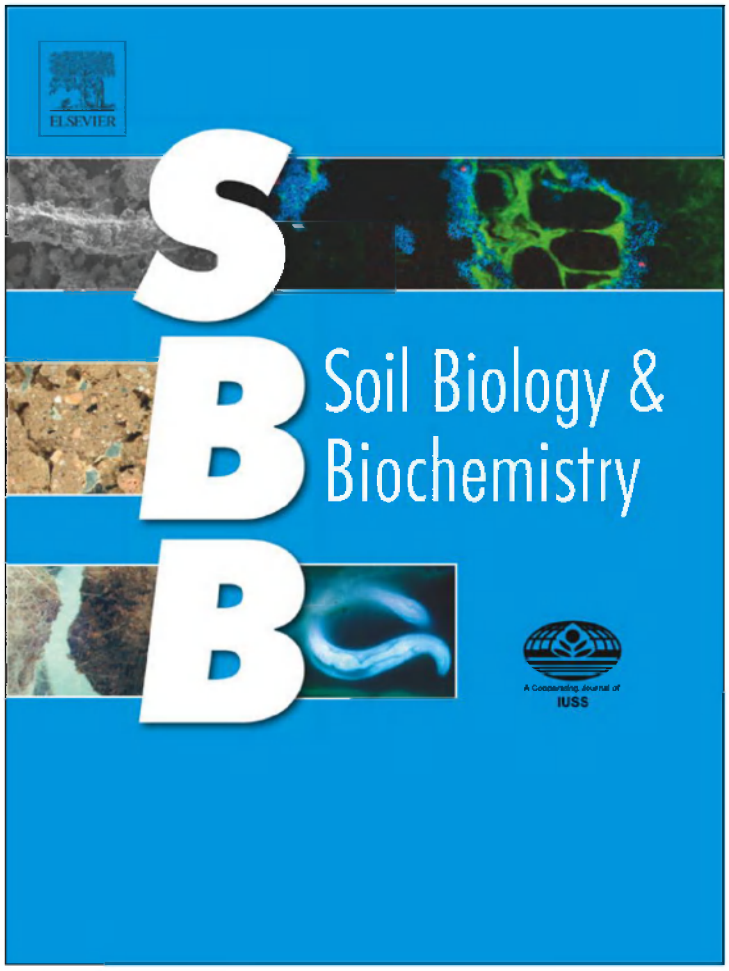

(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

Soil Biology & Biochemistry 58 (2013) 61–69

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Effects of canopy tree species on belowground biogeochemistry in a lowland wet tropical forest

Adrienne B. Keller [a], Sasha C. Reed [b], Alan R. Townsend [c], Cory C. Cleveland [a,*]

[a] Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA
[b] U.S. Geological Survey, Southwest Biological Science Center, 2290 S.W. Resource Blvd., Moab, UT 84532, USA
[c] Institute of Arctic and Alpine Research and Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80303, USA

ARTICLE INFO

Article history:
Received 28 June 2012
Received in revised form
30 October 2012
Accepted 31 October 2012
Available online 26 November 2012

Keywords:
Biogeochemistry
Carbon
Nitrogen
Soil phosphatase enzymes
Phosphorus
Species effect
Tropical rain forest

ABSTRACT

Tropical rain forests are known for their high biological diversity, but the effects of plant diversity on important ecosystem processes in this biome remain unclear. Interspecies differences in both the demand for nutrients and in foliar and litter nutrient concentrations could drive variations in both the pool sizes and fluxes of important belowground resources, yet our understanding of the effects and importance of aboveground heterogeneity on belowground biogeochemistry is poor, especially in the species-rich forests of the wet tropics. To investigate the effects of individual tree species on belowground biogeochemical processes, we used both field and laboratory studies to examine how carbon (C), nitrogen (N), and phosphorus (P) cycles vary under nine different canopy tree species – including three legume and six non-legume species – that vary in foliar nutrient concentrations in a wet tropical forest in southwestern Costa Rica. We found significant differences in belowground C, N and P cycling under different canopy tree species: total C, N and P pools in standing litter varied by species, as did total soil and microbial C and N pools. Rates of soil extracellular acid phosphatase activity also varied significantly among species and functional groups, with higher rates of phosphatase activity under legumes. In addition, across all tree species, phosphatase activity was significantly positively correlated with litter N/P ratios, suggesting a tight coupling between relative N and P inputs and resource allocation to P acquisition. Overall, our results suggest the importance of aboveground plant community composition in promoting belowground biogeochemical heterogeneity at relatively small spatial scales.

1. Introduction

Individual trees can exert a "sphere of influence" on soil properties (Zinke, 1962), and aboveground plant diversity can drive local patterns in soil heterogeneity (e.g., Binkley and Giardina, 1998). Research has shown the chemistry of these spheres is more similar between individuals of the same species than among species, and that tree species differentially affect leaf litter and soil properties beneath their crowns, thereby regulating fundamental biogeochemical processes (Hobbie, 1992; Hobbie et al., 2006; Reed et al., 2008). Accordingly, a more complete understanding of tree species controls over ecosystem-scale biogeochemical cycles is necessary for assessing how changes to plant diversity and community composition (such as those resulting from climate and/or land use change, for example) may affect ecosystem function.

Species effects on soil biogeochemistry can result from both above- and belowground controls, and may operate through multiple mechanisms. For example, fine litterfall (i.e., leaves and smaller woody fractions) represents the dominant input of carbon (C) and nutrients to forest soils (e.g., Clark et al., 2001), and interspecies variation in foliar nutrient concentration may translate to differences in litter chemistry that both directly and indirectly affect pools and fluxes of belowground C and nutrients (Binkley and Giardina, 1998; Reed et al., 2008). This could, in turn, affect ecosystem processes including nutrient cycling, decomposition and soil C storage, among others (Melillo et al., 1982; Hobbie, 1992; Hirobe et al., 2004; Hobbie et al., 2006; Wieder et al., 2009; Russell et al., 2010). Similarly, species-specific variations in nutrient demand and acquisition may drive local heterogeneity in soil biogeochemistry. In particular, species differences in fine root production, mycorrhizal fungal associations and enzyme production,

* Corresponding author. Department of Ecosystem and Conservation Sciences, CHCB 423B, University of Montana, Missoula, MT 59812, USA. Tel.: +1 406 243 6018; fax: +1 406 243 6656.
E-mail addresses: adrienne.keller@gmail.com (A.B. Keller), screed@usgs.gov (S.C. Reed), alan.townsend@colorado.edu (A.R. Townsend), cory.cleveland@umontana.edu (C.C. Cleveland).

0038-0717/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.soilbio.2012.10.041

among others, may significantly alter belowground C and nutrient availability via variations in nutrient uptake (Binkley et al., 2000; Rillig et al., 2001; Eviner and Chapin, 2003; Finzi et al., 2007).

Field studies comparing soil biogeochemical properties beneath different tree species offer insight into the nature and magnitude of species effects *in situ*, and evidence suggests that species exert important differences in belowground C and nutrient pools (e.g. Finzi et al., 1998; Berger et al., 2002; Lovett et al., 2004; Ayres et al., 2009; Cross and Perakis, 2011). However, the majority of research to date has focused on relatively species-poor temperate forests. Yet, tropical rain forests boast some of the greatest plant biodiversity of any biome on earth and are disproportionately important in global biogeochemical cycles (Field et al., 1998; Phillips et al., 1998; Townsend et al., 2011). Previous research has highlighted the importance of linkages between biodiversity and biogeochemistry in tropical forests (Townsend et al., 2008), and aboveground biodiversity is reflected in high interspecific variation in foliar leaf nutrient concentrations. For example, foliar nitrogen (N), phosphorus (P) and N/P ratios have been shown to vary more among species in a given tropical forest site than across all temperate forests combined (Townsend et al., 2008). Still, our understanding of the effects of such aboveground biogeochemical heterogeneity on key belowground biogeochemical properties in tropical forests remains poor.

