosynthetic zone in an aquatic system (*sensu* Redfield 1958). We constructed 45 modular towers at representative sites across the mature forest at La Selva Biological Station, Costa Rica, and collected all leaves intersecting each tower. We used this, the largest systematic, strati-

fied random sample of ground to top-of-canopy tropical forest foliage to date, to ask: (1) How does foliar chemistry vary horizontally across the landscape? (2) How does foliar chemistry vary with height in the canopy? and (3) What abiotic and biotic variables, if any, explain horizontal variation?

## METHODS

### Site Description

Data were collected at La Selva Biological Station, a 1536 ha forest preserve in northeastern Costa Rica (10° 26'N 84° 1'W, 37–150 m asl) with 515 ha of continuous mature tropical forest. La Selva has undulating topography, with relatively flat ridges descending to stream channels with a few tens of meters of topographic relief. Many ridgetop soils in the landscape are Ultisols or Oxisols, with Inceptisols found on steeper slopes and in alluvial valleys (Sollins and others 1994; Porder and others 2006). Soils on ridges retain a relatively high fraction of rock-derived nutrients, as has been observed in other relatively young geomorphic settings of the lowland tropics (Bern and others 2005; Porder and others 2006). Although in this region, as in other lowland tropical sites, ridgetops have substantially lower rock-derived nutrient availability than slopes and alluvial areas, La Selva has fairly high rock-derived nutrients in the soil compared with more stable, geologically quiescent lowland tropical forests. For example, total soil P to 100 cm depth ranges from ~ 500 ppm on ridges to over 1600 ppm in alluvial soils (Porder and others 2006, data collected as part of this study), whereas on the Brazilian shield total P concentrations may be as low as 100 ppm (Quesada and others 2010).

Annual rainfall at La Selva is ~ 4000 mm with no month receiving less than 200 mm of precipitation, and the mean annual temperature is 26 °C (Sanford and others 1994). There were 113 species of palm, tree, and liana identified among the plants whose branches we sampled at La Selva. As in many Central American forests with year-round precipitation, the leguminous tree *Pentaclethra macroloba* (Willd.) Kuntze is abundant; at La Selva, *Pentaclethra* is by far the most common plant species (Hartshorn 1983). Previously reported results from our sampling campaign showed that this species makes up  $14 \pm 2\%$  of leaf area at the 45 locations where we sampled, and 35% of total basal area within a 10 m radius of these locations (Clark and others 2008).

## Sampling & Analyzing Photosynthetic Tissue

In order to span the variability in soils at La Selva, 45 plots were identified via stratified random design (based on predictions of topsoil total soil P and slope) across the 515 ha of mature forest (Clark and others 2008). Forest heights at these locations ranged from 4 to 45 m. Between June 2003 to March 2005, we constructed a modular tower at each plot (Figure 1). All foliage intersecting the tower footprint was collected, from the ground to the canopy top. The sample area was 2.42 m<sup>2</sup> for the first 4 plots, after which we obtained a side platform that increased the tower footprint to 4.56 m<sup>2</sup> for the remaining 41 plots. Leaf area index (LAI) ranged from 1.2 to 12.9 m<sup>2</sup>m<sup>-2</sup>, with an overall average across all tower transects of  $6.0 \pm 0.3$  m<sup>2</sup>m<sup>-2</sup> (Clark and others 2008).

For each 1.86 m tall tower segment, leaves were collected and categorized into eight plant functional groups: *Pentaclethra*, other trees, palms, lianas, herbs, herbaceous vines, ferns, and epiphytes. Herbs, herbaceous vines, ferns, and epiphytes contributed only  $12 \pm 1\%$  of LAI across all 45 plots, and leaf chemistry was not measured for these groups at all plots. For the purposes of our analyses (described in Data Analysis and Statistics), we excluded the contribution of these minor functional groups to the total LAI and leaf mass of a tower or tower section and reweighted the four major functional groups (*Pentaclethra*, other trees, palms, and lianas) to 100%.

We measured leaf area with a LI-3100 benchtop leaf area meter (LI-COR Biosciences, Lincoln, NE, USA). Foliar samples were taken from each functional group at each height, homogenized with a Wiley mill and 20-mesh sieve, and weighed. For each foliar sample, a subsample was analyzed for foliar N at Colorado State University with a TruSpec CN Determinator (LECO, St. Joseph, MI, USA), and another subsample was digested by nitric acid and hydrogen peroxide to determine foliar P at MDS Harris Laboratories on a 4300 Optima Dual View inductively coupled plasma (ICP) spectrometer (PerkinElmer, Waltham, MA, USA). For two periods of foliar sampling (June 2003 to Mid-October 2003 and February 2004 to June 2004), only N and P were measured. For the rest of the study (Mid-October 2003 to January 2004 and July 2004 to Mid-March 2005), foliar concentrations were also determined for Potassium (K), Magnesium (Mg), Calcium (Ca), Sulfur (S), Sodium (Na), Zinc (Zn), Manganese (Mn), and Aluminum (Al). Thus, we have a full suite of foliar concentrations for 28

towers. Light conditions were highly correlated with the height from which a sample was collected in the canopy (log-linear regression:  $r^2 = 0.99$ ; Cavaleri and others 2010), so in this study we use higher leaves as a proxy for well-lit leaves.

