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# Functional traits determine tree growth and ecosystem productivity of a tropical montane forest: Insights from a long-term nutrient manipulation experiment

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## Abstract

Trait-response effects are critical to forecast community structure and biomass production in highly diverse tropical forests. Ecological theory and few observation studies indicate that trees with acquisitive functional traits would respond more strongly to higher resource availability than those with conservative traits. We assessed how long-term tree growth in experimental nutrient addition plots (N, P, and N + P) varied as a function of morphological traits, tree size, and species identity. We also evaluated how trait-based responses affected stand scale biomass production considering the community structure. We found that tree growth depended on interactions between functional traits and the type or combination of nutrients added. Common species with acquisitive functional traits responded more strongly to nutrient addition, mainly to N + P. Phosphorous enhanced the growth rates of species with acquisitive and conservative traits, had mostly positive effects on common species and neutral or negative effects in rare species. Moreover, trees receiving N + P grew faster irrespective of their initial size relative to trees in control or to trees in other treatment plots. Finally, species responses were highly idiosyncratic suggesting that community processes including competition and niche dimensionality may be altered under increased resource availability. We found no statistically significant effects of nutrient additions on aboveground biomass productivity because acquisitive species had a limited potential to increase their biomass, possibly due to their generally lower wood density. In contrast, P addition increased the growth rates of species characterized by more conservative resource strategies (with higher wood density) that were poorly represented in the plant community. We provide the first long-term experimental evidence that trait-based responses, community structure, and community processes modulate the effects of increased nutrient availability on biomass productivity in a tropical forest.

## KEYWORDS

biomass productivity, Ecuador, experimental nutrient manipulation, functional traits, nitrogen, phosphorus, tree growth, tropical montane forest

## 1 | INTRODUCTION

The Tropical Andes are an important global biodiversity hotspot, as they host very high numbers of vascular plants and other organisms

(Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). This biodiversity hotspot is threatened by various anthropogenic pressures, including increased rates of atmospheric nutrient deposition related to local and regional land-use change (Wilcke et al., 2013).

Atmospheric chemical deposition is increasing soil nutrient availability even in remote areas of the planet (Boy et al., 2008; Wilcke et al., 2013). Tree growth in tropical montane forests (TMF) is supposed to be limited by N or co-limited by N and P (Dalling, Heineman, González, & Ostertag, 2016; Santiago, 2015; Tanner, Vitousek, & Cuevas, 1998). Thus, altered nutrient availability can be problematic for the conservation of highly diverse TMF because nitrogen (N) and phosphorus (P) concentrations determine critical aspects of tree growth and forest functioning, including tree species distributions, functional trait expression, community structure, and dynamics at the landscape scale (Homeier, Báez, Hertel, & Leuschner, 2017). Moreover, there is growing experimental evidence that enhanced resource availability shifts of competitive interactions (Suding et al., 2005) and decrease species diversity due to the loss of niche dimensionality (Harpole et al., 2016). However, the combination of specific local conditions (i.e., climate, topography, soil type, and local biota) and geological history seem to determine whether or not a particular resource becomes limiting for plant growth (Cárate-Tandalla, 2015; Dalling, Heineman, González, et al., 2016; Werner & Homeier, 2015).

Given the high tree diversity of tropical forests, understanding trait-based responses to nutrient addition and linking them to patterns of community structure is perhaps the only way to forecast shifts in community composition, diversity, and ecosystem functioning under future global environmental change. However, we are far from understanding how functional traits determine tree growth under enhanced nutrient availability. Tree species often differ in their responses to increased nutrient availability in many tropical forests (Dalling, Heineman, González, et al., 2016; Dalling, Heineman, Lopez, Wright, & Turner, 2016; Santiago, 2015; Santiago et al., 2012) suggesting limitation by multiple nutrients, and differences in nutrient uptake strategies or nutrient economies (Dalling, Heineman, González, et al., 2016). In addition, trees in smaller size classes in tropical lowland forests have been shown to grow faster more consistently than larger size classes under increased nutrient availability (Alvarez-Clare, Mack, & Brooks, 2013; Wright et al., 2011).

Ecological theory and few observation studies suggest that trees with acquisitive strategies (fast resource acquisition and growth rates) are more responsive than trees with conservative strategies (slower resource acquisition and growth rates; Baribault et al., 2012; Holste, Kobe, & Vriesendorp, 2011; Reich, 2014; van der Sande et al., 2016). Tree functional traits linked to acquisitive strategies include high stem conductivity, high specific leaf area, high foliar N and P concentrations, and low wood density, whereas the opposite traits characterize trees exhibiting conservative strategies (Díaz et al., 2016; Kunstler et al., 2016; Reich, 2014). To our knowledge, no studies have yet explored trait-based responses to experimental long-term nutrient addition in tropical forests.

Community-level dynamics, including trait-based responses and shifts in species composition, can reduce or magnify the effects of environmental change on ecosystem performance, as proposed by trait-response effect frameworks (Díaz et al., 2013; Enquist et al., 2015; Suding et al., 2008; van der Sande et al., 2016). For example, traits including tree height and leaf mass area (LMA) are positively

correlated with aboveground carbon storage in tropical lowland forest in Panama, and N-fixing capacity and low LMA explain carbon storage in mixed species plantations (Ruiz-Jaen & Potvin, 2011). On the other hand, environmental factors including edaphic conditions overrule the effects of functional traits on biomass production in Amazonian forests (Baker et al., 2009). Thus, assessing over the long-term how trait-based responses affect ecosystem functioning is critical to understand nutrient limitation and to develop mechanistic models that can forecast community structure, species composition and ecosystem biomass production under altered resource availability due to anthropogenic activities (Ali, Medlyn, Aubier, Crous, & Reich, 2015; Hautier et al., 2016).