Relatively few studies have explored how individual tree species affect soil properties in tropical forests, and those that have report variable results. Some studies found significant species effects on belowground C and N cycling in southwestern Costa Rican and Brazilian rain forests (Reed et al., 2008; Wieder et al., 2008; Van Haren et al., 2010), while Powers et al. (2004) found no significant species effects in an eastern Costa Rican rain forest. Beyond C and N, species effects on P cycling in lowland tropical forests may be especially important to consider for several reasons: P is relatively immobile; tropical soil P availability is typically low (e.g., Sanchez, 1976; Sanchez et al., 1982; Vitousek and Sanford, 1986); and P has been shown to limit ecosystem processes in tropical forests (Cleveland et al., 2002; McGroddy et al., 2004; Wright et al., 2011; Santiago et al., 2012). In P-poor soils (like those that dominate much of the lowland tropics; Sanchez, 1976), both plants and microbes mineralize and acquire P largely via the production of extracellular phosphatases, enzymes that convert organic P into bio-available inorganic P (P_i) forms (McGill and Cole, 1981; Olander and Vitousek, 2000). Phosphatase production requires substantial quantities of N (Treseder and Vitousek, 2001) and N fertilization in low N soils has been shown to increase soil phosphatase activity (Olander and Vitousek, 2000), suggesting a tight coupling between soil N and P cycling and availability. Building on this idea, Houlton et al. (2008) suggested that interactions between N and P help explain the abundance of putative N-fixing legumes in tropical rain forests. From an N perspective, high N-fixer abundance in the relatively N-rich tropics represents something of a paradox, as N seems unlikely to limit plant growth and the ability to acquire N from the atmosphere should therefore not confer a competitive advantage. However, Houlton et al. (2008) proposed putative N-fixers (the majority of which are legumes) could indeed have a competitive advantage in P-poor tropical forests due to their ability to allocate excess N to produce phosphatases and acquire scarce P. While only a small minority of all legumes in the tropics are likely actively fixing N at a given time (Barron et al., 2010), unique physiological traits common to legumes – such as high foliar N – suggest the potential for a competitive advantage regardless of symbiotic N fixation. While there are insufficient data available to confirm this hypothesis, those that do exist suggest legumes and non-legumes may differentially affect belowground biogeochemistry through important N × P interactions (e.g., Marklein and Houlton, 2011).

The magnitude of species-specific effects on soil phosphatase activity may vary with differences in soil P availability (McGill and Cole, 1981), and may be particularly strong in the low P soils of many tropical forests. For example, while soil phosphatase activity did not vary by tree species in a relatively P-rich temperate forest (Weand et al., 2010), Ushio et al. (2010) reported a significant tree species effect on potential soil phosphatase activity in a montane tropical forest characterized by low soil P. In addition, species-specific strategies for procuring P may offer a competitive advantage in P-poor soils (Turner, 2008), such that different species may employ different P-acquiring enzymes to access different soil P pools. However, beyond the observation that soil phosphatase activity is higher under some legumes (Houlton et al., 2008), our understanding of the interactions and mechanisms behind the observed relationships between legumes and soil phosphatase activity is incomplete.

Here, our objective was to examine how soil C, N and P pools and fluxes vary under nine different lowland tropical forest canopy tree species, including three putative N-fixing legumes and six non-legumes. We hypothesized that individual canopy tree species would drive differences in belowground C, N and P pools due primarily to species-specific differences in litter chemistry. Next, we hypothesized that soil phosphatase activity would vary among species as well as by functional group, likely due to important belowground N × P interactions wherein legume trees would have access to greater N resources to allocate toward higher soil phosphatase production. We addressed these hypotheses using a combination of observational field studies and a laboratory incubation experiment and measured multiple pools of total and available C and nutrients as well as soil phosphatase activity.

2. Materials and methods

2.1. Study area

The study was conducted in a lowland tropical rain forest reserve on the Osa Peninsula in southwestern Costa Rica (8°24′ N 83°19′ W). Mean annual temperature at the site is ~26 °C, mean annual precipitation is 3450 mm, and the region experiences a dry season from December through April with heavy rains common throughout the rest of the year (as for a site ~30 km away described by Cleveland et al., 2004). The study area is located on upland soils classified as highly weathered, nutrient-poor Ultisols (Berrange and Thorpe, 1988). The Osa Peninsula is a biologically diverse ecosystem, home to approximately 700 different tree species and more than 4000 vascular plant species (Sanchez-Azofeifa et al., 2002; Kappelle et al., 2003). Although specific phenology varies by species in this semi-deciduous tropical rain forest, most tree species drop the majority of their leaves during the dry season and then leaf out again at the onset of the rainy season (Lobo et al., 2008).

2.2. Experimental design

Nine common canopy tree species were selected with 6–8 replicates per species for a total of 66 trees within a 1 km^2 study area. Tree species included three legume species (*Dialium guianense*, *Inga alba* and *Tachigali versicolor*) and six non-legume species (*Brosimum utile*, *Caryocar costaricense*, *Castilla tunu*, *Otoba novogranatensis*, *Pourouma bicolor* and *Socratea exorrhiza*). To investigate how variations in foliar and leaf litter chemistry relate to differences in belowground processes, we chose common species representing a wide spectrum of foliar nutrient concentrations (G.

Asner, unpublished results). Only trees with a diameter >10 cm and receiving full sun at some point during the day were included.

2.3. Soil and litter sampling

Soils were sampled under each tree twice – in April 2010 during the dry-to-wet season transition, and in July 2010 during the peak of the wet season – to capture some seasonal variability. Four 0–10 cm deep soil cores were taken with an 8 cm bulb corer at the four cardinal directions within 1 m of the base of each tree, likely capturing the most active horizon of belowground plant and soil microbial activity (Veldkamp et al., 2003). Soil samples were bulked by tree, homogenized by hand in the field, and sorted to remove roots and coarse fragments. All analyses were performed on these composite samples for each tree, giving a total of 66 samples. Recently fallen species-specific leaf litter (i.e., minimally decomposed standing litter composing the top-most portion of the litter layer) was also collected under each tree in April.

2.4. Soil and litter analyses

Within 12 h of collection, soil inorganic N (NH_4^+ and NO_3^-) was extracted from fresh soil samples by shaking 8 g soil in 25 mL of a 2 M KCl solution for 5 h. Extracts were filtered using Whatman glass microfiber filters (Grade GF/B, 47 mm), frozen and transported to the laboratory at the University of Montana for colorimetric analysis using a Synergy 2 Microplate Reader (BioTek, USA; Solorzano, 1969; Doane and Horwath, 2003). Fresh soil samples were also transported to the laboratory for soil microbial biomass analysis and stored at 4 °C to limit microbial activity after sampling until analyses were performed (within one week of field sampling). Microbial biomass C and N concentrations were determined using a chloroform fumigation-extraction method (Brookes et al., 1985) and 0.5 M K_2SO_4 extracts were analyzed using a Shimadzu TOC-V CPN/TNM-1 analyzer (Shimadzu Inc., Kyoto, Japan). Biomass estimates were calculated as the difference in C and N concentrations between fumigated and non-fumigated samples and standard k factor corrections (0.45 for C and 0.54 for N) were used.