## Quantifying Soil and Topographic Variables

At the time of foliar sampling, we collected eight to ten 100 cm soil cores of 3 cm diameter within 2 m of each tower base and homogenized them. Prior work at La Selva on total soil C, N, and P suggests that soil chemistry is likely similar for tens of meters beyond this soil sampling area (Espeleta and Clark 2007; Clark and others, unpublished data). Total P in the top 10 cm of soil was correlated at  $r^2 = 0.96$  with the 0–100 cm value. We use the latter in this analysis. Soil C and soil N were quantified by Vario EL Elemental Analyzer CNS (Elementar, Langensfeld, Germany). All other elements were analyzed by nitric acid digest followed by inductively coupled plasma spectrometry (SPECTRO Analytical Instruments, Kleve, Germany). Cation exchange capacity was recorded as the sum of charges from exchangeable H, Na, K, Ca, Mg, Mn, Fe, and Al (McKenzie and others 2004), and base saturation as the fraction of this occupied by Na, K, Ca and Mg. Dry soil was mixed with 1 M KCl in a 1:2.5 ratio for pH measurement with a combined electrode (Schlichting and others 1995). In addition, we used a high-resolution digital elevation model generated by aircraft-based LiDAR (Kellner and others 2009) for a post hoc categorization of the topographic position (ridge, slope, or valley) and to determine elevation below the local topographic high (Porder and others 2005).

## Data Analysis and Statistics

For a given foliar sample ( $i$ ), we measured leaf area ( $L_i$ ), LMA ( $H_i$ ), mass-based foliar N ( $N_{\text{mass}i}$ ), and mass-based foliar P ( $P_{\text{mass}i}$ ). The fundamental unit of analysis in this study is all foliar samples collected within the same 1.86 m tall section of the same collection tower (Figure 1). We calculated mean foliar chemistry by grouping these 1.86 m tall height sections (a) with the others from the same collection tower (plot) and (b) by aggregating 1.86 m tall sections with all others from the same height (canopy level). (a) To scale foliar measurements up to the plot, mass-basis foliar N (Eq. 1) and mass-basis foliar P (Eq. 2) values were weighted based on the relative contribution of the foliar





**Figure 1.** Within each 1.86 m tall tower section, we grouped leaves by functional group to measure LMA, LAI, and elemental concentrations. In the ground level tower section of plot 1 in this example, the traits of the liana leaves would be measured and recorded separately from those of the palm leaves. In plot 2, all leaves of the ground level segment would be analyzed together because they are all palm leaves. The data from these samples were aggregated by plot and by canopy level. LAI-weighted average of area-basis nutrient concentrations and leaf-mass-weighted average of mass-basis concentrations were calculated for both plots and canopy levels. For illustration purposes, here we show 2 plots spanning a maximum of 5 canopy layers. Our study encompassed 45 plots and 22 canopy layers. The unweighted, arithmetic mean of those two plot values would describe the “landscape” in this example.

sample leaf mass (the product of leaf area,  $L$ , and LMA,  $H$ ) to the total leaf mass captured in the tower ( $\sum_{i=1}^s L_i H_i$  where  $s$  is all foliar samples in a plot). To determine the resources available to the total ( $t$ ) photosynthetic surface at a plot, area-basis foliar N (Eq. 3), area-basis foliar P (Eq. 4), and N:P (Eq. 5) values were weighted based on the relative contribution of  $L_i$  to the total leaf area captured in the collection tower ( $\sum_{i=1}^s L_i$  where  $s$  is all foliar samples in a plot). Because plots were placed at representative locations across the mature forest at La Selva, the unweighted arithmetic mean across plots was taken to represent the landscape-scale foliar trait. (b) Weighted averages were also calculated for the mass of tissue at each canopy level (Eqs. 1 and 2, where  $s$  is all foliar samples in a

canopy layer), and for the photosynthetic surface at each canopy level (Eqs. 3, 4, and 5, where  $s$  is the index of foliar samples in a canopy layer).

$$N_{\text{mass},t} = \sum_{i=1}^s N_{\text{mass},i} \frac{L_i H_i}{\left( \sum_{i=1}^s L_i H_i \right)} \quad (1)$$

$$P_{\text{mass},t} = \sum_{i=1}^s P_{\text{mass},i} \frac{L_i H_i}{\left( \sum_{i=1}^s L_i H_i \right)} \quad (2)$$

$$N_{\text{area},t} = \sum_{i=1}^s N_{\text{mass},i} H_i \frac{L_i}{\left( \sum_{i=1}^s L_i \right)} \quad (3)$$

$$P_{\text{area}_i} = \sum_{i=1}^s P_{\text{mass}_i} H_i \frac{L_i}{\left(\sum_{i=1}^s L_i\right)} \quad (4)$$

$$\left(\frac{N}{P}\right)_{\text{area}_i} = \sum_{i=1}^s \frac{N_{\text{mass}_i}}{P_{\text{mass}_i}} \left(\frac{L_i}{\sum_{i=1}^s L_i}\right) \quad (5)$$

We focus on area-weighted values for horizontal analyses, but our results did not differ substantially when mass-weighted values were considered instead (Figure S1). This analysis excluded any samples for which one or more measurements were missing from any calculation that required the missing factor or factors, but these samples were included in all other calculations. Less than 1% of data was missing for leaf mass per area, but 3% of  $N_{\text{mass}}$  measures and 9% of  $P_{\text{mass}}$  were missing due to the additional logistics involved in performing these measures on rainforest foliage over years of sampling. There was no significant difference between the sampling heights of missing data and those of recorded data.

Finally, we used regression tree analysis (Breiman and others 1983; De'Ath and Fabricius 2000) to partition horizontal variation in foliar N, P, and N:P using the following independent variables: soil C:N, soil N, soil P, soil pH, cation exchange capacity, base saturation, topographic position, elevation difference from the local topographic maximum, forest height, and LAI. A regression tree classifies data dichotomously along a single categorical or continuous variable, to explain variation in the dependent variable, then continues splitting data to create a hierarchical model. Because this method can overfit, we only included splits that reduced the Akaike Information Criterion (AIC) of the model and that resulted in subsets that were significantly different ( $p \leq 0.05$ , as indicated by a 2-tailed heteroscedastic  $t$ -test for a single split tree, or by a one-way ANOVA followed by Tukey's HSD for a tree with multiple splits).