The main objective of this paper was to explore experimentally in situ tree responses to altered nutrient availability based on ten morphological traits, tree size, and species identity, and their relative effects on ecosystem biomass productivity in a highly diverse Andean forest in southern Ecuador. We expected that species with acquisitive functional traits would grow faster than individuals with conservative functional traits under nutrient addition, particularly with N + P amendments. Second, we hypothesized that smaller trees would respond more strongly in terms of growth than large trees in nutrient addition plots. Third, we expected that tree species would differ in their responses to nutrient additions as a result of their specific trait configuration, and possibly, due to shifts in the competitive hierarchies in the plant community. Finally, we expected that nutrient addition would increase productivity at the stand scale, and that trait-based responses to nutrient addition should explain stand-level aboveground biomass (AGB) change during the study period.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study was conducted in an Andean montane forest between 1800 and 2300 m of elevation in the Reserva San Francisco (3°58'S, 79°04'W) in southern Ecuador. The area receives a mean annual precipitation of 2,200 mm, with a less humid period between September and December, and has an annual mean temperature of 15°C (Bendix, Rollenbeck, Richter, Fabian, & Emck, 2008). Here, humid montane forests cover continuous extents of the Andean chain. Our study site has a rugged topography, with vegetated slopes between 20 and 50°. The most diverse families include Lauraceae, Melastomataceae, and Rubiaceae (Homeier, Breckle, Günter, Rollenbeck, & Leuschner, 2010). Soils are heterogeneous, mostly highly weathered, and generally nutrient-poor, with low N and P concentrations (Wilcke et al., 2008; Wolf, Veldkamp, Homeier, & Martinson, 2011) compared to other TMF (Unger, Leuschner, & Homeier, 2010). In our site average nutrient dry and bulk deposition rates were about 47 kg N ha<sup>-1</sup> yr<sup>-1</sup> and 2.5 kg P ha<sup>-1</sup> yr<sup>-1</sup> between 2007 and 2012 (Velescu, Valarezo, & Wilcke, 2016).

#### 2.1.1 | Nutrient addition experiment

We used data on tree growth over 7.7 years (February 2008–October 2015) of the ongoing Ecuadorian Nutrient Manipulation

Experiment (NUMEX, Homeier et al., 2012). The full-factorial experiment was set in a stratified random design that includes four blocks and 16 plots of 400 m<sup>2</sup> (20 × 20 m), with a minimum distance of 10 m between plots. Thus, each block has four plots randomly assigned to a treatment: N, P, N + P, and control. Nitrogen and phosphorus were added to the experimental plots at a moderate annual rate of 50 kg N/ha as urea, and 10 kg P/ha as monosodium phosphate. Both nutrients were distributed in solid form by hand, homogeneously within the plot area, twice a year.

The tree community of the NUMEX experimental plots is diverse (45 species), but dominated by a few species of trees. Indeed, 65% of the tree community is represented by five species (*Graffenrieda emarginata* Ruiz & Pav. (Melastomataceae), *Dictyocaryum lamarckianum* (Mart.) H. Wendl. (Arecaceae), *Alchornea lojaensis* Secco (Euphorbiaceae), *Myrcia* sp. nov. (Myrtaceae), and *Hieronyma fendleri* Briq. (Phyllanthaceae), whereas 27 species are represented by five or fewer individuals (Table 1).

In NUMEX, all trees measuring ≥10 cm dbh in the experimental plots were marked, identified to species, and their diameter was monitored at least every 6 months using permanent dendrometer tapes (D1, UMS, Munich, Germany). Tree height was estimated using a Vertex IV height meter and a T3 transponder (Haglöf, Langsele, Sweden).

## 2.1.2 | Functional traits

We evaluated functional traits in 158 tree species found between 1800 and 2300 m of elevation at our study site to assess how representative were the NUMEX species' traits of the trait variation

spectrum of the whole tree community. Thus, the following leaf and stem functional traits were measured for 158 tree species measuring dbh ≥10 cm: bark thickness (BS), stem vessel density (VDens) and vessel diameter (VDia), theoretical sapwood-specific conductivity (KS), wood-specific gravity (WSG), leaf area (LA), specific leaf area (SLA), leaf toughness (LT), and foliar nitrogen (N) and phosphorus (P) concentrations. The methods used to measure each trait are presented in Table S1.

## 2.2 | Data analyses

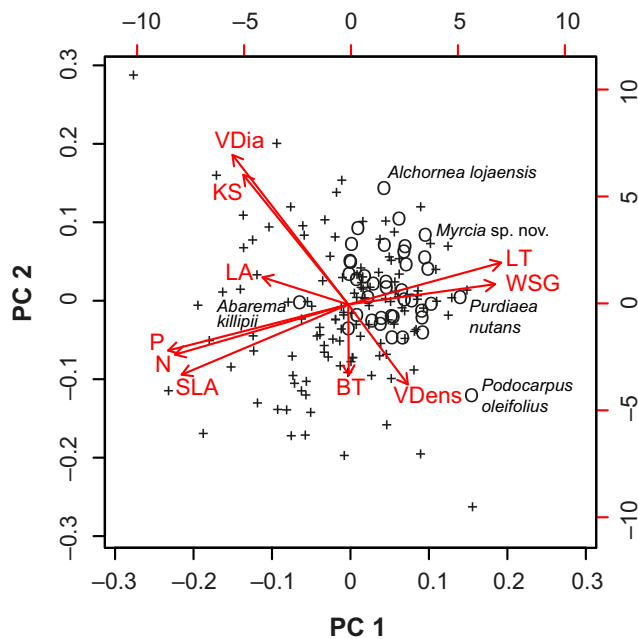
### 2.2.1 | Functional traits at the community scale and within the experimental plots

