REVIEW AND SYNTHESIS

Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis

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Abstract

Tropical rain forests play a dominant role in global biosphere-atmosphere CO_2 exchange. Although climate and nutrient availability regulate net primary production (NPP) and decomposition in all terrestrial ecosystems, the nature and extent of such controls in tropical forests remain poorly resolved. We conducted a meta-analysis of carbon-nutrient-climate relationships in 113 sites across the tropical forest biome. Our analyses showed that mean annual temperature was the strongest predictor of aboveground NPP (ANPP) across all tropical forests, but this relationship was driven by distinct temperature differences between upland and lowland forests. Within lowland forests (< 1000 m), a regression tree analysis revealed that foliar and soil-based measurements of phosphorus (P) were the only variables that explained a significant proportion of the variation in ANPP, although the relationships were weak. However, foliar P, foliar nitrogen (N), litter decomposition rate (k), soil N and soil respiration were all directly related with total surface (0–10 cm) soil P concentrations. Our analysis provides some evidence that P availability regulates NPP and other ecosystem processes in lowland tropical forests, but more importantly, underscores the need for a series of large-scale nutrient manipulations – especially in lowland forests – to elucidate the most important nutrient interactions and controls.

INTRODUCTION

More than a quarter century ago, Vitousek (1984) wrote that, '[inferential] analyses suggest that phosphorus (P) but not nitrogen (N) availability limits litterfall in a substantial subset of intact tropical forests.' Since then, several global syntheses of both foliar and litterfall nutrient data have indicated that P appears to be less abundant than N (relative to plant demand) in many tropical forest sites (McGroddy *et al.* 2004a; Reich & Oleksyn 2004; Townsend *et al.* 2007). Whether these patterns indicate P limitation of net primary production (NPP)

or not, however, remains an open question, as tropical forests often have sufficient labile P in surface soils to satisfy the growth requirements of NPP (Johnson *et al.* 2003). This incomplete understanding has global implications: tropical forests contain *c.* 25% of the world's terrestrial biomass and soil C (Jobbagy & Jackson 2000), exchange more water and carbon dioxide (CO_2) with the atmosphere than any other biome (Foley *et al.* 2005), and account for at least one-third of global annual terrestrial NPP (Grace *et al.* 1995; Phillips *et al.* 1998). Thus, identifying the relationships between nutrient availability and C cycling is critical for accurately predicting how these forests may

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respond to (and control) many aspects of natural and human-caused environmental change (Hungate *et al.* 2003; Thornton *et al.* 2007; Bonan & Levis 2010; Zhao & Running 2010; Townsend *et al.* 2011).

In temperate and high latitude ecosystems, a wealth of direct evidence (i.e. data from nutrient manipulation experiments) suggests widespread N or N/P co-limitations to NPP (Aber *et al.* 1991; Gough *et al.* 2000; Elser *et al.* 2007), and some data also suggest that N limitation may be common in montane tropical forests on minimally weathered soils (Tanner *et al.* 1998). Direct evidence of nutrient limitation in lowland tropical forests is rare, but indirect proxies indicate an abundance of N relative to P. These include: high foliar (McGroddy *et al.* 2004a; Reich & Oleksyn 2004; Townsend *et al.* 2007) and litter (Vitousek 1984) N : P ratios; potentially high N fixation (Cleveland *et al.* 1999; Houlton *et al.* 2008) and nitrification rates (Robertson 1984); large N trace gas emissions (Robertson & Tiedje 1988; Matson & Vitousek 1990) and N_2 fluxes (Houlton *et al.* 2006); elevated soil and foliar $\delta^{15}N$ values (Martinelli *et al.* 1999; Nardoto *et al.* 2008); rapid internal N cycling (Silver *et al.* 2005; Templer *et al.* 2008); and hydrological export of biologically available N (Hedin *et al.* 2009). These empirical data have been used in conjunction with the theoretical framework provided by Walker & Syers (1976) – which predicts P poverty on highly weathered soils such as the Oxisols and Ultisols that dominate the lowland tropics – to argue that P is likely to limit NPP in lowland tropical forests.

Nevertheless, there is some reason to question the prevailing model of 'N-rich' and 'P-poor' lowland tropical systems. For example, the Walker & Syers (1976) model may not be appropriate for the tropics as a whole, which vary widely in soil age (Porder & Hilley 2010), and virtually every other factor that could affect nutrient availability (Townsend *et al.* 2008). Walker & Syers (1976) focused exclusively on soil age and the idea of a steadily declining source of rock-derived nutrients through time, but more recent work has shown that this construct is too simplistic: wet sites can experience nutrient depletion in a relatively short time (i.e. 10^4–10^5 years; Chadwick *et al.* 1999), different substrates may lose P at very different rates (Porder *et al.* 2007), and thus time should be considered in concert with other state factors to explain nutrient depletion in tropical soils (Porder & Hilley 2010). In addition, erosion can remove highly weathered soils and expose fresh parent material to weathering, thereby maintaining a source of new rock-derived elements to the ecosystem (Bern *et al.* 2005; Porder *et al.* 2007). This phenomenon may help explain more pronounced responses to N than to P additions in tropical montane forests, where relatively rapid rates of erosion may replenish P, but not N (e.g. Tanner *et al.* 1998), although erosion rates can be rapid in lowland settings as well. Likewise, the deposition of putatively rock-derived nutrients via both marine aerosols and dust may provide large or even dominant inputs of P to some systems (Chadwick *et al.* 1999; Okin *et al.* 2004; Pett-Ridge *et al.* 2009). These data support the argument that the tropics exhibit tremendous biogeochemical heterogeneity (Townsend *et al.* 2008), and suggest that a blanket model of P poverty in the lowland tropics may be an oversimplification.