Differences in foliar nutrients could result from flexibility within functional groups, from functional group turnover, or both. To explore the possibility of functional group turnover as a mediating factor in horizontal trends, we quantified the relative contribution of each functional group to the foliage of each plot (percent of  $\sum_{i=1}^s L_i H_i$  for mass-basis foliar traits and percent of  $\sum_{i=1}^s L_i$  for area-basis foliar traits), and tested for a difference between plot groups identified by the regression tree model. We also used linear regression to see if functional group turnover was associated with fo-

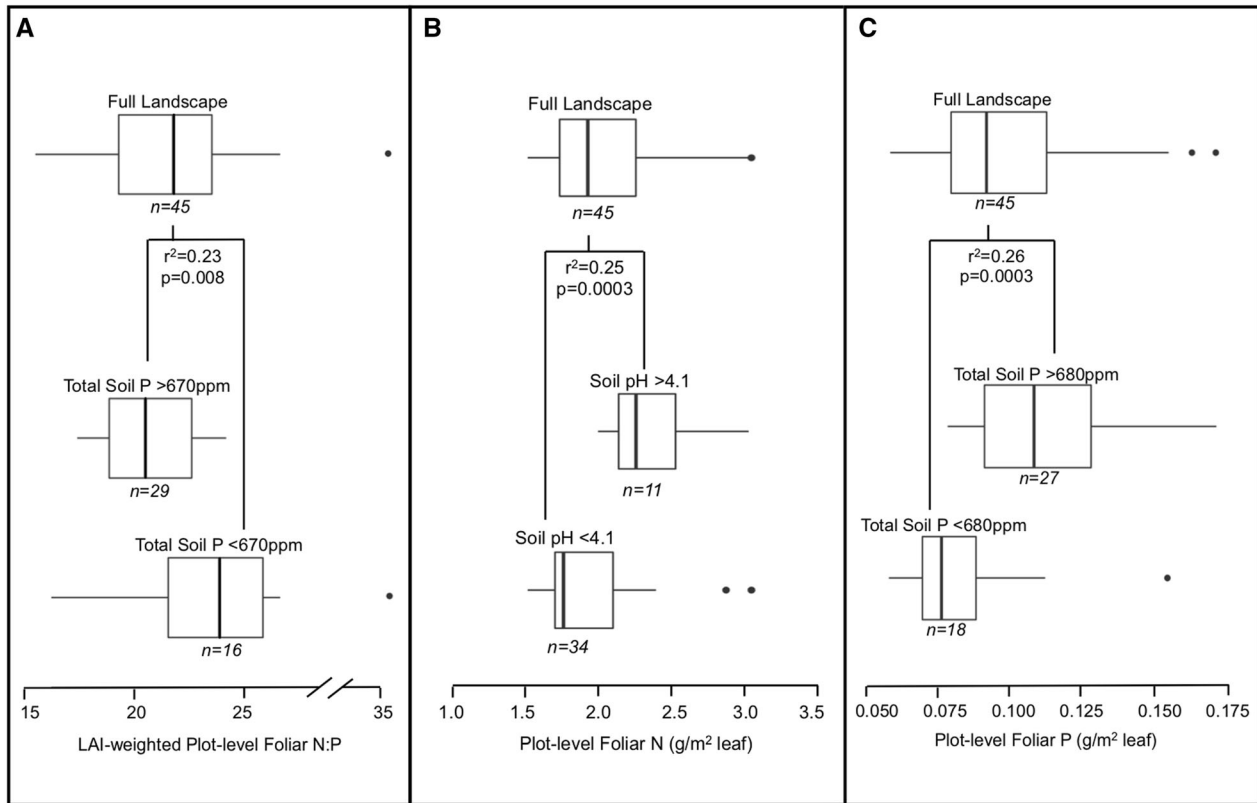
liar chemistry across all plots. The strength and direction of vertical trends within the canopy was assessed by linear regression as well. Where weighted means are reported, weighted mean standard errors are used (Cochran 1977; Gatz and Smith 1995). All statistics were performed in R version 1.1.453 (R Core Team 2013), using packages dplyr (Wickham and others 2021), rpart (Therneau and others 2019), regclass (Petrie 2020), weights (Pasek and others 2020), and Hmisc (Harrell and Dupont 2020). Figures 2, 3, and 4 were created with package ggplot2 (Wickham and others 2020). All R code is included in the supplemental material.

## RESULTS

### Horizontal Trends

Among individual foliar samples in this tropical rainforest, foliar N:P spanned 38% of the log-transformed global range (Wright and others 2004, see Isles 2020 for the reasons for log-transformation in stoichiometric comparisons). However, there was only modest variation among plots (that is, comparing all foliage captured in one sampling tower to all foliage captured in another). The arithmetic mean of plot-level foliar N:P was  $21.8 \pm 0.5$  ( $48 \pm 1$  molar). The highest plot-level foliar N:P we found in the canopy exceeded the lowest by about a factor of 2 (N:P molar-ratio range: 34 to 78, N:P mass-ratio range: 15.5 to 35.3). This variance in N:P was partially explained by total soil P (0–100 cm). Plots on soils with  $< 670$  ppm soil P had foliage with significantly higher foliar N:P ( $r^2 = 0.23$ ,  $p = 0.008$ , Figure 2) than those on more P-rich soils. No additional explanatory power resulted from including any other soil variables (C:N, total N, pH, cation exchange capacity, base saturation), topographic position, elevation difference from the local topographic maximum, forest height, or LAI.