We used species mean trait values to calculate a Principal Component Analysis (PCA) that collapsed trait variation among species onto a few main axes (Figure 1, Table S2). The first two axes described 56% of the trait variation in the tree community. The first axis (PC 1) captured 41% of the variation where positive values indicated high specific wood gravity and high leaf toughness, whereas negative values were related to high leaf concentration of N and P, and high SLA (Figure 1). Thus, it described an intuitive gradient of functional traits for species with potential for fast nutrient acquisition and growth (i.e., high leaf nutrient content, high SLA) to species with traits related to slow nutrient acquisition and growth (i.e., high wood density and leaf toughness; Reich, 2014). Conversely, PC 2 captured 15% of the variation reflecting investment in low to high hydraulic conductivity due to fewer and wider vessels vs. abundant and narrower sapwood vessels (and higher values of specific conductivity

**TABLE 1** Mean basal area change (cm<sup>2</sup>) over 7.7 years (±1 SE), number of individuals (in parentheses), and PC scores for tree species with at least one individual in each nutrient addition treatment

Species	Control	N	P	N + P	PC 1	PC 2
<i>Abarema killippii</i>	10.16 ± 7.31 (6)	5.56 (1)	7.06 ± 2.71 (3)	13.07 ± 4.54 (2)	-1.43	0.03
<i>Alchornea lojaensis</i>	11.4 ± 2.74 (20)	15.19 ± 2.56 (19)	17.65 ± 3.97 (16)	25.24 ± 10.28 (11)	1.17	2.18
<i>Alzatea verticillata</i>	7.02 ± 2.53 (12)	7.49 ± 1.58 (4)	27.68 ± 5.25 (5)	25.76 ± 6.05 (8)	1.77	1.00
<i>Clusia ducuoides</i>	16.65 ± 7.59 (3)	13.96 ± 2.85 (4)	37.23 ± 15 (6)	11.51 ± 4.5 (4)	1.02	1.12
<i>Endlicheria oreocola</i>	0.7 (1)	11.48 (1)	7.31 ± 6.2 (2)	6.03 (1)	0.88	-0.37
<i>Eschweilera sessilis</i>	2.32 ± 1.27 (5)	1.54 ± 0.65 (4)	4.21 ± 2.62 (3)	17.12 (1)	2.36	0.66
<i>Graffenrieda emarginata</i>	16.31 ± 2.13 (41)	19.35 ± 1.76 (45)	15.02 ± 1.9 (43)	23.99 ± 2.34 (47)	0.67	0.40
<i>Hieronyma fendleri</i>	9.03 ± 2.51 (8)	9.31 ± 1.85 (20)	5.28 ± 1.03 (14)	15.04 ± 4.18 (13)	1.07	0.32
<i>Myrcia</i> sp. nov.	13.63 ± 2.17 (17)	15.77 ± 1.72 (14)	8.61 ± 1.68 (16)	17.37 ± 3.18 (9)	2.27	1.30
<i>Ocotea</i> sp. 1	3.39 (1)	7.16 ± 2.66 (2)	14.24 (1)	6.79 ± 1.53 (2)	0.23	0.40
<i>Persea subcordata</i>	3.5 (1)	3.45 (1)	19.87 ± 5.44 (3)	2.8 (1)	1.52	0.75
<i>Persea weberbaueri</i>	4.51 ± 2.15 (4)	7.7 (1)	4.84 ± 4.59 (2)	19.71 ± 8.26 (3)	1.52	0.75
<i>Podocarpus oleifolius</i>	10.13 ± 5.71 (6)	3.53 ± 1.14 (4)	1.08 ± 0.6 (2)	0.98 ± 0.08 (2)	3.55	-1.65
<i>Prunus opaca</i>	5.65 ± 2.59 (4)	10.02 ± 3.88 (6)	6.82 (1)	14.37 ± 10.03 (4)	1.80	0.08
Rare	13.62 ± 4.64 (8)	6.96 ± 1.58 (13)	16.08 ± 5.69 (15)	12.2 ± 2.33 (29)	1.35 <sup>a</sup>	0.17 <sup>a</sup>

<sup>a</sup>Means calculated from PC scores of the following rare species: *Bejaria aestuans*, *Calytranthes pulchella*, *Clethra revoluta*, *Eugenia* sp., *Gordonia fruticosa*, *Graffenrieda harlingii*, *Licaria subsessilis*, *Matayba inelegans*, *Miconia calophylla*, *Miconia punctata*, *Myrsine coriacea*, *Naucleopsis francisci*, *Ocotea aciphylla*, *Ocotea andina*, *Ocotea* sp.2, *Ocotea* sp.3, *Purdiaea nutans*, *Tapirira guianensis*, *Weinmannia ovata*, *Weinmannia sorbifolia* and 12 unidentified individuals.



**FIGURE 1** Principal Component Analysis (PCA) of 158 tree species traits between 1,800 and 2,300 m of elevation at the Reserva San Francisco, Ecuador. Ten functional traits were used for the analysis: foliar N (N) and foliar P (P) concentrations, leaf area (LA), leaf toughness (LT), specific leaf area (SLA), bark thickness (BT), sapwood-specific conductivity (KS), stem vessel density (VDens), stem vessel diameter (VDia), and wood-specific gravity (WSG). Species occurring in the NUMEX experimental plots (O), other species at the study site (+). PC scores for NUMEX species are presented in Table 1. Loadings of functional traits in both PC axes are given in Table S2

(KS)), respectively (Figure 1). Therefore, trait variation in PC 2 described a gradient from more acquisitive (negative values) to more conservative (positive values) resource acquisition and use strategies (Poorter et al., 2010). For further statistical analyses, the PC 1 and PC 2 scores for the NUMEX species were used as predictive variables to model trait-based responses to nutrient addition at the scale of individual trees because they explained most of the trait variation in the tree community (Table S2).

