

## Variation in Canopy Litterfall Along a Precipitation and Soil Fertility Gradient in a Panamanian Lower Montane Forest

Katherine D. Heineman<sup>1,5</sup>, Pedro Caballero<sup>2</sup>, Arturo Morris<sup>2</sup>, Carmen Velasquez<sup>2</sup>, Kiria Serrano<sup>2</sup>, Nelly Ramos<sup>2</sup>, Jonathan Gonzalez<sup>2</sup>, Luis Mayorga<sup>2</sup>, Marife D. Corre<sup>3</sup>, and James W. Dalling<sup>1,4</sup>

<sup>1</sup> Department of Plant Biology and Program for Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, IL 61801, U.S.A.

<sup>2</sup> Departamento de Biología, Universidad Autónoma de Chiriquí, David, Panama

<sup>3</sup> Soil Science of Tropical and Subtropical Ecosystems, Büsgen Institute, Georg-August-University Göttingen, Büsgenweg 2, 37077 Göttingen, Germany

<sup>4</sup> Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

### ABSTRACT

Fertilization experiments in tropical forests have shown that litterfall increases in response to the addition of one or more soil nutrients. However, the relationship between soil nutrient availability and litterfall is poorly defined along natural soil fertility gradients, especially in tropical montane forests. Here, we measured litterfall for two years in five lower montane 1-ha plots spanning a soil fertility and precipitation gradient in lower montane forest at Fortuna, Panama. Litterfall was also measured in a concurrent nitrogen fertilization experiment at one site. Repeated-measures ANOVA was used to test for site (or treatment), year, and season effects on vegetative, reproductive and total litterfall. We predicted that total litterfall, and the ratio of reproductive to leaf litterfall, would increase with nutrient availability along the fertility gradient, and in response to nitrogen addition. We found that total annual litterfall varied substantially among 1-ha plots (4.78 Mg/ha/yr to 7.96 Mg/ha/yr), and all but the most aseasonal plot showed significant seasonality in litterfall. However, litterfall accumulation did not track soil nutrient availability; instead forest growing on relatively infertile soil, but dominated by an ectomycorrhizal tree species, had the highest total litterfall accumulation. In the fertilization plots, significantly more total litter fell in nitrogen addition relative to control plots, but this increase in response to nitrogen (13%) was small compared to variation observed among 1-ha plots. These results suggest that while litterfall at Fortuna is nutrient-limited, compositional and functional turnover along the fertility gradient obscure any direct relationship between soil resource availability and canopy productivity.

Abstract in Spanish is available in the online version of this article.

*Key words:* ectomycorrhizal trees; environmental gradients; fertilization experiment; Fortuna Forest Reserve; nutrient limitation; tropical forest productivity; tropical forest seasonality; tropical montane forest.

LITTERFALL IS THE DEPOSITION OF LEAVES, TWIGS, REPRODUCTIVE TISSUE, and other organic matter from the forest canopy onto the forest floor. Litterfall represents a large fraction (~30%) of forest net primary productivity (NPP; Aragão *et al.* 2009) with important impacts on soil microbial communities and soil carbon storage (Sayer *et al.* 2012). Litter production has also been used as an indicator of nutrient limitation to forest productivity. In tropical forests, total litter biomass has been shown to increase relative to unfertilized controls in response to experimental N addition (Adamek *et al.* 2009), P addition (Wright *et al.* 2011), or both (Tanner *et al.* 1992).

While experimental nutrient addition suggests that litterfall is sensitive to soil nutrient availability, comparisons of litterfall rates across natural fertility gradients show contrasting effects on canopy net primary productivity. In a comparison across 81 sites in South American tropical forests, Chave *et al.* (2010) found that annual rainfall did not explain any variation in annual litterfall.

Furthermore, litterfall did not vary consistently with soil type, except for reduced litterfall on the most infertile white sand soils. In a similar comparison across ten lowland Amazonian sites ranging from infertile white sand forest to fertile *terra preta* forest, Aragão *et al.* (2009) found that litterfall did increase significantly with soil P availability (see also Vitousek 1984, Silver 1994).

Not only does litterfall represent an important allocation of forest productivity, it also represents the primary means by which labile nutrients are returned to the soil and made available for plant nutrition. The production of low quality, difficult to decompose litter with high carbon to nutrient ratios is simultaneously an adaptation to a low nutrient environment and a perpetuator of nutrient limitation. In particular, the concentration of nitrogen in litterfall varies widely among forest types and correlates with the amount of nitrogen deposited by litterfall each year (Vitousek 1984). Recent studies have suggested that forests differing in the relative abundance of taxa with ectomycorrhizal (EM) versus arbuscular mycorrhizal (AM) fungal associations may have marked differences in nitrogen cycling related to differences in litter quality and decomposition in AM and EM stands (Phillips *et al.*

Received 23 September 2014; revision accepted 5 January 2015.