Ultimately, the best tests of potential nutrient limitation emerge from direct manipulations of nutrient supply, and analysing results from multiple experiments can lend greater insight into large-scale patterns. For example, a recent global meta-analysis of fertilisation experiments concluded that limitation by both N and P is more common across terrestrial ecosystems than is limitation by either element alone (Elser *et al.* 2007). However, the Elser *et al.* (2007) meta-analysis included results from only one fertilisation experiment conducted in a primary forest in the lowland tropics in which N and P were added in a full-factorial design, and where aboveground NPP (ANPP) (i.e. fine litterfall and/or biomass growth increment) was included as a response variable (Mirmanto *et al.* 1999). There are a few more studies from upland and secondary lowland forests (Tanner *et al.* 1998; Davidson *et al.* 2007), but the paucity of data from fertilisation experiments conducted in tropical forests precludes a meta-analysis of how NPP responds to direct manipulations of potentially limiting elements.

Given the lack of data from fertilisation experiments in tropical forests, here we used meta-analyses to ask, *How does NPP vary with climate, N and P availability across the tropical forest biome?* In addition, given the fact that P is widely hypothesised to limit NPP in many lowland tropical forests (Vitousek 1984; Lambers *et al.* 2008; Hedin *et al.* 2009), we were particularly interested in exploring possible relationships between soil P availability and multiple C cycling metrics among lowland forest sites. Like other researchers who have explored this question over the past three decades, we were forced to explore potential nutrient constraints using indirect metrics. Correlational analyses are not direct tests of nutrient limitation, and thus conclusions drawn using such approaches have inherent weaknesses. However, indirect analyses can provide important insight and help identify where our understanding is poor, and where direct tests are most needed (e.g. Vitousek 1984; Vitousek & Sanford 1986).

In addition, we note that elements other than N or P may also be important in regulating ecosystem function in tropical forests (Cuevas & Medina 1988; Barron *et al.* 2008; Kaspari *et al.* 2008), but we focused on relationships between N and P and the major features of the tropical C cycle for three reasons. First, recent global syntheses underscore a long-held belief that N, P or both of these elements limit multiple processes in many terrestrial ecosystems worldwide (Elser *et al.* 2007; LeBauer & Treseder 2008). Second, given the dominant role of the tropics in the global C cycle, multiple studies have highlighted the need to understand how N and P regulate tropical C storage and exchange (Bonan & Levis 2010; Townsend *et al.* 2011). Third, data describing N and P concentrations in plants and soils are relatively common, whereas those describing other nutrients are much more limited.

METHODS

We assembled data from the literature and accessible databases and conducted a meta-analysis of relationships between climate, nutrient status and multiple metrics of both above- and below-ground C cycling in upland and lowland moist and wet tropical forests. All data were obtained either from the literature or from accessible electronic databases (e.g. National Center for Ecological Analysis and Synthesis [NCEAS], Oak Ridge National Laboratory Distributed Active Archive Center [ORNL DAAC]). To locate published data sources, we conducted searches using online databases (e.g. the ISI Web of Science) or search engines (e.g. Google Scholar) using the search terms: tropical forest, nutrient, nutrient limitation, nitrogen, phosphorus, primary productivity, decomposition and soil respiration. Once relevant papers were located, references therein were checked in an attempt to locate others that may not have been accessible using the ISI database. We also included some data published in previous syntheses (Elser *et al.* 2007; Townsend *et al.* 2007; LeBauer & Treseder 2008; Quesada *et al.* 2009), and examined relevant references cited therein for additional data.

In some cases, values for a given characteristic (e.g. foliar P) for each site represent means of all available data for that characteristic. For example, within a site, when foliar nutrient concentrations were assessed for multiple species, we used those data to generate a simple (site) mean value for that characteristic. When multiple data were available for a single species characteristic (e.g. foliar nutrients), those data were averaged to generate a species mean, and species means were used to calculate the site mean for that characteristic. We did not weight the foliar nutrient data by the relative abundance of species. Data collected multiple times (e.g. seasonally) were averaged to generate a single mean. Finally, data from multiple sites within a single geographical region (e.g. spanning topographical, lithologic or pedogenic gradients) were treated as separate sites in the database.