Labile P and microbial biomass P were assessed using a NH_4F extraction (Bray and Kurtz, 1945; Oberson et al., 1997) and analyzed colorimetrically (D'Angelo et al., 2001). Labile P was calculated as the P present in non-fumigated samples and microbial biomass P was calculated as the difference between fumigated and non-fumigated samples and corrected for the efficiency of the digest (0.4 correction factor; Brookes et al., 1982), but not corrected to account for possible physical sorption of P mineralized during the fumigation (Oberson et al., 1997). Soil dry weights and percent moisture were determined gravimetrically by oven drying soils for 48 h at 105 °C. Total soil C and N were determined on dried and ground (using a mortal and pestle) samples using a CHNS-O elemental analyzer (CE Instruments EA 1110, Thermo Fisher, USA). Total soil P was determined on dried and ground samples using a nitric acid/hydrogen peroxide digest. Specifically, 16 mL of nitric acid were incrementally added to 0.4 g sample, heating to 95 °C after each addition until reaction was complete. After an additional 90 min at 95 °C, the samples were cooled and then 30% H_2O_2 was added incrementally until the sample no longer changed color. Samples were then heated at 85 °C for 2 h, after which 4 mL concentrated HCl were added to each sample and heated at 95 °C for 15 min. Finally, samples were diluted to 40 mL with deionized H_2O and left to settle overnight. Extracts were analyzed colorimetrically with a Synergy 2 Microplate Reader (Biotek Instruments, Inc., Winooski, VT USA; D'Angelo et al., 2001). Species-specific leaf litter samples were dried at 60 °C for two days and ground using a Wiley-Mill (20-mesh screen). Litter was ground to a fine powder using a mortal and pestle and total C, N and P of all litter samples were determined as described above for total C, N and P.

2.5. Enzyme assays

Potential rates of soil phosphatase activity were determined on subsamples of each composite soil sample that were frozen at −20 °C prior to analysis. Soil phosphatase activity was measured using a methylumbelliferyl (MUB)-linked substrate following the methodology of Saiya-Cork et al. (2002). Briefly, 1 g of fresh soil was homogenized with 125 mL of 50 mM sodium acetate buffer (pH 5) and 200 μL of the soil-buffer slurry was combined with 50 μL buffer and 50 μL of 200 μM 4-MUB phosphate. There were eight analytical replicates for each assay plus negative controls for sample and substrate fluorescence (i.e. quenching). Microplates were incubated in the dark for 3 h (an incubation time that was, after multiple tests, determined to correspond to the height of enzyme activity in the samples) and NaOH was not added prior to reading (365 nm excitation and 450 nm emission) due to the sensitivity of MUB fluorescence to NaOH over short time scales and the ability to acquire consistent results without NaOH addition (German et al., 2012). Enzyme activities were calculated as μmol h^{-1} g^{-1}.

2.6. Laboratory litter incubation experiment

To complement the field sampling and analyses, we also conducted a laboratory incubation experiment in an attempt to isolate the potential effects of species differences in litter chemistry on soil C, N and P pools, rates of C mineralization and soil phosphatase activity. Species-specific litter from six canopy tree species was incubated for 68 days with a composite soil from the site. Specifically, recently fallen leaf litter was collected in April under individuals for three legumes (*D. guianense*, *I. alba* and *T. versicolor*) and three non-legumes (*B. utile*, *C. tunu*, and *O. novogranatensis*), with three individual trees per species (for a total of 18 trees). Under each tree, litter was collected from the four cardinal directions within 1 m of the tree base and homogenized in the field, resulting in a total of 18 litter samples. At the start of the incubation, there were four replicates of each composite litter sample (for a total of 72 samples).

All litter samples were dried at 60 °C for two days and ground using a Wiley-Mill. Fresh soil collected in July from each tree as described above was composited using equal amounts of soil per tree (calculated by soil dry weight) to create a common bulk soil sample. In 50 mL plastic centrifuge tubes, 0.24 g of litter was mixed with 12 g of composite soil using a metal spatula for a 1:50 litter to soil ratio by mass. Samples were loosely covered with aluminum foil to allow for air flow and incubated in a dark cooler with moist paper towels (to maintain humidity) at 20 °C. Samples were maintained at field moisture by weighing tubes every seven days to determine moisture loss and adding sterilized deionized water with a micropipette as needed 24 h prior to measurement.

Rates of C mineralization were determined eight times across the 68-day experiment using a static-incubation procedure (Fierer et al., 2003). Six hours prior to sampling, tubes were opened to the atmosphere, gently fanned, and then sealed with air-tight plastic caps fitted with septa for gas-sampling. After the 6 h incubation period, headspaces were mixed with a syringe and a 5 mL sample from each tube was removed. C mineralization was measured using a gas chromatograph (Shimadzu Inc, Kyoto, Japan) equipped with a thermal conductivity detector and rates were calculated as CO_2 produced per gram sample per hour. On the same day C mineralization rates were measured, one replicate for each litter sample was destructively harvested and analyzed for inorganic N (as described above) and bicarbonate-extractable inorganic P

(Tiessen and Moir, 1993). Briefly, 30 mL 0.5 M $NaHCO_3$ was added to 1 g dry sample, shaken for 16 h, and centrifuged at 4500 rpm for 23 min. The supernatant was decanted and P content was analyzed colorimetrically (D'Angelo et al., 2001). Subsamples of each destructively harvested sample were stored at −20 °C for up to several months until being analyzed for potential rates of soil phosphatase activity (as described above).

2.7. Statistical analyses

All data were tested for normality and homoscedasticity using Shapiro–Wilk and Levene's tests, respectively. When assumptions of normality and variance homogeneity were not met, species differences were assessed using the Kruskal–Wallis non-parametric one-way analysis of variance test. Pairwise comparisons were performed using the Wilcoxon rank sum test with a Bonferroni correction. In cases with rank ties, exact *P*-values could not be calculated and approximate values are reported. Given that most of the data are non-normal, the median and a bootstrapped estimate of the standard error of the median (using 10,000 bootstrap samples) are provided along with the mean. A repeated measures general linear model was used to assess how rates of C mineralization varied among species and functional group through time, with species or functional group as the between-subject factor. Pearson correlation coefficients were calculated and simple linear regressions were used to determine relationships between pairs of quantitative data such as litter and soil chemistry. A significance threshold of $P < 0.05$ was used and all statistical analyses were performed using the open-source R software (R v. 2.13.0; R Development Core Team, 2010) or SPSS (v. 20.0; IBM Corporation).

3. Results

3.1. Field study

Litter and soil chemistry varied among canopy tree species but there was no direct relationship between the two (e.g., litter N/P ratios did not significantly correlate with soil N/P ratios). Chemical characteristics of species-specific litter and soil sampled below each canopy tree species are shown in Fig. 1 (see also Supplemental Table 1). Recently fallen species-specific standing leaf litter N and P concentrations and litter N/P ratios varied among all species ($P < 0.001$), as did leaf litter C/N ratios ($P < 0.001$) (Fig. 1; Supplemental Table 1). There were also significant differences in litter N concentrations and N/P ratios among functional groups: Legumes had higher N concentrations and higher N/P ratios compared to non-legume species ($P < 0.001$ for both %N and N/P ratios) and lower C/N ratios ($P < 0.001$) (Fig. 1). Species-specific leaf litter P content did not vary between legumes and non-legumes (Fig. 1).

There were significant differences in soil chemistry below different tree species, but not between functional groups. In all cases, tree diameter was not a significant factor in driving tree species differences. Total soil extractable organic C (TOC) and N (TN; both measured only in soils samples collected in April) varied significantly among species ($P < 0.001$ for both TOC and TN) but not between legumes and non-legumes (Supplemental Table 1). Soil TOC/TN ratios varied among species ($P = 0.009$) and showed marginally significant differences between functional groups ($P = 0.05$) (Supplemental Table 1). Soil inorganic N ($NH_4^+ + NO_3^-$) and Bray's extractable soil P concentrations did not vary significantly among species at either time point (Fig. 2; Supplemental Table 2). Overall, soil inorganic N concentrations were more than twice as large in April – during the dry-to-wet season transition – compared