## 2.2.2 | Tree growth

We used Linear Mixed Models (LMM) to evaluate individual tree growth because they can deal with grouped data in hierarchical structures, and provide estimates of the relative importance for fixed and random effects (Bates, Maechler, Bolker, & Walker, 2015). We built models that predicted tree growth considering the possible additive and multiplicative interactions between fixed factors (i.e., nutrient addition treatment and initial tree size as basal area at the beginning of the experiment) and functional trait variation summarized in two PC axes (as explained below). Thus, we run 16 models that included functional trait variation collapsed in PC 1 or PC 2, and five models that did not include functional traits. We did not test all the possible interactions between our fixed factors and the

two PCA axes because the complexity of the models could compromise their interpretability. We conducted these analyses using stem basal area change measured for each of the 545 dicotyledonous trees in the NUMEX plots that were alive throughout the study period.

In the LMM models, we included block as a random factor to account for possible spatial autocorrelation due to the design of the experiment. We also included species identity in the models as a random factor (to account for idiosyncratic responses) and allowed their intercepts and slope to vary across treatments (Bates et al., 2015; Metz, 2012); therefore species could have positive or negative responses to different experimental nutrient additions. To maintain the balance in the statistical models, tree species that had at least one individual in each of the four types of experimental plots were included in the analyses with their species identification (14 species, 449 individuals); all other trees were included in the category of 'rare species' (21 species, 96 individuals, Table 1). To assess what combination of nutrient addition, initial tree size, and functional traits best explained tree growth we used the Akaike Information Criterion (AIC; Burnham & Anderson, 2004; Symonds & Moussalli, 2011). The fit of the models were compared with  $\Delta AIC$  values ( $\Delta AIC = AIC \text{ model } i - \min AICc$ ; where  $\min AICc$  is the model with the smallest AIC value); considering that models with  $\Delta AIC < 6$  should not be rejected (Symonds & Moussalli, 2011). We also used the correlation between fitted and observed values to assess the explanatory power of each model through an approximation to  $R^2$  that measures explained variation in LMM (Xu, 2003).

Finally, we extracted prediction values to evaluate individual responses to nutrient addition, upper and lower confidence intervals for the fixed effects of the models with the lower AICs. Prediction means and intervals were calculated from 1000 simulated distributions of the treatment effect term to produce a distribution of predictions for each observation using merTools (Knowles & Frederick, 2016). We extracted species predicted growth across treatments (for the best models) to assess species responses. For caution, we only report nutrient addition effects for species represented by  $>1$  individual in control and any given treatment type. Statistical analyses and graphs were conducted in R Core Development Team (2014) using the packages ggplot2 (Wickham, 2009), lme4 (Bates et al., 2015), merTools (Knowles & Frederick, 2016), and pcaMethods (Stacklies, Scholz, Walther, & Selbig, 2007).

## 2.2.3 | Trait-response and effect on ecosystem functioning

We assessed the overall effect of nutrient addition on plot scale aboveground biomass (AGB). Individual tree AGB for the first and last year of the experiment was calculated using the following allometric equation  $AGB = 0.0673 \times (\rho D^2 H)^{0.976}$  where  $D$  = diameter in cm,  $H$  = height in m, and  $\rho$  = wood-specific gravity in  $g/cm^3$  (Chave et al., 2014). Next, we used repeated measures analyses to evaluate the relative response of each plot to nutrient addition in terms of aboveground biomass productivity.

### 3 | RESULTS

#### 3.1 | Trait variation in the tree community and experimental plots

The species in NUMEX held substantial trait variation compared to the tree community as a whole (47% and 46% in PC 1 and PC 2, respectively). Trees in NUMEX had statistically significantly more conservative strategies compared to the community when considering PC 1 (NUMEX mean =  $1.23 \pm 0.31$ , community mean =  $-0.27 \pm 0.16$ ,  $F_{1,165} = 18.39$ ,  $p < .001$ ); this pattern was not clear for PC 2 (NUMEX =  $0.35 \pm 0.20$ , community =  $-0.08 \pm 0.10$ ,  $F_{1,165} = 3.71$ ,  $p = .056$ ). Thus, tree species at NUMEX represented fairly well functional trait variation within the tree community of our site.

#### 3.2 | Trait-based responses to nutrient addition

As we predicted, functional traits were important predictors of tree responses to nutrient addition. Overall, species with more acquisitive resource use strategies responded more strongly to nutrient addition compared to more conservative species. Tree growth was best explained by two statistical models that included interactions between N, P, and tree functional traits (PC 1 or PC 2), plus the additive effect of initial tree size (Figures 2 and 3, Tables 2 and 3). In the best model ( $N \times P \times PC\ 2 + \text{tree size}$ ), nutrient addition favored the growth rates of species with more acquisitive resource use strategies (trees with higher PC 2 scores related to higher specific conductivity and higher vessel diameter), with a stronger positive effect of N + P than of N or P addition alone (Figure 2b).