As with foliar N:P, total soil P best explained variance from plot to plot in foliar P ( $r^2 = 0.26$ ,  $p = 0.0003$ , Figure 2). The optimal split selected by the regression tree model was 680 ppm, very similar to the result for foliar N:P. Notably, splitting the data by soil N did not significantly explain plot-level foliar N on a mass- ( $p = 0.21$ ) or area-basis ( $p = 0.37$ ). Plot-level foliar N variance was best explained by soil pH ( $r^2 = 0.25$ ,  $p = 0.0003$ , Figure 2). Soils of  $\text{pH} \geq 4.1$  supported more N-rich foliage, in comparison to the more acidic sites of  $\text{pH} 3.82\text{--}4.08$ . These soil conditions were not associated with one another ( $\chi^2$  of regression tree split:



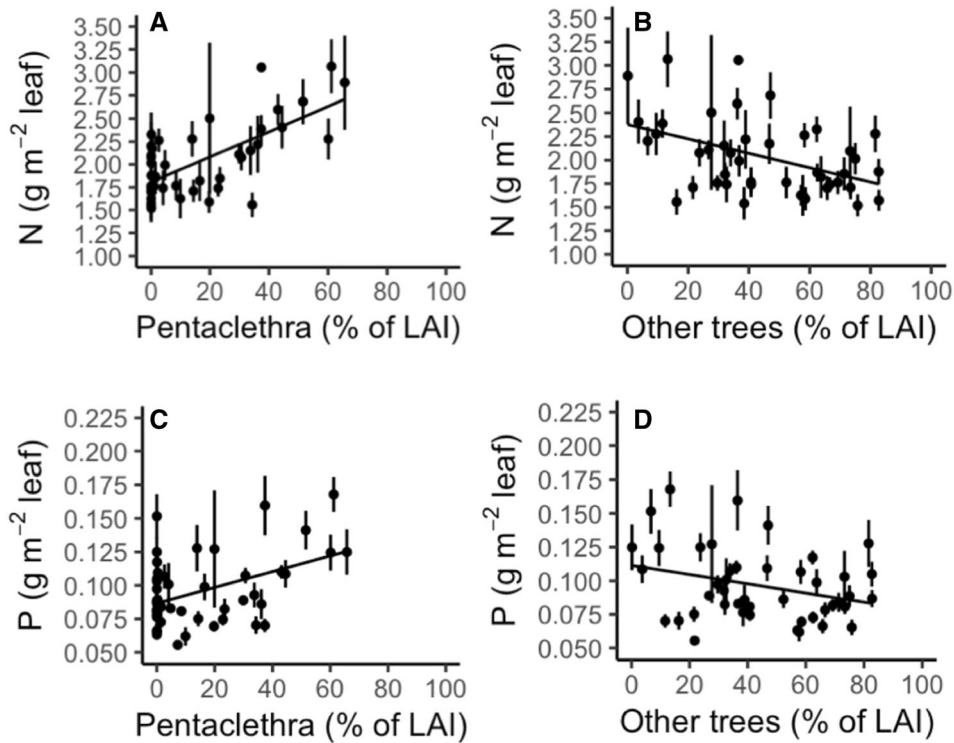
**Figure 2.** Boxplots showing LAI-weighted plot-level average **A** foliar N:P for the full landscape, **B** area-basis foliar N, and **C** area-basis foliar P, then for subsets of plots identified by regression tree analysis. Removal of the one anomalously high point (N:P = 35) does not eliminate the significant difference between the foliar N:P values on high vs. low P soils. See Figure S1 for boxplots of leaf-mass-weighted values.

$p = 0.51$ , linear regression:  $p = 0.52$ ). Foliar N, P, and N:P were thus each explained by a single factor, with no other factor adding explanatory power, and the results for mass-basis foliar traits were nearly identical (Figure S1).

The four plant functional groups differed in foliar chemistry (Table 1), so we asked whether functional group turnover was associated with the soil condition thresholds determined above. At total soil P < 670 ppm, 10% of leaf area was from *Pentaclethra*, but *Pentaclethra* became relatively more important at high soil P: 20% from *Pentaclethra* ( $p = 0.05$ ). When comparing functional groups' relative contribution to leaf mass, the change in *Pentaclethra* was similar (from 11% of leaf mass at low soil P to 25% at high soil P,  $p = 0.04$ ). For soil pH, the only significant association was that *Pentaclethra* accounted for 15% of leaf mass at the most acidic plots and 38% of leaf mass at soil pH  $\geq 4.1$  ( $p = 0.04$ ).

Across all plots, the relative abundance of *Pentaclethra* foliage was positively correlated with plot-level area-basis foliar N ( $p < 0.0001$ ,  $r^2 = 0.43$ ,

Figure 3) and P ( $p = 0.003$ ,  $r^2 = 0.19$ , Figure 3). This corresponded to a weak, but significant, decrease in the relative abundance of other tree foliage ( $p = 0.02$ ,  $r^2 = 0.13$  and  $p = 0.05$ ,  $r^2 = 0.09$ , respectively, Figure 3). On a mass-basis, the correlation of *Pentaclethra* abundance with plot-level foliar N was weaker ( $p = 0.008$ ,  $r^2 = 0.15$ , Table S5), and rather than supplanting other trees ( $p = 0.28$ ), there was a decrease in the percent of leaf mass from palms as plot-level mass-basis foliar N increased ( $p = 0.009$ ,  $r^2 = 0.15$ ). There was no significant association of any functional group with plot-level foliar N:P ( $p \geq 0.09$ ), nor with mass-basis P ( $p \geq 0.16$ ). It is worth noting that there is less variance to be explained for mass-basis foliar chemistry. From plot to plot, area-basis foliar P ( $0.096 \pm 0.004 \text{ g m}^{-2}$ , range: 0.055–0.168  $\text{g m}^{-2}$ ) and area-basis N ( $2.0 \pm 0.06 \text{ g m}^{-2}$ , range: 0.97–3.1  $\text{g m}^{-2}$ ) varied by a factor of  $\sim 3$ , whereas mass-basis P ( $0.10 \pm 0.003\%$ , range: 0.06–0.15%) and mass-basis N ( $2.1 \pm 0.04\%$ , range: 1.6–2.8%) were more constrained, with the highest plot-level value exceeding the lowest by a factor of  $\sim 2$ .