In sum, the final database included data from 113 tropical forest sites, although not all data were available from all sites. Our analysis included data from both upland ($n = 32$) and lowland forests ($n = 81$) located within tropical latitudes ($\pm 23.5°$N and S), and all sites in the database were either moist or wet tropical forests receiving a minimum of 1300 mm mean annual precipitation (MAP) (See Table S1). The majority of data were from sites in the Amazon Basin – the largest tract of remaining tropical forest in the world – with fewer sites in North and Central America and Asia, and only one site in Africa and Australia respectively (Fig. 1). Data were entered on separate online accessible electronic data entry forms available through NCEAS and imported into a single database prior to analysis. We selected data that were obtained using consistent sampling (e.g. soil depth) and measurement techniques, and all data were converted to common units prior to analysis. Data used in this analysis are available at the public repository at NCEAS (http://knb.ecoinformatics.org/knb/style/skins/nceas/).

To assess relationships between nutrient availability and NPP, we assembled data on the following C cycle components: (1) total fine litterfall (sum of leaves, twigs < 2 mm diameter and reproductive parts, (2) biomass growth increment (based on measured increases in tree stem diameters), (3) ANPP, calculated as the sum of observed litterfall and biomass growth increment, (4) litter decomposition rate (k; the decomposition rate constant, a value that describes the rate of decomposition of litter on the forest floor) and (5) soil respiration (soil CO_2 flux). For sites in which data describing only one component of ANPP were available, ANPP was modelled using the observed relationships between litterfall or biomass increment and ANPP and equations generated using data from sites where they were available (Figure S1).
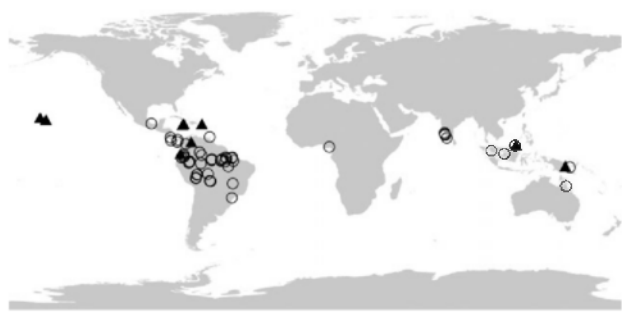
Figure 1 Map illustrating the global distribution of the tropical forest sites used in the meta-analysis. Open circles denote lowland forest sites (< 1000 m) and triangles denote upland forest sites (> 1000 m).

Next, we explored relationships between ANPP (the response variable) and a number of predictors, including climate (mean annual temperature [MAT] and MAP), soil type, nutrient cycling variables (foliar N and P, surface soil [0–10 cm] inorganic N (nitrate [NO_3^-] and ammonium [NH_4^+]) content), decomposition (k) and total surface soil N and P content. Estimates of 'available soil P' may be more appropriate than total soil P, but the diverse indices of P availability meant that comparable data were too sparse to include in the meta-analysis. Moreover, Silver (1994) found that total P and indices of available P were similarly related to litterfall nutrient use efficiency in a wide range of tropical forests, probably due to the exchange between labile and refractory soil P pools (Richter et al. 2006; Syers et al. 2008). Finally, we excluded data from two sites in the Hawaiian Islands (Thurston [300 years] and Laupahoehoe [20 kyr]), due to a combination of very young soil ages, substantial element inputs from rapidly weatherable volcanic ash and low overall tree diversity (Vitousek 2004), and because these two sites are in many ways significantly dissimilar from the majority of tropical forest sites used in the analysis. Data from more successionally advanced sites with more weathered substrates in the Hawaiian Archipelago (e.g. Maui and Kaua'i) were included in the analysis.

Statistical analysis

The relationship between the response variable (ANPP) and each of the predictor variables was first analysed using a classification and regression tree (CART) analysis (McCune & Grace 2002). We performed the regression tree analysis in two steps. First, we related ANPP to all predictor variables including a number of broadly defined variables (e.g. soil type). Next, we conducted a second CART analysis in which we analysed upland and lowland forests separately (see below). CART was implemented using the rpart library in R 2.11.1 (R development Core team). Regression trees were initially over-fit, and optimal tree sizes were determined using cost-complexity pruning based on 10-fold cross-validation (Venables & Ripley 2002).

We chose to use CART for several reasons. First, CART is ideally suited for ascertaining the relative importance of predictors in explaining variation in the response variable. CART can handle unbalanced data with missing values – a characteristic of this dataset – and one that can preclude analysis using other regression or structural equation approaches (De'ath & Fabricius 2000). Regression trees are also invariant to monotonic transformations of the predictor variables. Finally, CART effectively handles data that contain higher order interactions among variables (like the nutrient interactions that have been hypothesised in tropical forests; Townsend et al. 2011). However, CART also has some limitations. CART produces a hierarchical tree-like classification of a dichotomous form to classify observations into defined groups, and thus it can be difficult to assess the functional form (e.g. linear, curvilinear, etc.) of the relationship between the response and the predictors at each split. In addition, CART can have difficulty modelling smooth functions, and is prone to over-fitting such that small changes in training data can result in a different series of splits (Elith et al. 2008).