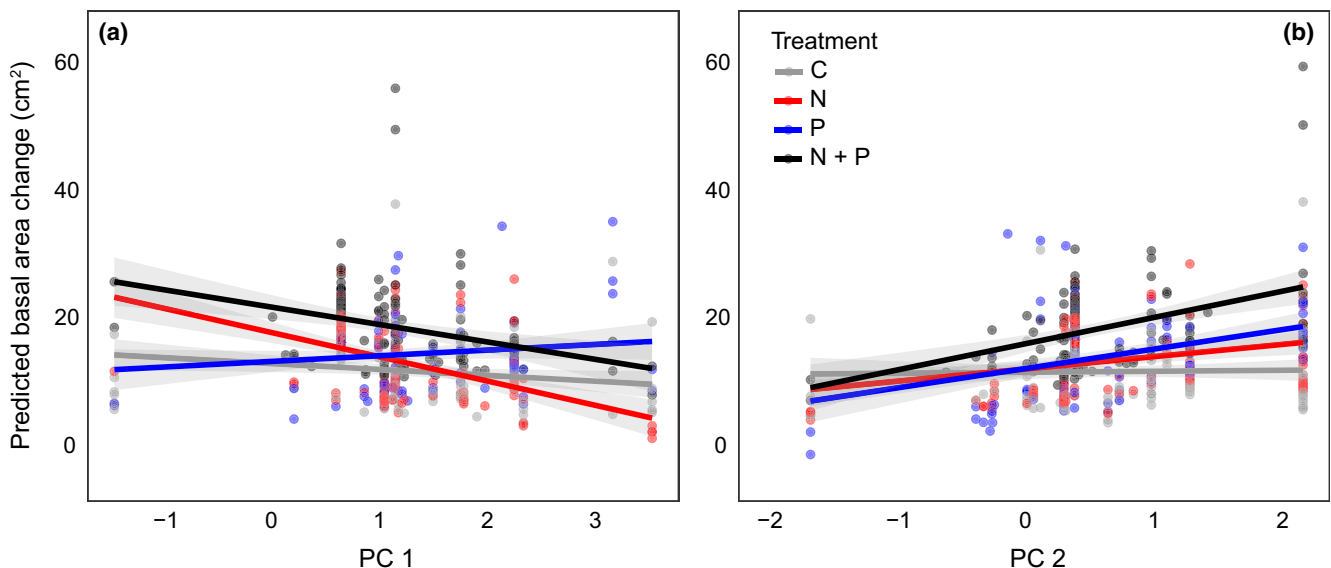
In the second best model ( $N \times P \times PC\ 1 + \text{tree size}$ ), trees with more acquisitive strategies (lower PC 1 scores related to high leaf concentration of N and P, and high SLA) grew faster after N + P and N addition than in control plots (Figures 2 and 3, Tables 2 and 3). However, N addition tended to decrease the growth rates of species with conservative resource use strategies (higher PC 1 scores due to higher specific wood gravity and leaf toughness) compared to trees in control plots (Figure 2a). On the contrary, addition of P alone enhanced the growth rates of species with higher PC 1 values, characterized by functional traits typical of species with conservative resource use strategies.

#### 3.3 | Tree size and responses to nutrient addition

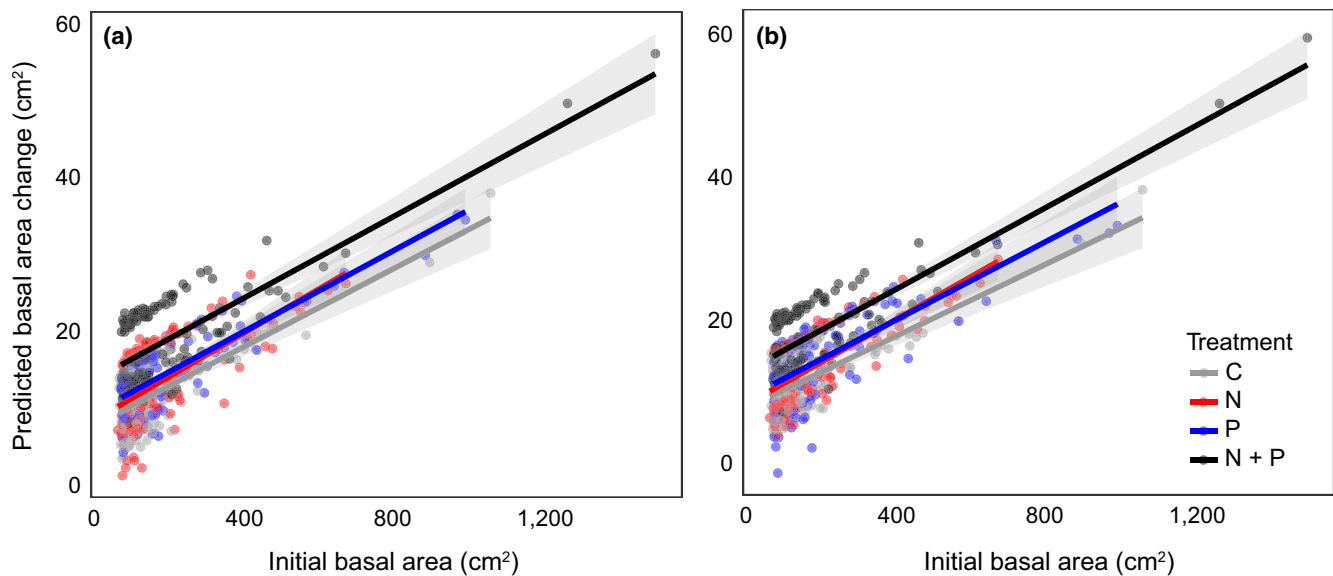
Contrary to our prediction, we did not find evidence that experimental nutrient addition enhanced the growth rates of smaller rather than of bigger trees. The two best models (Table 2) indicated that in N + P addition plots trees across the whole-tree size spectrum grew faster compared to trees in control plots (Figure 3). Addition of N or P alone did not have size dependent effects on tree growth either.