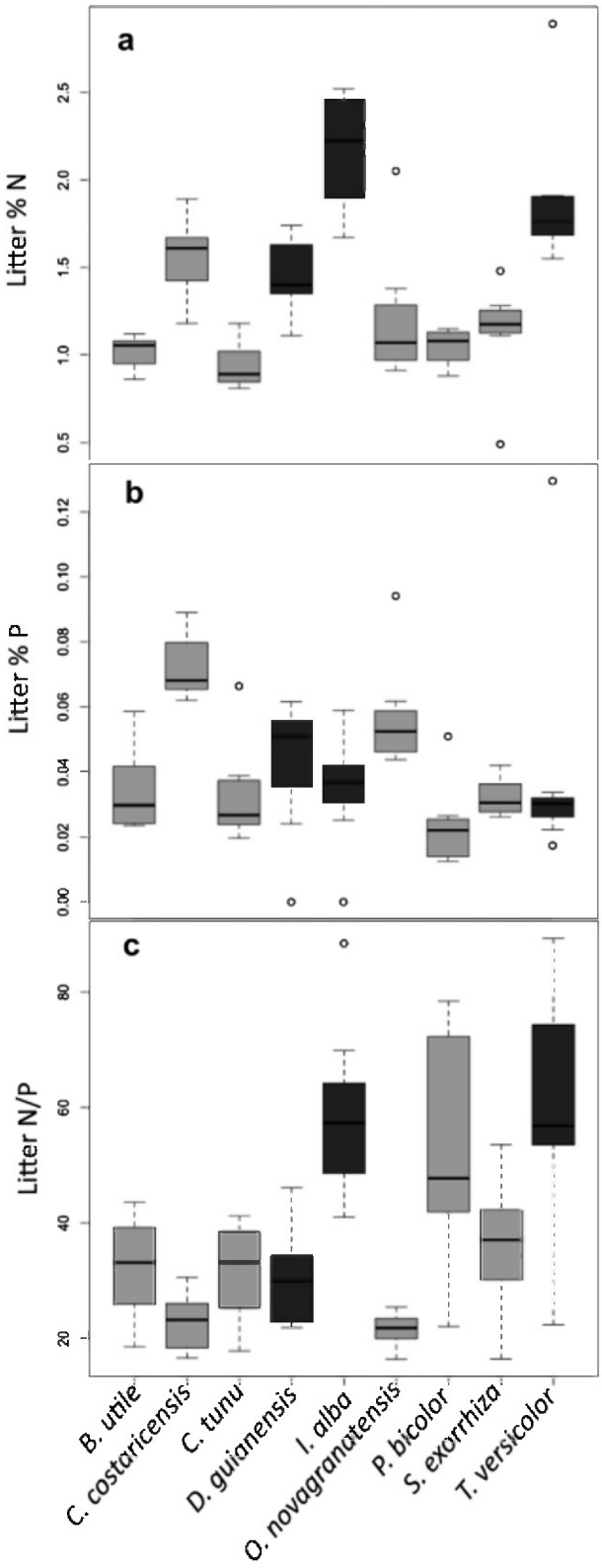

Fig. 1. Box-whisker plot showing species variation in total concentrations of leaf litter (a) N concentrations (b) P concentrations, and (c) N/P ratios. Plots show sample minimum, lower quartile, median, upper quartile, and sample maximum; outliers are depicted as open circles. Individual tree species on the *x*-axis are as follows: *Brosimum utile*, *Caryocar costaricensis*, *Castilla tunu*, *Dialium guianensis*, *Inga alba*, *Otoba novagranatensis*, *Pourouma bicolor*, *Socratea exorrhiza*, *Tachigali versicolor*. Light gray boxes correspond to non-legume species and dark gray boxes correspond to putative N-fixing species.

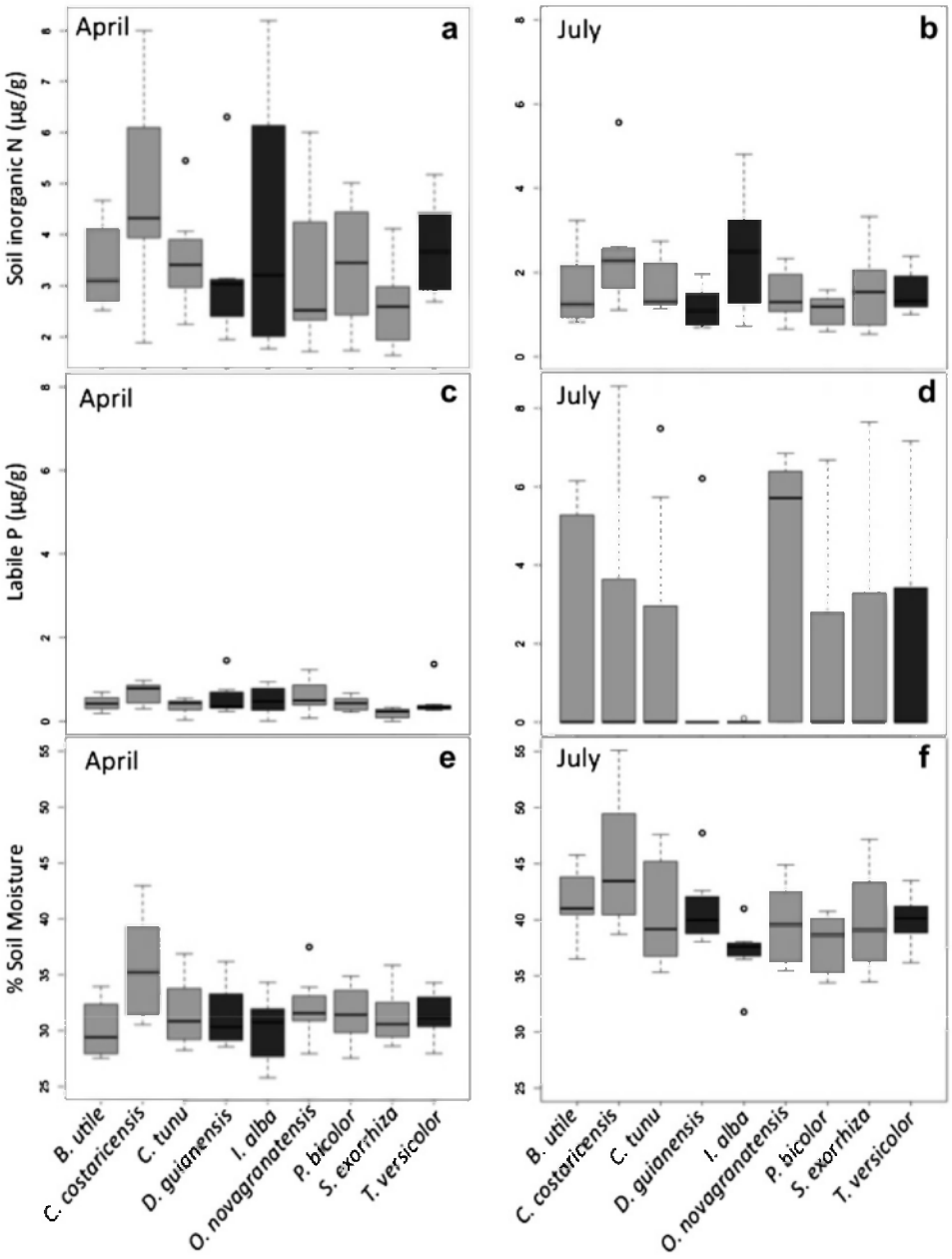

Fig. 2. Species variation in soil (a,b) extractable inorganic N, (c,d) extractable inorganic P and (e,f) soil moisture in April (left panels) and July (right panels). Plots show sample minimum, lower quartile, median, upper quartile, and sample maximum; outliers are depicted as open circles. Individual tree species on the *x*-axis as follows: *Brosimum utile*, *Caryocar costaricensis*, *Castilla tunu*, *Dialium guianensis*, *Inga alba*, *Otoba novagranatensis*, *Pourouma bicolor*, *Socratea exorrhiza*, *Tachigali versicolor*. Light gray boxes correspond to non-legume species and dark gray boxes correspond to putative N-fixing species.

to the peak of the wet season in July. Soil pH (measured on soils collected in April only) varied significantly among species ($P < 0.001$) and between functional groups ($P = 0.002$): soil pH under legumes was lower than soil pH under non-legumes (Supplemental Table 1). Mean soil moisture across all species was significantly higher in July ($P < 0.001$) and there was a marginally significant species effect on soil moisture in April ($P = 0.05$) and a stronger effect in July ($P = 0.02$) (Fig. 2). There were no significant differences in soil moisture content between functional groups at either time point.