Given this, following the CART analysis, we used regression and correlation analysis (Pearson-product moment) to more thoroughly investigate the relationships that emerged in the CART analysis of the lowland forest site data. We focused on lowland forests for several reasons. First, they play a dominant role in the global C cycle, yet the nature and extent of nutrient limitation of NPP in lowland forests is

poorly understood. Second, lowland tropical forests represent a much larger proportion of the tropical forest biome area than do montane forests (Bruijnzeel *et al.* 2011). Finally, the relatively large number of lowland sites (i.e. 81) in the database allowed us to confidently explore multiple possible relationships between C cycling, climate and nutrients. Correlation analyses were performed using SPSS version 19 for Windows (SPSS, Chicago, IL, USA), and in all cases significance was determined at $P < 0.05$.

RESULTS

The first regression tree (including climate and soil variables from all sites in the database) explained 29% of the variance in tropical ANPP (Fig. 2A), and MAT was the most important predictor, explaining the majority (20%) of the explained variance in ANPP (Fig. 1). In cool sites (< 18.1 °C), ANPP averaged 8.92 Mg ha^{-1} year^{-1}, whereas ANPP in warmer sites (> 18.1 °C) was higher (> 14 Mg ha^{-1} year^{-1}). In warm sites, the next split, which explained 9% of the remaining variance, was based on soil type: one branch included sites with Ultisols or Oxisols with relatively low ANPP (14.74 Mg ha^{-1} year^{-1}), and the other consisted of forests growing on other soil types (e.g. Entisols, Inceptisols or Histosols) with relatively high ANPP (18.76 Mg ha^{-1} year^{-1}) (Fig. 2A).

The emergence of soil order as a significant predictor of ANPP among the warm tropical forest sites in the initial CART analysis reflects potential influences of soil fertility on productivity. In addition, because of the strong relationship between temperature

and elevation, and in light of the widely held belief that P limits ANPP in lowland tropical forests, we analysed the data from upland and lowland forests separately. In classifying 'lowland' forests, we chose a threshold elevation of 1000 m (sensu Holdridge *et al.* 1971). This threshold corresponded to an MAT breakpoint of 20.7 °C (as opposed to the 18.1 °C suggested by the CART analysis); 'upland' forests included all forests above 1000 m (20.7 °C MAT). In contrast to the importance of temperature in explaining variations in ANPP observed across all the data (Fig. 1), MAT did not emerge as a strong or significant predictor of ANPP in either the upland or the lowland
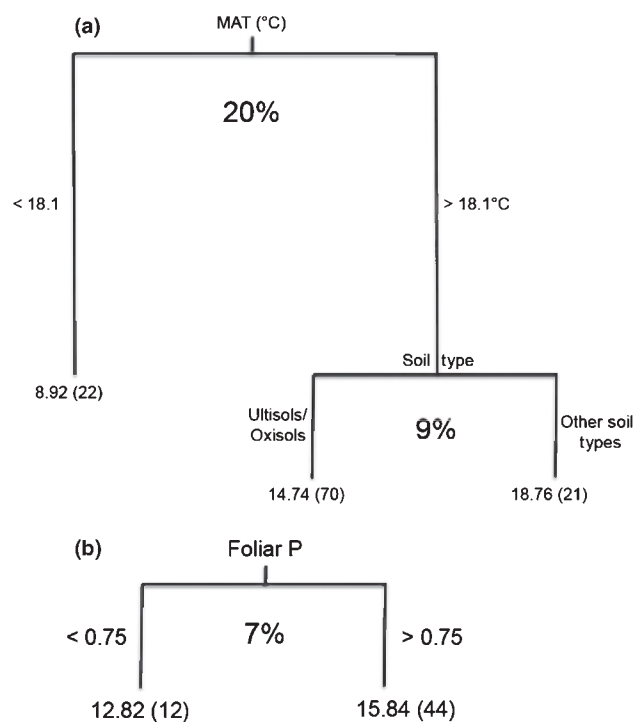
Figure 2 Regression tree showing: (a) how climate and soil type explain variance in ANPP across the tropical forest biome; and (b) how foliar P explains variance in ANPP across lowland tropical forests. Predictor variables are depicted at the top of each branch, predictor variable thresholds at the side of each branch and the mean ANPP (including the number of observations in parentheses) is reported below the terminal nodes. The height of each branch indicates the relative proportion of the total sum of squares explained by that split.
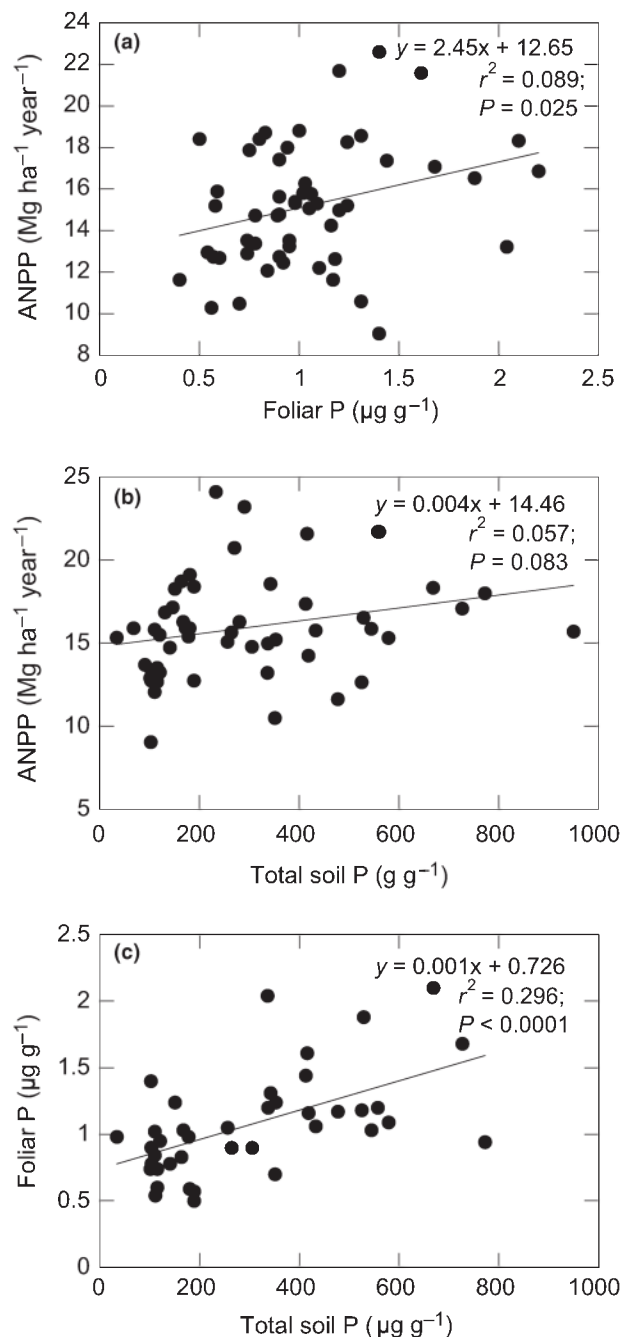
Figure 3 Relationships among P cycling variables and ANPP in lowland tropical forests. (a) Foliar P vs. ANPP; (b) total soil P vs. ANPP; (c) total soil P vs. foliar P.