**Figure 3.** Plot-level, area-basis foliar N is associated with the relative leaf area contribution of *Pentaclethra* (**A**,  $p < 0.0001$ ,  $r^2 = 0.43$ ) and other tree foliage (**B**,  $p = 0.02$ ,  $r^2 = 0.13$ ). Plot-level, area-basis foliar P is also associated with the relative leaf area contribution of *Pentaclethra* (**C**,  $p = 0.003$ ,  $r^2 = 0.19$ ) and other tree foliage (**D**,  $p = 0.05$ ,  $r^2 = 0.09$ ).

## Vertical Trends

Weighted averages of area-based foliar N ( $\text{g m}^{-2}$  leaf) and P ( $\text{g m}^{-2}$  leaf) increased with height in the canopy ( $r^2 = 0.82$ ,  $p < 0.0001$  and  $r^2 = 0.65$ ,  $p < 0.0001$ , respectively; Figure 4). In contrast, the weighted average of mass-based foliar N (percent of leaf mass) and P (percent of leaf mass) were not significantly correlated with height ( $p = 0.87$ ,  $p = 0.79$ , respectively; Figure 4). K was the only other leaf nutrient whose area-based concentration increased with height ( $r^2 = 0.26$ ,  $p = 0.01$ ; Figure 4), and there was significant vertical depletion of mass-basis K (percent of leaf mass;  $r^2 = 0.55$ ,  $p < 0.0001$ ; Figure 4). In fact, N and P were the only foliar nutrients that were not significantly depleted with height on a mass-basis, even though N and P were analyzed in  $\sim 50\%$  more foliar samples than the other elements and thus, we had greater statistical power to detect a relationship with height (Tables S3-S4).

## DISCUSSION

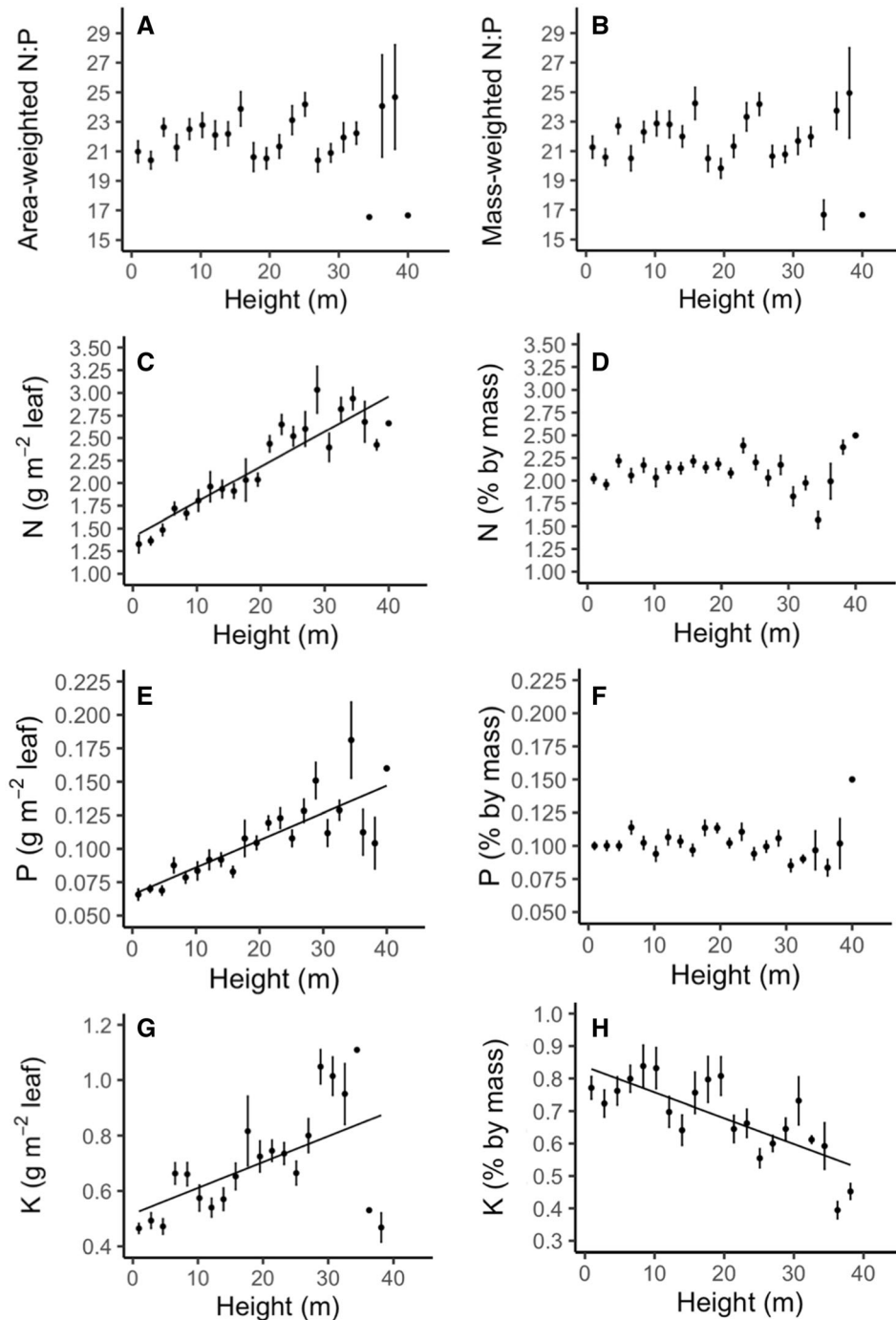
Measures of foliar chemistry, combined with vertical structure of leaves and light, has promise to efficiently model NPP across tropical rainforest