#### 3.4 | Species responses to nutrient addition

Tree species had positive or negative responses depending on the type and combination of nutrient added (Figure 4, Table 3). Addition of N + P increased the growth rates of a higher number tree species than separate N or P amendments. Our two best models indicated that N + P enhanced the growth rates of nine species (*Abarema killipii*, *Alchornea lojaensis*, *Alzatea verticillata*, *Clusia ducoides*, *Graffenrieda*



**FIGURE 2** Predicted tree growth and SE as a function of functional traits. Predictions values were extracted from the two best models in Table 3 that consider growth over 7.7 years as a function of the interactions between the nutrients added (N, P, N + P) and tree functional traits (PC 1 or PC 2) and the additive effect of initial tree size. (a) Model using PC 1. (b) Model using PC 2. PC 1 describes a gradient of acquisitive functional traits (high leaf nutrient content, high SLA) to conservative traits (wood density and leaf toughness). PC 2 describes a gradient from conservative to acquisitive functional traits (low and high sapwood-specific conductivity, respectively)



**FIGURE 3** Predicted tree growth and SE as a function of initial tree size. Predictions values were extracted from the two best models in Table 3 that consider growth over 7.7 years as a function of the interactions between the nutrients added (N, P, N + P) and tree functional traits (PC 1 or PC 2), and the additive effect of initial tree size. (a) Model using PC 1. (b) Model using PC 2. PC 1 describes a gradient of acquisitive functional traits (high leaf nutrient content, high SLA) to conservative traits (wood density and leaf toughness). PC 2 describes a gradient from conservative to acquisitive functional traits (low and high sapwood-specific conductivity, respectively)

*emarginata*, *Hieronyma fendleri*, *Myrcia* sp. nov., *Persea weberbaueri*, and *Prunus opaca*). Furthermore, N + P increased the growth rates of the group of rare species (only in the second best model, Figure 4a). Similarly, N addition increased the growth rates of up to six species (*A. lojaensis*, *A. verticillata*, *C. ducuoides*, *Eschweilera sessilis*, *G. emarginata*, *Myrcia* sp. nov.), and decreased the growth (relative to trees in control plots) of *Podocarpus oleifolius* (Figure 4). Phosphorous addition had positive effects in seven species (*A. lojaensis*, *A. verticillata*, *C. ducuoides*, *E. sessilis*, *G. emarginata*, *Myrcia* sp. nov., and *P. weberbaueri*), the group of rare species, and had negative effects in *P. oleifolius*.

### 3.5 | Effects of nutrient addition on ecosystem productivity

As expected, all experimental plots increased in aboveground biomass (AGB) ( $199.39 \pm 19.60$  kg) over the study period (Figure 5). However, there were no statistically significant differences among experimental treatments (Treatment:  $F_{3,12} = 0.435$ ,  $p = .731$ , Treatment  $\times$  Time:  $F_{3,12} = 1.133$ ,  $p = .374$ ). Plots receiving N + P gained more AGB ( $261 \pm 47$  kg), followed by plots receiving P ( $183 \pm 29$  kg), and N ( $176 \pm 47$  kg); control plots increased AGB at intermediate values ( $177 \pm 50$  kg) between N and P experimental plots.

## 4 | DISCUSSION

Functional traits were strong determinants of individual species responses to nutrient addition in our study system. The effect of increased nutrient availability on tree growth depended on

interactions between functional traits and the type or combination of nutrients added. Common species with more acquisitive resource use strategies responded more strongly to nutrient addition, mainly to N + P. However, trait-based responses did not affect stand-level AGB increment because responsive individuals, that increased their growth rates under nutrient additions, had limited potential to strongly enhance AGB, most likely due to their low wood density. As a consequence, trait-based responses buffered the effect of increased nutrient availability on productivity, a critical component of ecosystem functioning.

In agreement with our second hypothesis, N and P added together had the strongest positive effect on tree growth (Figure 2, Table 3). Furthermore, trees with acquisitive functional traits (i.e., high sapwood-specific conductivity, high SLA, high foliar N, and P concentration) benefited most from higher N and P availability (Figure 2). Addition of N alone resulted in the same pattern of trait-based responses as N + P, although the magnitude of the effect was smaller. It is noteworthy that almost 8 years of experimental N + P additions did not change substantially the growth rates of species with more conservative resource use strategies, suggesting that these species are well adapted to the local soil nutrient status. Alternatively, more conservative species may lack morphological and physiological plasticity—features commonly found in acquisitive species—to respond to enhanced nutrient availability (Chmura, Modrzyński, Chmielarz, & Tjoelker, 2017; Portsmouth & Ninemets, 2007). Furthermore, other mechanisms may limit growth responses of conservative species to N + P addition, including their interactions with mycorrhizal fungi (Camenzind et al., 2014), differences in nutrient resorption efficiency (Hättenschwiler, Aeschlimann, Coüteaux, Roy, & Bonal, 2008) and other factors discussed below.

**TABLE 2** Comparison of 21 Linear Mixed Models predicting tree basal area change over 7.7 years as a function of nutrient addition treatment (N, P, N + P), initial tree size, functional traits collapsed in two PCA axes (PC 1 and PC 2), species identity and block are included as random factors

Model	df	AIC	$\Delta$ AIC	R <sup>2</sup>
Models including PC 1				
N × P × Tree size × PC 1	19	4399.93	47.34	0.25
N × P × Tree size + PC 1	12	4378.80	26.24	0.23
N × P × PC 1 + Tree size	12	<b>4356.36</b>	<b>3.78</b>	0.21
N × P + Tree size + PC 1	9	4361.46	8.87	0.21
N + P + Tree size + PC 1	8	4365.14	12.55	0.21
N × P × PC 1	11	4402.32	49.73	0.12
N × P + PC 1	8	4409.07	56.49	0.12
N + P + PC 1	7	4412.08	59.50	0.12
Models including PC 2				
N × P × Tree size × PC 2	19	4403.11	50.52	0.24
N × P × Tree size + PC 2	12	4375.44	22.85	0.23
N × P × PC 2 + Tree size	12	<b>4352.58</b>	<b>0</b>	0.21
N × P + Tree size + PC 2	9	4358.60	6.10	0.21
N + P + Tree size + PC 2	8	4362.21	9.62	0.21
N × P × PC 2	11	4397.48	44.89	0.12
N × P + PC 2	8	4405.07	52.48	0.11
N + P + PC 2	7	4407.92	55.34	0.11
Models without a PC axis				
N × P × Tree size	11	4379.05	26.46	0.23
N × P + Tree size	8	4361.59	9.00	0.21
N + P + Tree size	7	4365.27	12.69	0.21
N × P	7	4409.74	57.15	0.12
N + P	6	4412.71	60.13	0.11

AIC and  $\Delta$ AIC values for the two best models are in bold.