Soil microbial biomass C concentrations varied significantly among species in both April and in July ($P = 0.02$ for both), but not between functional groups. A similar pattern was observed for microbial biomass N, with a significant species effect in April ($P = 0.004$) and a marginally significant effect in July ($P = 0.05$). However, there were no significant functional group differences in microbial biomass N for either April or July, and there were no significant species or functional group effects on microbial C/N ratios, microbial P or microbial N/P ratios at either time point (Supplemental Tables 2 and 3).

Soil phosphatase activity varied both among species ($P = 0.02$) and functional groups ($P < 0.001$) in April and July ($P < 0.01$ for both species and functional group) with higher activity under legumes (Fig. 3). There were also significant relationships between leaf litter nutrient stoichiometry (measured only on samples collected in April) and phosphatase activity (measured in April and in July). Litter N/P ratios from April positively correlated with soil phosphatase activity from both April and July ($r = 0.38$, $P = 0.002$

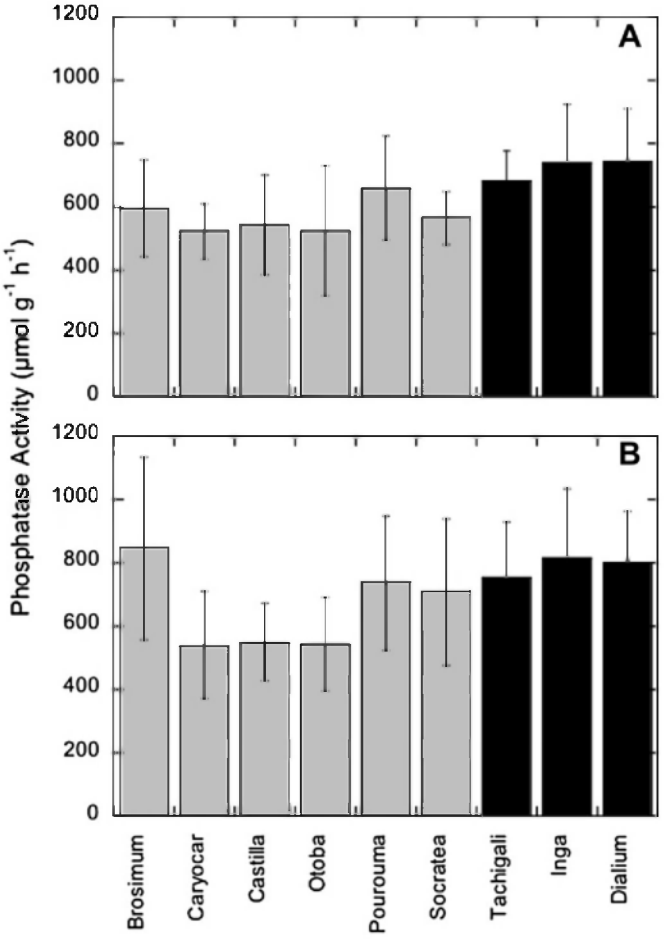

Fig. 3. Comparison of potential rates of soil acid phosphatase activity below nine different canopy tree species in April (A) and July (B). Bars represent means and error bars depict standard deviations. Putative N-fixing species are denoted by dark gray bars while light gray bars indicate non-N-fixers. No significant differences were found between individual species.

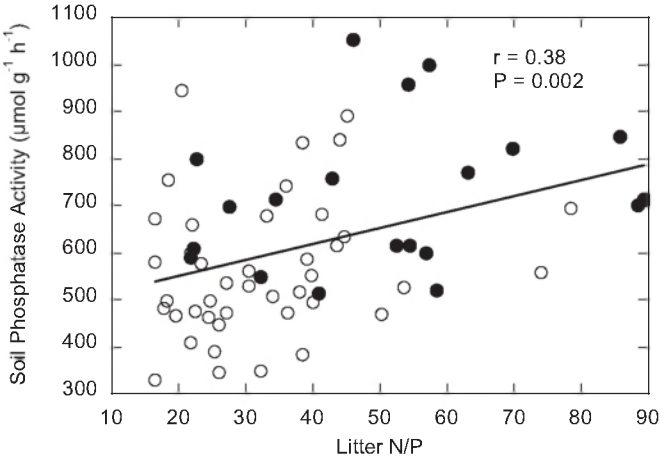

Fig. 4. Relationship between species-specific litter N/P and potential rates of soil acid phosphatase activity in April. Each point represents litter and soil enzyme data from under an individual tree. Putative N-fixing species are represented with black circles and non-legumes are shown with open circles. Significance and the correlation coefficient (r) are shown.

for each; Fig. 4). Litter N concentrations were also significantly related to potential soil phosphatase activity in April ($r = 0.25$, $P = 0.043$) while litter P concentrations were negatively correlated with soil phosphatase in July ($r = -0.29$, $P = 0.02$). However, when functional groups were analyzed separately, leaf litter N/P ratios were not a significant predictor of soil phosphatase activity for either legumes or non-legumes alone.

3.2. Laboratory incubation experiment

We observed species-specific differences in soil inorganic N concentrations on days 19, 43, and 68 ($P < 0.001$ for all time points), and both litter C/N and N/P ratios were significantly related to inorganic N availability at these time points ($P < 0.05$ in all cases). C/N ratios were negatively correlated with soil inorganic N at all time points, and litter N/P ratios showed inconsistent patterns. Soil inorganic bicarbonate-extractable P (P_i) varied by species at all time points ($P = 0.02$, $P < 0.001$, $P = 0.027$, $P = 0.033$ on days 1, 19, 43, and 68 respectively), but there were no significant relationships between litter C, N and P concentrations or ratios and soil extractable P_i at any time point.

Rates of C mineralization varied significantly by species ($P < 0.001$) and time ($P < 0.001$), such that the highest rates of mineralization were observed at the beginning of the incubation and generally decreased over time. There was also a significant interaction between species and time ($P = 0.003$): significant species effects on C mineralization rates were present during the initial stages of the incubation ($P = 0.01$, $P = 0.006$, $P = 0.02$, $P = 0.04$ on days 6, 8, 13, 19, respectively), but this species effect then disappeared until the final time point (day 68, $P = 0.02$). There was also a significant functional group × time interaction ($P < 0.001$) and although a significant functional group effect was not observed over the course of the incubation ($P = 0.392$), the final time point also marked the only time during which a significant functional group effect ($P = 0.018$) was apparent. Litter N/P ratios were the best predictor of cumulative C mineralization over the course of the experiment, with low litter N/P related to high cumulative C mineralization rates ($r = -0.56$, $P = 0.031$), although this relationship did not hold at all time points. There were no significant species or functional group differences in soil phosphatase activity at any time point during the incubation (Fig. 5). Litter P was the only significant predictor of soil phosphatase activity in the laboratory incubation and only on day 19.

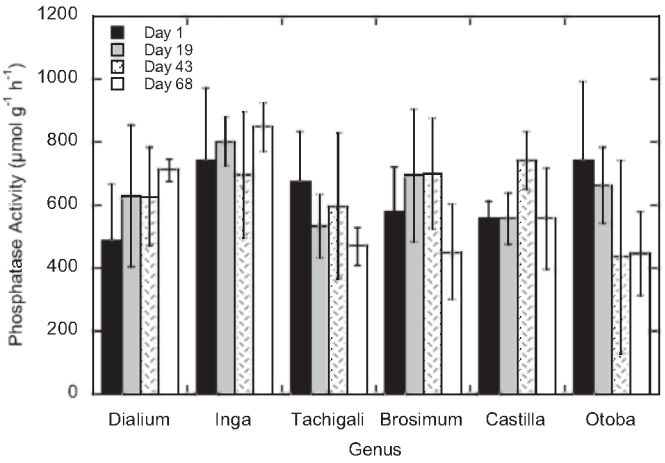

Fig. 5. Effects of species-specific litter on soil acid phosphatase activity in a laboratory incubation experiment. Bars represent means and error bars depict standard deviations. No significant species or functional group effect on enzyme activity was observed at any time point.