landscapes (Wieczynski and others 2021). However, to our knowledge, ours is the first systematic sampling of vertical nutrient distribution in lowland tropical rainforest foliage. This comprehensive foliar sampling (Figure 1) shows that LMA increase is the driver of vertical nutrient distribution, and that plot-level foliar N:P is marginally sensitive to total soil P, at least across the La Selva landscape.

## Horizontal Trends

Latitudinal differences in foliar stoichiometry have been invoked to suggest that P is particularly important to the tropics. However, lowland tropical rainforest is highly heterogeneous as a biome, and the assumption of P limitation across the biome is likely an over-generalization (Cuevas and Medina 1986; Porder and Hilley 2011; Sanchez 2019; Quesada and others 2020). Soils at La Selva, for instance, have higher total P than many other lowland tropical sites (Porder and others 2006). Yet even across La Selva's relatively P-rich soils, landscape foliar N:P was  $21.8 \pm 0.5$  ( $48 \pm 1$  molar). This is almost double the estimate for temperate broadleaf forests,  $12.6 \pm 0.7$  ( $28.2 \pm 1.5$  molar, 18% lower than our value on a logarithmic scale, McGroddy and others 2004). From plot to plot





**Figure 4.** Height versus canopy-level **A** LAI-weighted average foliar N:P, **B** mass-weighted average foliar N:P, **C** LAI-weighted average area-basis foliar N, **D** mass weighted mean mass-basis foliar N, **E** LAI-weighted average area-basis foliar P, **F** mass-weighted average mass-basis foliar P, **G** LAI-weighted average area-basis foliar K, and **H** mass-weighted average mass-basis foliar K. Each point shows a canopy level, binning leaf height by 1.86 m increments (the height of a sampling tower module). Error bars show  $\pm 1$  SE, calculated with weighted variance (Cochran 1977; Gatz and Smith 1995). Black lines indicate significant regression at  $p < 0.05$ . Significant linear trends were found for area-basis N ( $r^2 = 0.83$ , slope =  $0.04 \{ \text{g m}^{-2} \text{ leaf} \} \text{ m}^{-1}$ ), area-basis P ( $r^2 = 0.67$ , slope =  $0.002 \{ \text{g m}^{-2} \text{ leaf} \} \text{ m}^{-1}$ ), area-basis K ( $r^2 = 0.30$ , slope =  $0.009 \{ \text{g m}^{-2} \text{ leaf} \} \text{ m}^{-1}$ ), and mass-basis K ( $r^2 = 0.58$ , slope =  $-0.008 \{ \% \text{ by mass leaf} \} \text{ m}^{-1}$ ). All regression results for all 10 foliar concentrations are available in Table S3. LMA trends with height were previously reported (Cavaleri and others 2010), as were LAI distribution with height (Clark and others 2008).