forest data analysis (Supplementary Figure S2). In the lowlands, the optimal tree explained *c.* 7% of the variance in ANPP and was based on a single split of foliar P (Fig. 2B). In the low foliar P sites (i.e. < 0.75 μg P g^{-1}), ANPP averaged 12.82 Mg ha^{-1} year^{-1}, whereas ANPP in the high foliar P sites (> 0.75 μg P g^{-1}) averaged 15.84 Mg ha^{-1} year^{-1} (Fig. 2B). Given that CART allows surrogate splits to be assessed, we note that soil P was the next best predictor for the primary split of the lowland forest data and had similar explanatory power to foliar P. This apparent relationship was confirmed using regression analysis (Fig. 3), which showed a positive linear relationship between foliar P and ANPP and ($P = 0.025$) and a similar (though not significant) relationship between total soil P and ANPP ($P = 0.083$). There was also a stronger direct relationship between soil P and foliar ($P < 0.0001$; Fig. 3).

Informed by the initial CART analysis (which revealed relationships between P metrics and ANPP), we subsequently conducted a series of bivariate comparisons using correlation analyses to explore potential relationships between total soil P and foliar N, total soil N, decomposition rate (k) and soil respiration in the lowland forest sites (Table 1). There were significant positive relationships between total soil P and both foliar N and total soil N, and across all lowland forest sites from which data were available, total soil P was strongly related with both decomposition rate (k) and soil respiration rate (Fig. 4; Table 1).

DISCUSSION

Direct climate controls over ANPP are well established (e.g. Chapin *et al.* 2002; Zhao & Running 2010), and substantial variations in both temperature and precipitation across the tropical forest biome have been shown to influence multiple aspects of the tropical C cycle (e.g. Saleska *et al.* 2003; Schuur 2003; Powers *et al.* 2009). Our analysis showed that MAT explains the largest proportion of the variance in ANPP across all tropical forests (Fig. 2a). However, temperature was only important in broadly distinguishing tropical forest types; the first split in the regression tree analysis effectively separated upland (i.e. cool forests with low ANPP) from lowland (i.e. warm forests with higher ANPP) sites (Fig 2A). When analysing upland or lowland forests in isolation, the relationship between temperature and ANPP was not significant (Figure S2). Thus, although climate organises plant productivity globally (Chapin *et al.* 2002) and helps explain large-scale variations in ANPP across tropical forests as a whole, our analysis shows that within still large regions (e.g. upland or lowland tropical forest), MAT had little explanatory power. Similarly, there was not a significant relationship between MAP and ANPP in either the pan-tropical or the upland/lowland tropical forest analyses (Figure S2). This was somewhat surprising, given the decline in NPP in sites with

Table 1 Summary of Pearson correlation coefficients between total soil P and covariates, *P*-values for individual pair-wise comparisons and adjusted *P*-values for multiple comparisons. *P*-values were adjusted using Holm's sequential Bonferroni correction (Holm 1979)