<sup>5</sup>Corresponding author; e-mail: kheineman@life.illinois.edu

2013). Lower montane Neotropical forests represent an ecotone where lowland AM-associated communities transition to montane communities dominated by EM-associated members of the Fagales and, therefore, present an opportunity to explore differences in litterfall patterns between tree communities with contrasting functional groups that are related to nutrient acquisition.

Despite the large number of litter collection studies, canopy productivity remains relatively poorly estimated for montane forests relative to lowland tropical forest. The Chave *et al.* (2010) meta-analysis of 81 South American forests contained data from only five montane plots located in two study sites (Veneklaas 1991, Röderstein *et al.* 2005). Another pan-tropical compilation of litterfall datasets (Leigh 1999) includes more montane sites (14 of 52 sites have >800 m elevation; replicate plots and years excluded); however, interpretation of differences in litterfall rates among these more diverse sites is potentially confounded by differences in litterfall collection methods and litter classification (Proctor 1983).

Litterfall rates might be expected to be low in montane forests relative to lowland forests because total NPP generally declines with elevation (Raich *et al.* 1997, Kitayama & Aiba 2002, Moser *et al.* 2011). For example, Girardin *et al.* (2010) found that no sites >1000 m asl had higher NPP than any lowland Amazonian site, including sites located in infertile white sand forests. Furthermore, canopy NPP is positively correlated with stem NPP across lowland and montane sites (Aragão *et al.* 2009), and also declined with elevation in the Girardin *et al.* (2010) study. Constraints on productivity resulting from reduced irradiance or nutrient availability in montane forest might also be expected to impact reproductive allocation. Although data on fruit production are more limited than leaf or total litterfall, production of reproductive organs has been shown to decline strongly with elevation, and as a proportion of total canopy NPP from 1000 to 3000 m elevation (table 2 in Moser *et al.* 2011). Comparisons across soil gradients also suggest that proportional reproductive allocation increases with increasing fertility (van Schaik & Mirmanto 1985, Chave *et al.* 2010).

In this study we compare total, vegetative, and reproductive litterfall rates across five one-hectare plots in lower montane forest in western Panama with contrasting soil fertility and precipitation regimes, and across a replicated nitrogen addition experiment at one site. We hypothesized that if soil nutrient availability is a strong driver of forest productivity in montane forest, and if leaf production is prioritized over investment in reproduction under nutrient poor conditions, then total litter biomass, and the ratio of reproductive to vegetative biomass will increase with soil fertility, and with nitrogen addition. In contrast, we predicted that in these wet forests, rainfall regime would have a stronger effect on seasonality of litterfall rather than on total litterfall production.

## METHODS

**STUDY SITE.**—Fieldwork was conducted at the Fortuna Forest Reserve (19,500 ha), located in western Panama in the province of Chiriqui, and the adjacent Palo Seco Forest Reserve

(125,000 ha) in the province of Bocas Del Toro (Fig. S1). The area encompasses lower montane forests ranging between 700 and 1500 m asl. Mean annual rainfall at the study sites ranges between ~5100 and 7200 mm depending on orographic position (Table 1). There is seasonality in rainfall, but mean monthly rainfall in the drier months (January to April) exceeds 100 mm at all the sites. Mean annual temperature ranges from 19 to 22°C across the study sites (Andersen *et al.* 2009).

Within the study region, we measured litterfall in five one-hectare permanent forest inventory plots (Fig. S1). The plots differ in canopy tree species composition (J. Dalling, unpubl. data), reflecting underlying geology and soils (Table 1). Two plots occur on low fertility rhyolitic tuff (Honda and Chorro), and support forests dominated by the ectomycorrhizal tree *Oreomunnea mexicana* and the canopy palm *Colpothrinax apbenopetala*, respectively. Two plots occur on intermediate fertility andesite, and support high diversity mixed forest (Samudio and Palo Seco), and one plot occurs on high fertility porphyritic dacite, supporting mixed Lauraceae and oak forest (Hornito).

We conducted a detailed inventory of soil samples in each 1-ha plot in 2008 to evaluate the influence of soil variables in structuring understory palm communities. We took soil samples from 0 to 10 cm depth from 13 locations per plot and analyzed in the STRI soil analysis lab. Soil properties measured included extractable inorganic nitrogen (NH<sub>4</sub> and NO<sub>3</sub>), exchangeable phosphorus and cations (Al, Ca, Fe, K, Mg, Zn) concentrations (Mehlich-3 extraction), pH, bulk density, net nitrogen mineralization, and nitrification rates. A subset of these measures are listed in Table 1. For detailed methods of each soil property measured, see Andersen *et al.* (2009).