**Table 1.** Plot-level foliar chemistry, disaggregated by functional group values with standard errors

| Area-basis (g m <sup>-2</sup> leaf), Area-weighted |  |  |                                       |                                    |
|--|--|--|---------------------------------------|------------------------------------|
|  | Lianas                                 | Palms                                  | Pentaclethra                          | Other trees                        |
| N  | 2.03 <sup>b</sup> ± 0.02, n = 34       | 1.69 <sup>b</sup> ± 0.01, n = 45       | 2.9 <sup>a</sup> ± 0.2, n = 33        | 1.77 <sup>b</sup> ± 0.06, n = 45   |
| P  | 0.094 <sup>b</sup> ± 0.001, n = 32     | 0.091 <sup>b</sup> ± 0.006, n = 45     | 0.13 <sup>a</sup> ± 0.01, n = 32      | 0.086 <sup>b</sup> ± 0.005, n = 44 |
| N:P  | 23.3 <sup>b</sup> ± 0.1, n = 32        | 19.22 <sup>a</sup> ± 0.09, n = 45      | 24.6 <sup>b</sup> ± 0.9, n = 33       | 22.4 <sup>b</sup> ± 0.7, n = 44    |
| K  | 0.701 <sup>a</sup> ± 0.01, n = 21      | 0.522 <sup>a</sup> ± 0.008, n = 28     | 0.71 <sup>a</sup> ± 0.02, n = 19      | 0.68 <sup>a</sup> ± 0.07, n = 28   |
| Ca   | 0.57 <sup>a</sup> ± 0.02, n = 21       | 0.50 <sup>a</sup> ± 0.01, n = 28       | 0.43 <sup>a</sup> ± 0.07, n = 19      | 0.61 <sup>a</sup> ± 0.05, n = 28   |
| Mg   | 0.223 <sup>a</sup> ± 0.007, n = 21     | 0.261 <sup>a</sup> ± 0.009, n = 28     | 0.19 <sup>a</sup> ± 0.02, n = 19      | 0.26 <sup>a</sup> ± 0.09, n = 28   |
| S  | 0.147 <sup>a</sup> ± 0.0032, n = 21    | 0.363 <sup>a</sup> ± 0.006, n = 28     | 0.24 <sup>a</sup> ± 0.02, n = 19      | 0.28 <sup>a</sup> ± 0.09, n = 28   |
| Na   | 0.053 <sup>b</sup> ± 0.002, n = 21     | 0.066 <sup>b</sup> ± 0.002, n = 28     | 0.05 <sup>b</sup> ± 0.01, n = 19      | 0.11 <sup>a</sup> ± 0.01, n = 28   |
| Mn   | 0.045 <sup>b</sup> ± 0.02, n = 21      | 0.064 <sup>a</sup> ± 0.002, n = 28     | 0.026 <sup>b</sup> ± 0.004, n = 19    | 0.029 <sup>b</sup> ± 0.004, n = 28 |
| Al   | 0.0063 <sup>a</sup> ± 0.00001, n = 21  | 0.0068 <sup>a</sup> ± 0.0003, n = 28   | 0.0039 <sup>a</sup> ± 0.0006, n = 19  | 0.4 <sup>a</sup> ± 0.2, n = 28     |
| Zn   | 0.00153 <sup>a</sup> ± 0.00002, n = 21 | 0.00201 <sup>a</sup> ± 0.00003, n = 28 | 0.0019 <sup>a</sup> ± 0.0002, n = 19  | 0.02 <sup>a</sup> ± 0.02, n = 28   |
| Mass-basis (% by mass), Mass-weighted              |  |  |                                       |                                    |
|  | Lianas                                 | Palms                                  | Pentaclethra                          | Other trees                        |
| N  | 2.35 <sup>b</sup> ± 0.01, n = 34       | 1.890 <sup>a</sup> ± 0.008, n = 45     | 2.45 <sup>b</sup> ± 0.06, n = 33      | 2.34 <sup>b</sup> ± 0.06, n = 45   |
| P  | 0.106 <sup>a</sup> ± 0.02, n = 32      | 0.1029 <sup>a</sup> ± 0.0005, n = 45   | 0.11 <sup>a</sup> ± 0.01, n = 32      | 0.110 <sup>a</sup> ± 0.004, n = 44 |
| N:P  | 23.4 <sup>b</sup> ± 0.1, n = 32        | 19.29 <sup>a</sup> ± 0.09, n = 45      | 24.6 <sup>b</sup> ± 0.9, n = 32       | 22.4 <sup>b</sup> ± 0.2, n = 44    |
| K  | 0.84 <sup>bc</sup> ± 0.02, n = 21      | 0.615 <sup>ac</sup> ± 0.008, n = 28    | 0.56 <sup>a</sup> ± 0.06, n = 19      | 0.92 <sup>b</sup> ± 0.08, n = 28   |
| Ca   | 0.64 <sup>bc</sup> ± 0.02, n = 21      | 0.563 <sup>b</sup> ± 0.009, n = 28     | 0.31 <sup>a</sup> ± 0.03, n = 19      | 0.83 <sup>c</sup> ± 0.06, n = 28   |
| Mg   | 0.259 <sup>b</sup> ± 0.009, n = 21     | 0.293 <sup>b</sup> ± 0.004, n = 28     | 0.14 <sup>a</sup> ± 0.01, n = 19      | 0.34 <sup>b</sup> ± 0.03, n = 28   |
| S  | 0.171 <sup>b</sup> ± 0.004, n = 21     | 0.426 <sup>a</sup> ± 0.006, n = 28     | 0.184 <sup>b</sup> ± 0.006, n = 19    | 0.35 <sup>ab</sup> ± 0.08, n = 28  |
| Na   | 0.063 <sup>b</sup> ± 0.003, n = 21     | 0.078 <sup>b</sup> ± 0.002, n = 28     | 0.030 <sup>b</sup> ± 0.006, n = 19    | 0.15 <sup>a</sup> ± 0.02, n = 28   |
| Mn   | 0.047 <sup>b</sup> ± 0.001, n = 21     | 0.098 <sup>a</sup> ± 0.002, n = 28     | 0.018 <sup>b</sup> ± 0.002, n = 19    | 0.040 <sup>b</sup> ± 0.005, n = 28 |
| Al   | 0.0074 <sup>ab</sup> ± 0.0002, n = 21  | 0.0104 <sup>a</sup> ± 0.0003, n = 28   | 0.0034 <sup>ab</sup> ± 0.0005, n = 19 | 0.6 <sup>b</sup> ± 0.2, n = 28     |
| Zn   | 0.00182 <sup>b</sup> ± 0.00004, n = 21 | 0.00236 <sup>a</sup> ± 0.00003, n = 28 | 0.0015 <sup>a</sup> ± 0.0002, n = 19  | 0.02 <sup>a</sup> ± 0.01, n = 28   |

Significant differences ( $p \leq 0.05$ ) are indicated by letters, among the same element and the same basis of measuring concentration.

across La Selva, foliar stoichiometry responded to total soil P (regression tree:  $r^2 = 0.23$ ). That said, total soil P explained a greater portion of foliar N:P variance in a temperate rainforest (linear regression:  $r^2 = 0.55$ , Richardson and others 2008). Thus, our data do not suggest that lowland tropical foliar stoichiometry is unusually responsive to soil P.

We recognize that total P is not the only metric for soil P status. However, in many cases, total P and available P are correlated, including in a survey of the isthmus of Panama ( $r^2 = 0.68$ , Turner and others 2018). Across our plots, which have relatively homogenous parent material (Porder and others 2006), we also expect available and total soil P to be well correlated. Furthermore, the elevated foliar N:P that we observed at P-poor plots was driven by lower foliar P rather than higher foliar N (Figure 2). This landscape-scale finding is consistent with analyses of individual plants (Reich and others 2010) and plant communities (Guo and others 2020; Sardans and Peñuelas 2015), which have shown that decreases in mass-basis foliar N

are accompanied by steeper decreases in foliar P. Thus, given our results, we posit that plots with even lower soil P, which are relatively common in tectonically stable, ancient cratons on granitic material (Porder and Hilley 2011; Porder and Ramachandran 2013), might have even higher foliar N:P.