	Total soil P		
	r	*P*-value	Corrected *P*-value
Soil respiration	0.60	0.03	0.03
Total soil N	0.34	0.012	0.024
k	0.70	0.007	0.021
Foliar N	0.44	0.004	0.016
Foliar P	0.55	< 0.0001	< 0.00005
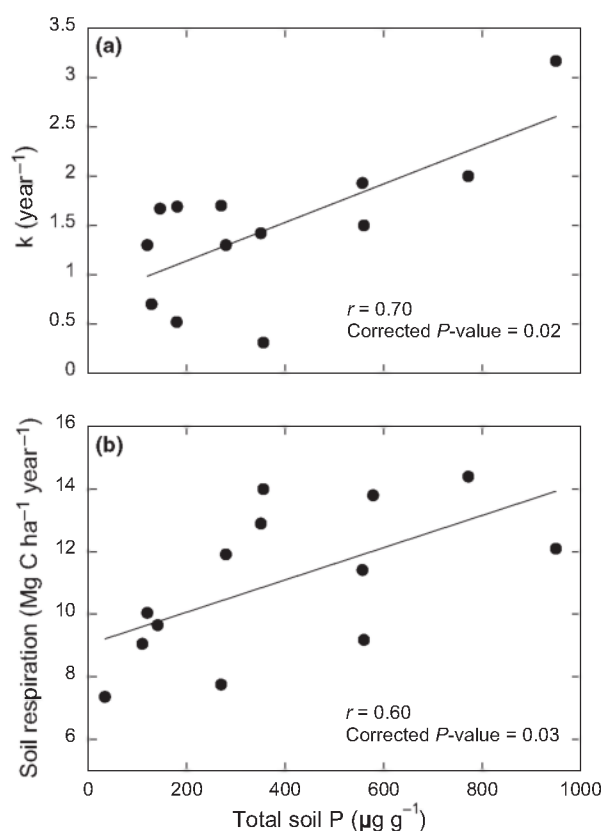
Figure 4 Total soil P vs.: (a) decomposition (k); and (b) soil respiration in lowland tropical forest. *R*-values represent Pearson correlation coefficients.

high MAP previously reported (e.g. Schuur 2003). However, our analysis included more data from very wet lowland sites (i.e. > 3500 mm year^{-1}) – sites that had higher ANPP than most of the wet upland forest sites included in Schuur (2003), perhaps accounting for the difference (See Table S1).

If MAT and MAP do not explain variations in tropical forest ANPP, what does? The regression tree analysis indicated that none of the climate or nutrient predictor variables we used explained a significant proportion of the variability in upland forest ANPP, despite direct evidence of N limitation in some upland tropical forests on young substrates (reviewed in Tanner *et al.* 1998). However, it is important to note that the upland forest database included a relatively small number of sites (i.e. 32), perhaps limiting our ability to detect possible relationships. In addition, other work has shown that N limitation may not exist in high elevation forests that occupy unusually stable surface soils (e.g. Vitousek & Farrington 1997) or in upland forests on older substrates (Silver *et al.* 2011).

Direct tests of nutrient limitation in primary lowland tropical forests are rare, but in the three experiments that have been done, two showed that P limits fine litterfall production (Wright *et al.* 2011). In this analysis, after MAT, soil type was next in importance in explaining variance in ANPP across all sites (Fig. 2a), which is consistent with data showing that soil nutrient availability varies with soil developmental stage (Walker & Syers 1976; Vitousek & Farrington 1997). That said, we note that the Walker & Syers (1976) model – and subsequent generalizations about lowland forest nutrient limitation – have focused on P-constraints with soil age. However, total soil P in

the lowland sites represented in our database varied by more than an order-of-magnitude, suggesting that simple assumptions about nutrient availability or nutrient limitation based on soil developmental stage may be overly simplistic (Table S1).

The only metrics that predicted lowland forest ANPP to any extent were P cycling metrics (foliar and soil P), implying that P may play a role in broadly structuring lowland tropical forest ANPP (Fig. 3). It is important to note, however, that the relationships were weak. For example, the best predictor of ANPP (foliar P) explained < 10% of the variation (Fig. 3A) in both the CART (Fig. 2) and regression analyses (Fig. 3). Similarly, there was an apparent relationship between soil P and ANPP, but that relationship was also weak ($r^2 = 0.057$) and did not meet our threshold for significance ($P = 0.083$; Fig. 3b). As with past inferential studies (e.g. Vitousek 1984; Martinelli *et al.* 1999; Townsend *et al.* 2007), we stress that our analyses do not provide evidence – either for or against – nutrient limitation *per se*. That said, despite a wealth of indirect evidence (e.g. Vitousek 1984; McGroddy *et al.* 2004a; Paoli *et al.* 2005; Paoli & Curran 2007; Townsend *et al.* 2007; Reich *et al.* 2009), and some direct evidence (Mirmanto *et al.* 1999; Wright *et al.* 2011) for widespread P limitation in the lowland tropics, our analysis revealed only weak relationships between metrics of P cycling and ANPP.