**TABLE 3** Results of linear mixed effects models predicting changes in basal area of individual trees as a function the interactions between experimental nutrient addition (N, P and N + P), functional traits (PC 1 or PC 2), and the additive effect of initial tree size (initial basal area). Random effects included in the model are tree species identity and block. Model PC 1 (AIC = 4356.4), model PC 2 (AIC = 4352.6)

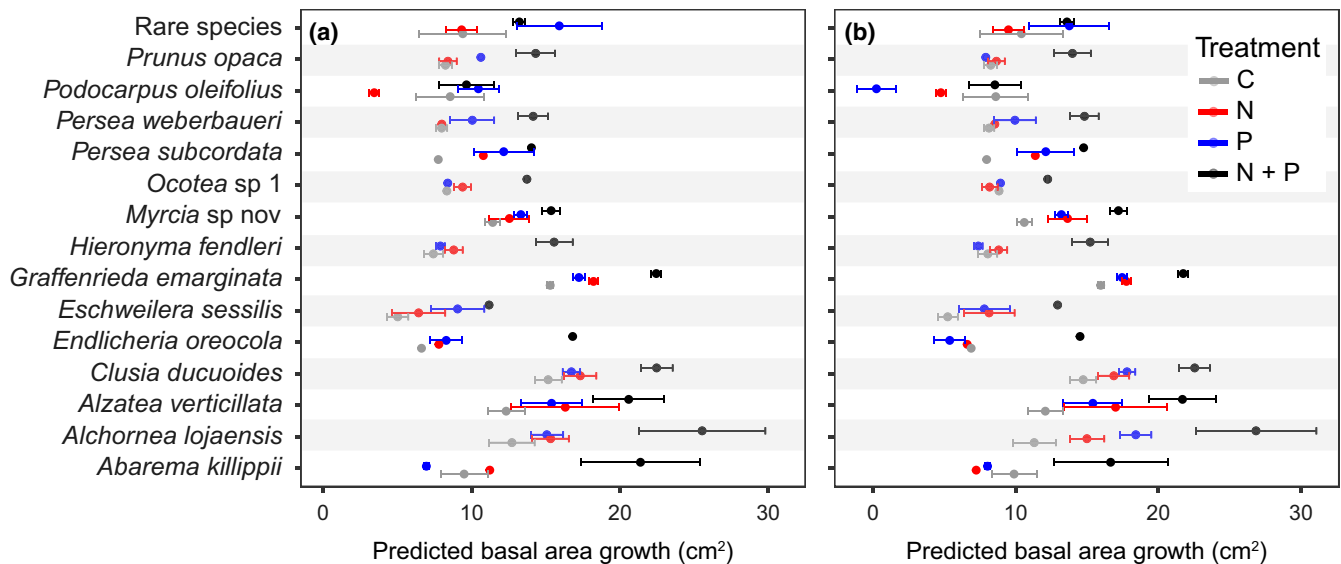
Model PC 1				Model PC 2			
Fixed effects	Estimate	SE	t-value	Fixed effects	Estimate	SE	t-value
(Intercept)	5.23	2.52	2.07	(Intercept)	4.87	2.00	2.43
N	2.83	2.90	0.97	N	0.43	2.05	0.21
P	-0.04	2.75	-0.01	P	-1.04	2.15	-0.48
PC 1	-0.05	1.44	-0.03	PC 2	0.86	1.76	0.49
Tree size	0.02	0.00	7.76	Tree size	0.02	0.00	7.71
N × P	4.52	4.06	1.11	N × P	4.82	2.97	1.62
N × PC 1	-1.42	1.95	-0.72	N × PC 2	0.84	1.91	0.44
P × PC 1	1.10	1.82	0.60	P × PC 2	3.24	2.02	1.60
N × P × PC 1	-1.12	2.83	-0.39	N × P × PC 2	-2.16	2.98	-0.72
Random effects	Parameter	Variance	SD	Random	Parameter	Variance	SD
Species	Intercept	15.855	3.98	Species	Intercept	14.04	3.747
Block	Intercept	0	0	Block	Intercept	0	0
Residual		166.681	12.91	Residual		166.07	12.887

We did not anticipate that a given nutrient would benefit equally trees with opposite resource use strategies. However, P enhanced growth rates of trees with more acquisitive (i.e., high sapwood-specific conductivity in PC 2) and more conservative functional traits (i.e., high wood-specific gravity and leaf toughness in PC 1; Figure 1). Previous lowland studies report increased growth in higher soil P sites (Quesada et al., 2012), and strong interspecific growth variation as a response to soil P and N availability (Baribault et al., 2012). To our knowledge, positive responses of conservative species to increased P availability have not been reported previously. Thus, our results highlight the fact that functional traits determine the nature of nutrient limitation in this ecosystem. Furthermore, our findings support the idea that trait-based responses to nutrient addition may differ for N and P (Dalling, Heineman, González, et al., 2016).

Our hypothesis that smaller trees would experience higher growth rates compared to large trees under increased nutrient availability was not supported (Figure 3, Table 3). Indeed, trees receiving N + P grew faster irrespective of their initial size relative to control or to other treatment plots (Figure 3). Thus, our study supports the notion that total resource availability determines growth in individual trees (Field, Chapin, Matson, & Mooney, 1992). Our statistical approach allowed us to detect treatment effects even in larger trees because we did not consider discrete size classes where statistical power decreases for large individuals. In consequence, size independent tree responses to nutrient addition may have been undetected in previous studies (see, e.g., Adamek, Corre, & Hölcher, 2009; Alvarez-Clare et al., 2013; Wright et al., 2011).