Community shifts in response to the environment can alter stoichiometry (Sternner and Elser 2002). Given the low foliar N:P of palms (Table 1), a pronounced increase in palm abundance could theoretically reduce landscape foliar N:P. With the more frequent and intense hurricanes expected with climate change (Fraza and Elser 2013; Emanuel 2017), palms may become more abundant in affected tropical forests (Comita and others 2018). However, in our study, the relative abundance of functional groups did not have a clear effect on plot-level foliar N:P. Both foliar N and foliar P (g m<sup>-2</sup> leaf) tended to be higher in plots with a greater percent of leaf area from *Pentaclethra* (Figure 3). *Pentaclethra* abundance also contributed

to the relationship between soil and foliar chemistry: the average percent of leaf mass from *Pentaclethra* doubled across the two unrelated soil thresholds selected by our model to explain plot-level foliar N and P (soil pH of 4.1 and 670 ppm soil P respectively,  $p = 0.04$  for each). *Pentaclethra* form a large majority of the symbiotic N-fixers at La Selva (Menge and Chazdon 2016), suggesting a possible mechanism of this species effect. N-fixation demands P so that the plant's rhizobial partners can incorporate  $N_2$  from the air into foliage (Houlton and others 2008), and the symbiosis is stressed below a soil pH of 4 (Bordeleau and Prévost 1994). Because we did not separate the leaves of symbiotic N-fixers from the rest of trees and lianas, we can only speculate that overall N-fixer abundance tracks *Pentaclethra* abundance.

Community shifts have been shown to maintain tropical forest productivity across soil conditions (Turner and others 2018), with a corresponding turnover in some plant functional traits (Umaña and others 2021). Our findings beg the question of whether foliar stoichiometry changes across soil nutrient gradients as well. Nutrient addition to tropical seedlings has shown little flexibility of foliar N:P within species, though the stoichiometry of stems and roots was more responsive to nutrients (Schreeg and others 2014). This suggests that, without community turnover, strict foliar stoichiometric requirements might lead to nutrient storage in other tissues. In a group of temperate forests with only 26 tree species, large trees appeared to store P in wood rather than substantially alter foliar stoichiometry (Sardans and Peñuelas 2014). It is plausible that, with the diversity of lowland tropical rainforests, community turnover could help to align foliar stoichiometry with soil conditions. Rather than denoting limitation to productivity, as has long been theorized, foliar stoichiometric differences could be another mechanism by which lowland tropical rainforests maintain relatively constant productivity across a wide range of soil conditions.

## Vertical Trends

Many studies have theorized that foliar nutrients (especially N) are optimized across vertical gradients of forest canopies in response to light environment (Takenaka 1989; Hikosaka and others 2016), but others have found weak evidence of this optimization theory (Bond and others 1999) and some suggest that vertical gradients in nutrients minimize the damage due to excess light, rather than optimize light utilization (Kitao and others

2018). At La Selva, however, the remarkably consistent vertical gradients of LMA across the tower transects were more strongly related to height than to light, which points to hydraulic constraints on leaf morphology due to gravity rather than optimization due to light (Cavaleri and others 2010). Because the area-basis concentrations of N, P, and K increase with height, but the mass-basis concentrations do not, these patterns are driven by the LMA gradient. This has also been observed in individual tropical plants (Niinemets and others 2015; Poorter and others 2019). LMA increase with height, in turn, is likely driven by hydraulic constraint. This consistent pattern of LMA increases with height, which drives N, P, and K (Figure 4), as well as foliar respiration (Cavaleri and others 2008), has the potential to greatly simplify the modeling of physiological processes in tropical forests.

In contrast to N and P, foliar concentrations of all other elements decreased with height on a mass-basis (Tables S3 and S4). This is similar to findings from across the Amazon (Lloyd and others 2010) and from a montane rainforest in New Guinea (Grubb and Edwards 1982) where shorter trees had greater mass-basis foliar Ca and Mg. In the Amazon, Mg was enriched on an area-basis in the taller trees, but in our study at La Selva, only N, P, and K were vertically enriched. In the case of K, the mass-basis decrease was small enough relative to the change in LMA that area-basis K increased with height, both across the Amazon and in our study at La Selva. Potassium leaches more readily than foliar N or foliar P, presumably because of the very small size of  $K^+$  (Sardans and Peñuelas 2015), and the uppermost leaves experience the most leaching (Adriaenssens and others 2012). Given the importance of these elements for photosynthesis (Mercer and others 1962; Epstein and Bloom 2005), these results bear further consideration as the vertical distribution of leaves and their chemistry is integrated into photosynthetic models.

## CONCLUSION

Our comprehensive foliar sampling of a lowland tropical rainforest suggests that plot-level variability of foliar chemistry reflects soil conditions, and that plot-level foliar N:P in particular is an indicator of soil P status. Furthermore, we show that landscape-scale vertical nutrient enrichment is the result of LMA increase, as has previously been reported within individual tropical plants. Landscape photosynthetic models often consider foliar N alone, but we show concomitant vertical increase

of foliar P and K. Finally, our data hint that stoichiometric flexibility may help to maintain productivity on low P soils. Testing this idea will require additional work in lower P sites.

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## Declarations

**Conflict of Interest** The authors declare no conflict of interest.

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