4. Discussion

Overall, our results show that even in this diverse lowland tropical rain forest, individual species have multiple measurable effects on belowground biogeochemistry. In addition to effects on soil C and nutrient pools and stoichiometry, species also appear to differentially regulate belowground nutrient cycling through N × P interactions. For example, phosphatase activity in soil collected under legumes was higher than in soil collected under non-legumes, and species with higher litterfall N/P ratios were associated with higher rates of soil phosphatase activity (Fig. 4). These results are not only some of the first from a wet lowland tropical forest to support the hypothesis that legumes may promote higher soil phosphatase activity than non-legumes (Houlton et al., 2008), but they also add nuance to our understanding of what drives variation in soil phosphatase activity. In particular, the pattern we observed between litterfall N/P ratios and soil phosphatase activity (Fig. 4) only holds when assessing both legumes and non-legumes together, suggesting that higher litter N/P ratios may result in elevated soil phosphatase activity regardless of the capacity to fix N. This relationship between litterfall N/P ratios and soil phosphatase activity may also lend insight into tropical species-specific canopy-to-soil biogeochemical 'footprints' (Reed et al., 2008), such that higher N/P ratios may result in higher soil phosphatase activity due to relatively more N and less P entering the soil.

While most studies that have investigated plant species effects on soil conducted to date have focused on temperate ecosystems (e.g., Boettcher and Kalisz, 1990; Finzi et al., 1998; Washburn and Arthur, 2003; Lovett et al., 2004; Cross and Perakis, 2011), the nature of such plant–soil relationships may be fundamentally different in lowland tropical forests. For example, litterfall chemistry – which varied significantly among species (Fig. 1) – may be particularly important in regulating belowground biogeochemistry in lowland tropical forests, where fine litterfall can account for ~ 50% of all aboveground net primary production (Clark et al., 2001), and complete litter turnover can occur over relatively short time scales (Gholz et al., 2000; Cleveland et al., 2006). Moreover, a large proportion of the nutrient pool in many nutrient-poor tropical forests is actively cycled through litterfall over relatively short timescales. Thus, litterfall plays an especially critical role in nutrient cycling in these ecosystems (Vitousek, 1982), implying that species differences in litter chemistry, and/or differences in resorption efficiency (Reed et al., 2012), could have a particularly strong effect on belowground nutrient heterogeneity and availability in lowland tropical forests. This suggests the presence of a strong plant–soil relationship, whereby observed belowground biogeochemical differences are largely a result of tree species effects on local soil properties. However, it may also be the case that such belowground differences favored the establishment of specific tree species due to their unique edaphic habitat preferences (John et al., 2007).

The litter incubation experiment was designed to isolate the potential effects of litter chemistry versus other possible belowground effects (e.g., species differences in root dynamics such as root exudates) on soil C, N and P pools and fluxes. Results showed species differences in litter chemistry drove significant differences in cumulative C mineralization and inorganic N availability. Species effects on C mineralization have been reported across multiple forest types (Wieder et al., 2008; Ayres et al., 2009; Yohannes et al., 2011) and could represent an important species-level control over ecosystem functioning, as C mineralization dynamics strongly influence both C and nutrient cycles (Wieder et al., 2008). Similarly, the direct relationship we observed between litter chemistry and inorganic N availability in the laboratory mirrors field study results obtained in other ecosystems (Finzi et al., 1998; Kamei et al., 2008; Ayres et al., 2009; but see Washburn and Arthur, 2003; Cross and Perakis, 2011). The absence of such a direct relationship in our field study may be due in part to rapid plant nutrient uptake. In particular, while larger available N pools may be expected under species with high litter N, high rates of N uptake can act to reduce variation in belowground N availability.

In the field, low soil P availability may drive species-specific differences that help explain the difference in phosphatase activity in the soils beneath legumes versus non-legumes. Low P availability may promote allocation of excess available N to soil phosphatase production (Houlton et al., 2008), directly from root-derived enzymes, indirectly from microbial phosphatase activity or a combination of both pathways. In contrast to the positive relationship observed between litter N/P and soil phosphatase activity in the field, we did not observe a significant relationship between litter P, microbial P or inorganic labile P in either the lab or the field. The lack of differences (in spite of species differences in litter P; Fig. 1) is not necessarily surprising given the relatively low P content of these highly weathered tropical soils (Bern et al., 2005; Townsend et al., 2002), and that much of P mineralized in soil may be rapidly occluded via P geochemical adsorption (Cleveland et al., 2002). Although movement of P and other nutrients into the soil via leaching from the litter layer may be high, rates of nutrient uptake and immobilization may also be high, resulting in low available soil nutrient concentrations. The consistently low extractable nutrient pools we observed across all tree species support this idea (Fig. 2; Supplemental Tables 2 and 3). At a nearby site Reed et al. (2008) did observe a significant relationship between leaf litter P and labile soil P, and the shallower soil depths used in that study could help explain the tighter coupling between litter and soil available P. In a study conducted in another tropical rain forest site, Powers et al. (2004) found no significant differences in soil chemistry, including extractable P, under four different tree species compared to a common putative N-fixing species (*Pentaclethra macroloba*). Yet, a lack of statistical power may have hindered the detection of an ecologically important species effect in the Powers et al. (2004) study. Taken together, our data and those of others suggest that available P pools in P-poor soils may not lend a great deal of insight into how P becomes available or how it is used, and investigations of processes such as P mineralization may offer more direct information into how P demand and acquisition vary.

In fact, potential soil phosphatase activity was the only belowground pool or flux measured in this study to show a significant direct relationship with litter chemistry. Species drove differences in several metrics of belowground biogeochemistry (namely TOC, TN and microbial biomass C and N), yet there were not direct relationships between species-specific litter chemistry and belowground inorganic or total C, N and P pools. These results differ from other studies showing a strong relationship between litter and soil N (Stump and Binkley, 1993; Van Cleve et al., 1993; Ferrari, 1999) and P concentrations (Reed et al., 2008) although the majority of these studies were carried out in low diversity, cool and relatively dry ecosystems.

Species can affect soil pH and soil moisture – edaphic factors that have been shown to indirectly affect belowground biogeochemistry by altering rates of decomposition, weathering and nutrient cycling, among others (Chapin et al., 2002). Such effects may combine to limit the direct relationship between litter and soil chemistry, and yet contribute to the overall observed species effect in important ways. For example, in an analysis of soils across the western hemisphere, Fierer and Jackson (2006) found that soil pH was a strong predictor of microbial community composition, which can affect rates of decomposition and nutrient cycling (Strickland et al., 2009; McGuire and Treseder, 2010). This result persisted at small scales, with soils from sites similar in climate and vegetation but varying in pH exhibiting different microbial communities.

Specifically, more acidic soils were characterized by lower microbial diversity and richness. Interestingly, here we found soil pH varied by species with more acidic soils generally found under legumes. Differences in microbial community composition can affect rates of decomposition as well as the retention of nutrients in the soil (Schimel et al., 2001; Zak et al., 2003). Thus, tree species effects on soil pH may drive differences in microbial community composition that in turn may locally affect C and nutrient pools and fluxes belowground.

Similarly, soil moisture affects rates of decomposition and nutrient cycling, with low soil moisture restricting diffusion of C and nutrients to microbes and high soil moisture limiting oxygen diffusion (Chapin et al., 2002). In both cases, microbial activity is reduced and decomposition and nutrient cycling slows. Here we found significant species effects on soil moisture as well as a seasonal effect with higher mean soil moisture in July. Thus, effects of species on edaphic soil properties as seen in this study may also contribute to species-driven variation in belowground biogeochemistry.