Two types of explanations exist for the weak relationships between P availability and ANPP we observed across the lowland tropics, and it is likely that both contribute to some extent. First, methods for measuring both the predictor (e.g. climate or soil nutrient availability) and response variables (i.e. ANPP) have multiple known limitations. For example, ANPP in tropical forests is notoriously difficult to measure, methods for assessing ANPP vary widely between sites, and ANPP is frequently estimated from an incomplete set of measured ANPP metrics (Clark *et al.* 2001). In addition, measured estimates of ANPP frequently reflect fine litterfall inputs and biomass increment, and often do not acknowledge the potential importance of other aspects of ANPP (e.g. losses to herbivores, contributions of coarse woody debris), potentially biasing estimates. Complicating matters, in many sites, only one metric of ANPP is measured regularly (e.g. litterfall or biomass increment), and for more than half the sites in our database, we were forced to estimate ANPP based on relatively weak relationships between biomass increment or litterfall and ANPP. Moreover, these methodological concerns are not restricted to ANPP; as has been suggested elsewhere, logistical difficulties in accurately sampling and assessing nutrient availability (Stark & Hart 1997) may combine to mask stronger associations that actually do exist across environmental gradients. For example, current methods for assessing soil N or P availability (e.g. episodic measurements using chemical extractions) may not accurately reflect true availability to either microbes or plants. Such methodological concerns can challenge meta-analyses for any biome, but are likely to be especially problematic in tropical forests, especially for ANPP (see Clark *et al.* 2001).

Second, it is possible that a sizable fraction of the variance in tropical ANPP may be explained by factors other than those directly considered here. For example, although few multi-nutrient manipulations exist, in those that do, some evidence has emerged indicating control by nutrients other than N or P (Cuevas & Medina 1988; Barron *et al.* 2008; Kaspari *et al.* 2008; Wright *et al.* 2011). Furthermore, the stature and complexity of tropical forest canopies drives considerable variation in photosythetically active radiation, and light availability may directly limit ANPP across gradients in both climate

and nutrient availability (Wright & van Schaik 1994). Next, although relatively easy to measure and readily available in the literature, simple climate metrics like MAT and MAP may be insufficient to capture the most important effects of climate on ANPP (e.g. the effects of seasonal variations in precipitation that are not reflected in MAP). Finally, the high species diversity of most tropical canopies promotes local and regional heterogeneity in N and P allocation and cycling (Townsend *et al.* 2008) that is linked to a broad suite of life history and evolutionary constraints; how those factors, along with variation in other levels of ecological organisation (e.g. herbivory and other plant-animal interactions; Fine *et al.* 2004), combine to regulate ANPP in the tropics remains poorly understood. The existence of such heterogeneity, along with multiple possible drivers of the C cycle at both local and regional scales, implies that detecting broad, ecosystem-level correlates will require a thorough systematic sampling at any given site (Townsend *et al.* 2008). Such thorough sampling is rarely reflected in available data, including many of those used in the current database, but our analysis suggests that such a strategy may be critical.

Although P metrics accounted for a small proportion of the observed variance in ANPP, our analysis does provide stronger evidence of links between P availability and belowground C cycling. For example, we found significant relationships between total soil P and both decomposition (k) and soil respiration rates (Table 1; Fig. 4). Data from experiments directly investigating the effects of nutrients on decomposition in the tropics are nearly as scarce as those on aboveground responses (but see Hobbie & Vitousek 2000; McGroddy *et al.* 2004b; Cleveland *et al.* 2006; Kaspari *et al.* 2008; Powers *et al.* 2009), but previous research at the plot scale has shown similar direct relationships between litter decomposition and P availability. For example, Wieder *et al.* (2009) showed that although litter lignin : N ratios most strongly predict decomposition rates in temperate ecosystems (Melillo *et al.* 1982), lignin : P ratios were the best predictor of litter decomposition rates in a P-poor tropical forest in Costa Rica. In another experiment, Kaspari & Yanoviak (2008) showed that litter C : P ratios positively correlated with increases in forest floor organic matter accumulation, suggesting that decomposition and nutrient turnover slow with increasing C : P. Similarly, Hobbie & Vitousek (2000) showed that P limits litter decomposition in forests on highly weathered, P-poor sites in Hawaii. Other studies have observed high P immobilization during decomposition in P-poor soils (McGroddy *et al.* 2004b) without simultaneous increases in mass loss rates, but litter P immobilization could translate into more rapid and complete decomposition of dissolved organic matter leached from litter in P-poor soils (Cleveland *et al.* 2002). Finally, P availability has been shown to limit soil respiration in low-P tropical soils (Cleveland & Townsend 2006). Although this result could indicate plant root responses to soil P availability (e.g. Ostertag 2001), these studies are consistent with our results showing that decomposition broadly scales with P availability across the lowland tropical forest sites in the database. Given the relatively high P demand and low stoichiometric plasticity of decomposers relative to plants (Cleveland & Liptzin 2007), it is perhaps not surprising that P-constraints over cellular growth and metabolism may be more apparent in metrics of decomposition than in those used to assess ANPP.