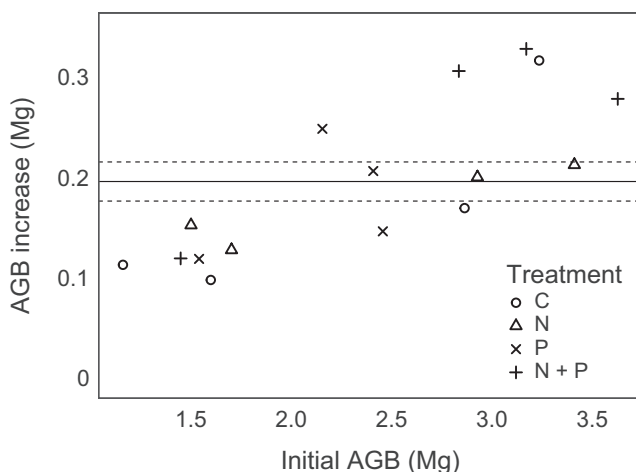
Consistent with our third hypothesis, tree species differed in their responses to increased nutrient availability. The vast majority of species had increased growth rates under N + P amendments, and only a subset of those species responded positively to N or P addition (Figure 4). Possibly, *P. oleifolius*, a species characteristic of





**FIGURE 4** Predicted mean growth and SE of tree species in experimental nutrient addition plots. Predictions values were extracted from the two best models in Table 3 that consider growth over 7.7 years as a function of the interactions between the nutrients added (N, P, N + P) and tree functional traits, and the additive effect of initial tree size. (a) Model using traits in PC 1 (fast nutrient acquisition and growth due to high leaf nutrient content and high SLA, to slow nutrient acquisition and growth related to high wood density and leaf toughness), and (b) model using traits in PC 2 (slow to fast nutrient acquisition related to low and high sapwood-specific conductivity, respectively)

old growth forests, had reduced growth rates under additions of N and P due to enhanced competition with more acquisitive species. Furthermore, NUMEX seedlings of rare species growing in nutrient addition plots have lower survival rates than seedlings of common species despite of having comparable levels of herbivory (Cárate-Tandalla, 2015), which suggests that niche processes may be at play (Harpole et al., 2016). As a result, in our site as in other lowland and TMF sites, species responses to increased nutrient availability were highly idiosyncratic (Dalling, Heineman, González, et al., 2016; Santiago, 2015), perhaps due to internal physiological controls (Major, Wright, & Turner, 2014) and changes in the interactions with other species, including competition, mutualism, and herbivory.



**FIGURE 5** Relationship between the increment of aboveground biomass (AGB) over 7.7 years and mean AGB in 16 experimental plots in NUMEX in 2008. Overall means and standard errors are presented by solid and dashed lines, respectively

Our results demonstrate that most of the species in the community will be able to respond positively to higher N and P availability due to increased nutrient deposition rates from Amazonian vegetation fires and fossil fuel burning, and Saharan dust deposition, respectively (Mahowald et al., 2008; Wilcke et al., 2013). Furthermore, our results indicate that rare species have acquisitive or conservative resource use strategies that could (Figure 4a) or could not (Figure 4b) profit from increased N + P and P availability (but not from N addition alone). Rare species responses are important to maintain plant community diversity; they represent 60% of the tree species ( $n = 21$ ), but only 18% of the individuals in NUMEX. Over time, under higher N + P availability or more likely higher N deposition, some rare and one common species (*P. oleifolius*) with conservative resource use strategies could be eliminated from the community. Indeed, a regeneration study in NUMEX found that 5 years of N addition reduced seedling richness relative to control plots (Cárate-Tandalla, 2015). In this TMF, as it occurs in grasslands worldwide, higher nutrient availability may reduce species diversity through mechanisms that include competitive exclusion (Suding et al., 2005), and elimination of trade-offs that allow species coexistence (Harpole et al., 2016).

The current trait distribution of our plant community suggests that in the long-term tree species adapted and currently restricted to more fertile soils (more acquisitive local species with low and high PC 1 and PC2 values, respectively, see Figure 1), may displace current dominants of areas with poorer soil nutrients (Werner & Homeier, 2015). This shift in species composition would strongly alter the physiology, carbon dynamics, and other ecosystem functions in this TMF.

As we expected, addition of N and P together increased AGB biomass, although differences were not statistically significant (Figure 4). Addition of N, and N and P together increased the growth

rates of virtually all species in the community (Figure 4) but to a larger extent of species with traits related to more acquisitive resource use strategies that have a limited potential to increase their biomass due to their generally lower wood density, a key parameter for biomass gain (Fig. S1). In contrast, P addition increased the growth rates of species characterized by more conservative resource strategies, with higher wood density. However, these species were poorly represented in the plant community; indeed many of them were rare species, and therefore could not make a substantial contribution to stand scale AGB increment. Furthermore, nutrient enrichment decreased the growth rates (relative to control plots) of conservative species (rare or common), which counterbalanced AGB increases given by acquisitive species. As a result, trait-based responses and community structure determined the effects of nutrient addition on AGB in NUMEX.

Our study demonstrates that functional traits related to acquisitive and conservative resource use strategies, and variation in nutrient economies determine nutrient limitation in this ecosystem. We also show that trait-based responses, community structure, and probably also interspecific interactions have the potential to modulate the effects of increased nutrient availability on ecosystem functioning. We conclude that trait-response effect frameworks are powerful approaches to study the effects of global environmental change on ecosystem functioning.

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