Overall, our results show tropical rain forest community composition can drive important differences in belowground biogeochemistry, including effects on soil C mineralization rates, P acquisition via soil phosphatase, and the stoichiometry of litterfall inputs. This study revealed significant variation in soil properties among nine canopy tree species, suggesting tropical species-specific influences on belowground heterogeneity at relatively small spatial scales. Such local variability and the importance of community composition on belowground processes should therefore be considered when extrapolating plot-level measurements across larger scales and when attempting to predict how these forests will respond to perturbations such as climate change (Pastor and Post, 1988; Prentice et al., 1993). It is expected that tree species will differentially respond to environmental changes and developing a more nuanced understanding of belowground biogeochemistry that considers the effects of the aboveground plant community will help us better predict –and mitigate – future changes to the biogeochemical cycles of these forests. In addition, shifts in aboveground plant community composition as a result of environmental changes – such as the predicted increase in drought across much of the tropics (Li et al., 2008; Malhi et al., 2009) or increased atmospheric N deposition (Galloway et al., 2004; Hietz et al., 2011) – may affect ecosystem processes in variable, non-random ways depending on the nature of change to the tree community composition. Finally, the strong species and functional group differences in soil phosphatase activity observed in this study add to a growing body of work suggesting that belowground N × P interactions are driven to a large extent by aboveground community composition. Developing a mechanistic understanding of these interactions is critical to broadly predicting aboveground-belowground linkages and the effects of environmental change on tropical ecosystem processes.

Acknowledgments

We thank Osa Conservation, F. Campos Rivera, the Organizacion para Estudios Tropicales (OET) and the Ministerio de Ambiente y Energia (MINAE) for access to field sites, assistance with research permits and logistical support in Costa Rica. We are grateful for field and laboratory assistance from Reinaldo Aguilar, Jay Aylward, Sarah Castle, Walkom Combronero-Castro, Tell Dietzler, Patrick Funk, Jonathan Leff, Megan Keville, Phillip Taylor, Samantha Weintraub, and William Wieder. Grants from the Andrew W. Mellon Foundation and the National Science Foundation supported this research. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2012.10.041.

References

Ayres, E., Steltzer, H., Berg, S., Wallenstein, M.D., Simmons, B.L., Wall, D.H., 2009. Tree species traits influence soil physical, chemical, and biological properties in high elevation forests. Plos One 4, e5964.
Barron, A.R., Purves, D.W., Hedin, L.O., 2010. Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. Oecologia 165, 511–520.
Berger, T.W., Neubauer, C., Glatzel, G., 2002. Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (*Picea abies*) and mixed species stands in Austria. Forest Ecology and Management 159, 3–14.
Bern, C.R., Townsend, A.R., Farmer, G.L., 2005. Unexpected dominance of parent material strontium in a tropical forest on highly weathered soils. Ecology 86, 626–632.
Berrange, J.P., Thorpe, R.S., 1988. The geology, geochemistry, and emplacement of the Cretaceous–Tertiary ophiolitic Nicoya Complex of the Osa Peninsula, southern Costa Rica. Tectonophysics 147, 193–220.
Binkley, D., Giardina, C., 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42, 89–106.
Binkley, D., Giardina, C., Bashkin, M.A., 2000. Soil phosphorus pools and supply under the influence of *Eucalyptus saligna* and nitrogen-fixing Albizia facaltaria. Forest Ecology and Management 128, 241–247.
Boettcher, S., Kalisz, P., 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. Ecology 71, 1365–1372.
Bray, R., Kurtz, L., 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Science 59, 39–46.
Brookes, P.C., Kragt, J.F., Powlson, D.S., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: the effects of fumigation time and temperature. Soil Biology and Biochemistry 17, 831–835.
Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement of microbial biomass phosphorus in soil. Soil Biology and Biochemistry 14, 319–329.
Chapin, F.S.I., Matson, P.A., Mooney, H.A., 2002. Principles of Terrestrial Ecosystem. Ecology. Springer, New York.
Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., Holland, E.A., 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications 11, 371–384.
Cleveland, C.C., Reed, S.C., Townsend, A.R., 2006. Nutrient regulation of organic matter decomposition in a tropical rain forest. Ecology 87, 492–503.
Cleveland, C.C., Townsend, A.R., Constance, B.C., 2004. Soil microbial dynamics in Costa Rica: seasonal and biogeochemical constraints. Biotropica 26, 184–195.
Cleveland, C.C., Townsend, A.R., Schmidt, S.K., 2002. Phosphorus limitation of microbial processes in moist tropical forests: evidence from short-term laboratory incubations and field experiments. Ecosystems 5, 680–691.
Cross, A., Perakis, S., 2011. Tree species and soil nutrient profiles in old-growth forests of the Oregon Coast Range. Canadian Journal of Forest Research 41, 195–210.
D'Angelo, E., Crutchfield, J., Vandiviere, M., 2001. Rapid, sensitive, microscale determination of phosphate in water and soil. Journal of Environmental Quality 30, 2206–2209.
Doane, T.A., Horwath, W.R., 2003. Spectrophotometric determination of nitrate with a single reagent. Analytical Letters 36, 2713–2722.
Eviner, V., Chapin, F.S., 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology, Evolution, and Systematics 34, 455–485.
Ferrari, J.B., 1999. Fine-scale patterns of leaf litterfall and nitrogen cycling in an old-growth forest. Canadian Journal of Forest Research 29, 291–302.
Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281, 237–240.
Fierer, N., Allen, A.S., Schimel, J.P., Holden, P.A., 2003. Controls on microbial CO_2 production: a comparison of surface and subsurface soil horizons. Global Change Biology 9, 1322–1332.
Fierer, N., Jackson, R., 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences 103, 626–631.
Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Ceulemans, R., 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. Proceedings of the National Academy of Sciences 104, 14014–14019.
Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecological Applications 8, 440–446.
Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michael, A.F., Porter, J.H., Townsend, A.R., Vorosmarty, C.J., 2004. Nitrogen cycles: past, present, and future. Biogeochemistry 70, 153–226.
German, D.P., Weintraub, M.N., Grandy, A.S., Lauber, C.L., Rinkes, Z.L., Allison, S.D., 2012. Response to Steen and Ziervogel's comment on "Optimization of