Our data also provide evidence suggesting that interactions between the N and P cycles in lowland tropical forests (e.g. Treseder & Vitousek 2001) may also have implications for C uptake and loss (Vitousek *et al.* 2009; Townsend *et al.* 2011). For example, we found correlations between total soil P and both soil N and foliar N

(Table 1), and we suggest these links may emerge because of an underlying control by P that is expressed in two ways. First, N fixation rates often increase with P availability (e.g. Pearson & Vitousek 2001; Reed *et al.* 2007), and under high P conditions, relatively high N inputs via N fixation could result in both higher soil and foliar N content. Second, our data suggest that P regulation of the N cycle goes beyond its effects on N fixation, and that P exerts a broader level of control over soil N turnover. For example, the observed links between total soil P and both litter decomposition (k) and soil respiration (Fig. 4) imply that rates of decomposition in sites where P is abundant may drive parallel increases in the rate at which N becomes available for plant uptake, helping to explain the observed relationship between soil P and foliar N (Table 1).

As a whole, our analysis provides some evidence that soil P effects on the tropical C cycle may be manifested in both direct and indirect ways, as has been hypothesised elsewhere (Reich *et al.* 2008, 2009; Vitousek *et al.* 2010; Townsend *et al.* 2011). First, the relationship between metrics of P availability and ANPP (Fig. 2) are at least consistent with previous claims of direct P controls on ANPP in lowland tropical forests. In addition, the links between soil P and both decomposition (Fig. 4) and N pools (Fig. 3 and Table 1) imply that P-constraints may also operate indirectly via controls on N turnover and N availability. Given the widely recognised importance of foliar N content to photosynthetic rates (Field & Mooney 1986; Reich *et al.* 1997; Wright *et al.* 2004; Warren *et al.* 2005), the soil P-foliar N correlation suggests an additional mechanism by which P may act as the underlying constraint on ecosystem C uptake (*sensu* Vitousek *et al.* 2010). Vitousek *et al.* (2010) described differences between proximate and ultimate nutrient limitation, and argued that in many ecosystems, proximate constraints by N may 'mask' an ultimate limitation by P. Based on our results, low soil P may pose a broad constraint on litter decomposition and soil organic matter turnover in the tropics, with the highest rates of decomposition occurring where P is relatively abundant. In turn, rapid decomposition of P-rich organic matter should lead to simultaneous increases in rates of N mineralisation and/or in relatively high rates of N fixation (Reed *et al.* 2007; Houlton *et al.* 2008), promoting both higher soil N availability and greater overall ecosystem N stocks. Similarly, elevated N may also enhance P availability, mainly by meeting the high N requirements of phosphatase production (Olander & Vitousek 2000; Treseder & Vitousek 2001; Houlton *et al.* 2008).

However, although our analysis does provide additional evidence suggesting the importance of P in ecosystem processes in lowland tropical forests, perhaps more importantly, it also highlights that our understanding of the role of nutrients (and climate) in regulating ecosystem processes in tropical forests is far from complete. In 1998, Tanner and colleagues stated: 'Many more experiments, especially in lowland forests, are needed to test our speculation that P usually limits productivity in tropical lowland rain forests and that N limits productivity in tropical montane rain forests.' More than a decade later and with only a handful of notable exceptions (e.g. Mirmanto *et al.* 1999; Kaspari *et al.* 2008; Wright *et al.* 2011), we still lack such experiments, and we thus lack the ability to make broad generalizations about the nature of nutrient limitation in this important biome.

Thus, to more clearly identify the nature and strength of nutrient limitation in the lowland tropics, and to distinguish the role of nutrients from other potential drivers (e.g. climate, species traits, soil physical properties, community-level interactions, etc.), multiple manipulative experiments that span important environmental gradients are urgently needed. These are especially important in the lowlands, given both the paucity of data and the enormous importance of lowland forests to the global C cycle and climate (e.g. Zhao & Running 2010). As a starting point, given the evidence presented here and elsewhere of the multiple potential ways in which P may constrain both the C and N cycles throughout the lowlands, we would recommend a series of fertilisation experiments that span the more than order-of-magnitude variation in soil P that exists across lowland tropical forests (Supplementary Table S1). In addition, a series of nutrient manipulations spanning temperature, precipitation and/or soil fertility gradients would be particularly valuable in elucidating how tropical forests may respond to global change. We also note that given the significant variance in canopy nutrient contents (Fyllas *et al.* 2009; Gleason *et al.* 2009) and life history strategies (Denslow 1980) that occur in most tropical forests, manipulation experiments that can capture complete ecosystem scale feedbacks and consequences will require large plots, thorough sampling protocols across species and long-time horizons. These facts pose significant challenges on both financial and logistical fronts, but such efforts are critical to an improved understanding of how tropical forests will respond to a suite of global changes, including both current (e.g. Li *et al.* 2008) and forecasted climate and atmospheric change (Thornton *et al.* 2007; Loarie *et al.* 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Linear relationships between (a) litterfall and (b) biomass increment and ANPP. Relationships were used to generate ANPP values when either component was unavailable in the literature.

Figure S2 ANPP vs. MAT (a and b) and MAP (c and d) in the upland and lowland forest sites in the database.

Table S1 Maximum (Max.), minimum (Min.) and median values for the climate, carbon and nutrient cycling variables used in the analysis. The 'uplands + lowland' column represents calculated values for all sites in the database. The 'lowlands' column represents values from sites with MAT > 20.7 °C, and the 'uplands' column represents values from sites with MAT < 20.7 °C.

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