hydrolytic and oxidative enzyme methods to ecosystem studies." Soil Biology & Biochemistry 43, 1387–1397.
Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6, 751–765.
Hietz, P., Turner, B.L., Wanek, W., Richter, A., Nock, C.A., Wright, S.J., 2011. Long-term changes in the nitrogen cycle of tropical forests. Science 334, 664–666.
Hirobe, M., Sabang, J., Bhatta, B.K., Takeda, H., 2004. Leaf-litter decomposition of 15 tree species in a lowland tropical rain forest in Sarawak: dynamics of carbon, nutrients, and organic constituents. Journal of Forest Research 9, 347–354.
Hobbie, S., Reich, P., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288–2297.
Hobbie, S.E., 1992. Effects of plant-species on nutrient cycling. Trends in Ecology & Evolution 7, 336–339.
Houlton, B.Z., Wang, Y., Vitousek, P.M., Field, C.B., 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature 454, 327–330.
John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M., Foster, R.B., 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences of the United States of America 104, 864–869.
Kamei, J., Pandey, H.N., Barik, S.K., 2008. Tree species distribution and its impact on soil properties, and nitrogen and phosphorus mineralization in a humid subtropical forest ecosystem of northeastern India. Canadian Journal of Forest Research 39, 36–37.
Kappelle, M., Marco, C., Acevedo, H., Gonzalez, L., Monge, H., 2003. Ecosistemas del Area de Conservacion Osa (ACOSA). Instituto Nacional de Biodiversidad, San Jose.
Li, W., Fu, R., Juárez, R.I.N., Fernandes, K., 2008. Observed change of the standardized precipitation index, its potential cause and implications to future climate change in the Amazon region. Philosophical Transactions of the Royal Society Biological Sciences 363, 1767–1772.
Lobo, J., Aguilar, R., Chacon, E., Fuchs, E., 2008. Phenology of tree species of the Osa Peninsula and Golfo Dulce region, Costa Rica. Stapfia 88, 547–555.
Lovett, G.M., Weathers, K.C., Arthur, M.A., Schultz, J.C., 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochemistry 67, 289–308.
Malhi, Y., Aragao, L.E.O.C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., McSweeney, C., Meir, P., 2009. Exploring the likelihood and mechanism of a climate change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences of the United States of America 106, 20610–20615.
McGill, W.B., Cole, C.V., 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26, 267–286.
McGuire, K.L., Treseder, K.K., 2010. Microbial communities and their relevance for ecosystem models: decomposition as a case study. Soil Biology & Biochemistry 42, 529–535.
Marklein, A.R., Houlton, B.Z., 2011. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytologist 193, 696–704.
McGroddy, M.E., Daufrense, T., Hedin, L.O., 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. Ecology 85, 2390–2401.
Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.
Oberson, A., Friesen, D., Morel, C., Tiessen, H., 1997. Determination of phosphorus released by chloroform fumigation from microbial biomass in high P sorbing tropical soils. Soil Biology Biochemistry 29, 1579–1583.
Olander, L.P., Vitousek, P.M., 2000. Regulation of soil phosphatase and chitinase activity by N and P availability. Biogeochemistry 49, 175–191.
Pastor, J., Post, W.M., 1988. Response of northern forests to CO_2-induced climate change. Nature 334, 55–58.
Phillips, O., Malhi, Y., Higuchi, N., Laurance, W., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 16, 439–442.
Powers, J., Kalicin, M., Newman, M., 2004. Tree species do not influence local soil chemistry in a species-rich Costa Rica rain forest. Journal of Tropical Ecology 20, 587–590.
Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecological Modeling 65, 51–70.
Reed, S.C., Cleveland, C.C., Townsend, A.R., 2008. Tree species control rates of free-living nitrogen fixation in a tropical rain forest. Ecology 89, 2924–2934.
Reed, S.C., Townsend, A.R., Davidson, E.A., Cleveland, C.C., 2012. Stoichiometric patterns in foliar nutrient resorption across multiple scales. New Phytologist 196, 173–180.
Rillig, M.C., Wright, S.F., Nichols, K.A., Schmidt, W.F., Torn, M.S., 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. Plant and Soil 233, 167–177.
Russell, A.E., Raich, J.W., Arrieta, R.B., Valverde-Barrantes, O., Gonzalez, E., 2010. Impacts of individiual tree species on carbon dynamics in a moist tropical forest environment. Ecological Applications 20, 1087–1100.
Saiya-Cork, K.R., Sinsabaugh, R.L., Zak, D.R., 2002. The effects of long term nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. Soil Biology and Biochemistry 34, 1309–1315.
Sanchez, P.A., Bandy, D.E., Villachica, J.H., Nicholaides, J.J., 1982. Amazon Basin soils: management for continuous crop production. Science 216, 821–827.
Sanchez, P., 1976. Properties and Management of Soils in the Tropics. John Wiley & Sons, New York.
Sanchez-Azofeifa, G.A., Rivard, B., Calvo, J., Moorthy, I., 2002. Dynamics of tropical deforestation around national parks: remote sensing of forest change on the Osa Peninsula of Costa Rica. Mountain Research and Development 22, 352–358.
Santiago, L.S., Wright, S.J., Harms, K.E., Yavitt, J.B., Korine, C., Garcia, M.N., Turner, B.L., 2012. Tropical tree seedling growth responses to nitrogen, phosphorus, and potassium addition. Journal of Ecology 100, 309–316.
Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W., Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R.A., Melillo, J.M., Moore, B., Murdiyarso, D., Noble, I., Pacala, S.W., Prentice, I.C., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L., Wirth, C., 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414, 169–172.
Solorzano, L., 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnology and Oceanography 14, 799–801.
Strickland, M.S., Lauber, C., Fierer, N., Bradford, M.A., 2009. Testing the functional significance of microbial community composition. Ecology 90, 441–451.
Stump, L.M., Binkley, D., 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Canadian Journal of Forest Research 23, 492–502.
Tiessen, H., Moir, J.O., 1993. Characterization of available P by sequential extraction. In: Carter, M.R. (Ed.), Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton.
Townsend, A.R., Asner, G.P., Cleveland, C.C., Lefer, M.E., Bustamante, M.C., 2002. Unexpected changes in soil phosphorus dynamics following tropical deforestation to cattle pasture. Journal of Geophysical Research 107. http://dx.doi.org/10.1029/2001JD000650.
Townsend, A.R., Asner, G.P., Cleveland, C.C., 2008. The biogeochemical heterogeneity of tropical forests. Trends in Ecology & Evolution 23, 424–431.
Townsend, A.R., Cleveland, C.C., Houlton, B.Z., Alden, C.B., White, J.W., 2011. Multi-element regulation of the tropical forest carbon cycle. Frontiers in Ecology and the Environment 9, 9–17.
Treseder, K.K., Vitousek, P.M., 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. Ecology 82, 946–954.
Turner, B.L., 2008. Resource partitioning for soil phosphorus: a hypothesis. Journal of Ecology 96, 698–702.
Ushio, M., Kitayama, K., Balser, T.C., 2010. Tree species effects on soil enzyme activities through effects on soil physicochemical and microbial properties in a tropical montane forest on Mt. Kinabalu, Borneo. Pedobiologia 53, 227–233.
Van Cleve, K., Yarie, J., Erickson, R., 1993. Nitrogen mineralization and nitrification in successional ecosystems on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research 23, 970–978.
Van Haren, J.L.M., De Oliveira, R.C., Restrepo-Coupe, N., Hutyra, L., De Camargo, P.B., Keller, M., Saleska, S.R., 2010. Do plant species influence soil $CO_2$and N_2O fluxes in a diverse tropical forest? Journal of Geophysical Research 115, G03010.
Veldkamp, E., Becker, A., Schwendenmann, L., Clark, D.A., Schulte-Bisping, H., 2003. Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest. Global Change Biology 9, 1171–1184.
Vitousek, P.M., 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119, 553–572.
Vitousek, P.M., Sanford, J.R.L., 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecological Systems 17, 137–167.
Washburn, C.S.M., Arthur, M.A., 2003. Spatial variability in soil nutrient availability in an oak-pine forest: potential effects of tree species. Canadian Journal of Forest Research 33, 2321–2330.
Weand, M.P., Arthur, M.A., Lovett, G.M., Sikora, F., Weathers, K.C., 2010. The phosphorus status of northern hardwoods differs by species but is unaffected by nitrogen fertilization. Biogeochemistry 97, 159–181.
Wieder, W.R., Cleveland, C.C., Townsend, A.R., 2008. Tropical tree species composition affects the oxidation of dissolved organic matter from litter. Biogeochemistry 88, 127–138.
Wieder, W.R., Cleveland, C.C., Townsend, A.R., 2009. Controls over leaf litter decomposition in wet tropical forests. Ecology 90, 3333–3341.
Wright, S., Yavitt, J.B., Wurzburger, N., Turner, B.L., Tanner, E.V.J., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E., Garcia, M.N., Corre, M.D., 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92, 1616–1625.
Yohannes, Y., Shibistova, O., Abate, A., Fetene, M., Guggenberger, G., 2011. Soil CO_2 efflux in an Afromontane forest of Ethiopia as driven by seasonality and tree species. Forest Ecology and Management 261, 1090–1098.
Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84, 2042–2050.
Zinke, P., 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43, 130–133.