**STUDY PLOTS AND SAMPLING REGIME.**—We spaced thirteen 0.71 m<sup>2</sup> litter traps equally across each 1-ha plot in a stratified random design. Traps were constructed of polyvinyl chloride tubing, raised 1 m above the ground with 2 mm nylon mesh suspended to capture falling litter. We collected litter from each trap every 2 weeks from August 2008 to December 2010 and sorted them into six categories: leaf, bark, branch, fruit, flowers, and other (principally epiphytes and canopy soil). We dried litter samples at 60°C for 72 h and weighed them. Based on repeated weighing of litter samples after 72, 96, and 120 h for the first four collection periods, we determined that 72 h of drying was sufficient for samples to achieve constant mass. In addition, on three sampling dates between November 2008 and July 2009, we collected random subsamples of leaf litter from each site, pooled within a site, ground and analyzed them for total carbon and nitrogen using a Thermo Flash EA112 analyzer (CE Elantech, New Jersey, U.S.A.).

In addition to litterfall data collected across the five plots representing a natural gradient in soil fertility, we also included data on litterfall collected using the same methodology in four 0.16-ha paired control and nitrogen-addition plots, which are part of an on-going nitrogen manipulation experiment ‘NITROF’ ~150 m from the Honda plot (Adamek *et al.* 2009). NITROF plots were established in 2006. Fertilized plots received 125 kg

TABLE 1. Compositional, structural, and environmental characteristics of the five-one-hectare permanent forest inventory sites. Sites are ordered by increasing soil fertility. Rainfall data are means from 2007 to 2013. Dry-season rainfall covers 1 January–30 April. Soil variables were measured at 13 locations per plot in the top 10 cm of soil (Andersen et al. 2009, 2012) and are presented in volumetric units to account for variation in bulk density among sites. Litter data ( $\pm 1$  SD).

Site	Chorro	Honda <sup>1</sup>	Samudio	Palo Seco	Hornito
Substrate	Rhyolitic tuff	Rhyolitic tuff	Andesite	Andesite	Dacite
Dominant species	<i>Colpothrinax aphanopetala</i>	<i>Oreomunnea mexicana</i>	Mixed forest	Mixed forest	Mixed forest
Basal Area (m <sup>2</sup> )	34.2	42.2	39.7	32.5	52.9
% Ectomycorrhizal basal area	7%	24%	1%	0%	3%
% Palm basal area	42%	0.5%	0.5%	2%	0%
Elevation (m)	1100	1074	1232	878	1330
Annual temperature (°C)	20.5	20.2	19.7	21.8	19.2
Annual rainfall (mm)	5434	7246	5105	6032	5477
Proportion of rainfall in dry season (mm)	26%	22%	17%	29%	15%
Soil pH	3.91	4.63	5.06	5.08	5.76
Soil inorganic N ( $\mu\text{g N}/\text{cm}^3$ )	0.63	3.40	1.42	2.90	4.52
NH <sub>4</sub> :NO <sub>3</sub>	5.47	4.65	7.09	10.30	10.08
Nitrification rate ( $\mu\text{g N}/\text{cm}^3/\text{day}$ )	0	−0.03	0.10	0.29	0.12
Mehlich extractable soil P ( $\mu\text{g P}/\text{cm}^3$ )	2.74	1.70	3.67	3.91	10.92
Litter N (% N)	1.18 (0.15)	1.39 (0.14)	1.38 (0.22)	1.81 (0.22)	1.66 (0.14)
Litter C:N	38.0 (4.9)	33.0 (3.6)	32.4 (4.6)	24.5 (3.3)	27.1 (2.8)

<sup>1</sup>Honda A in Andersen et al. (2009).

urea-N/ha/yr, applied four times per year. We collected litterfall every 2 weeks from four 0.5 m<sup>2</sup> traps per plot. We constructed traps in the same way as those used in the 1 ha plots and sorted, dried and weighed litter using the same criteria.

Previous authors have suggested that traditional measures of canopy productivity underestimate the litterfall contribution of palm fronds that are too large to fit into standard litterfall baskets (Chave et al. 2010). A comparison of palm litterfall accumulation in three Brazilian forest plots found that 0.32 m<sup>2</sup> litter fall baskets collected 18–30 times less palm litter biomass per unit area than 5 m × 5 m ground plots (Villela & Proctor 1999). To estimate leaf litterfall produced by canopy palms at Chorro, we measured leaf production in the canopy palm *Colpothrinax aphanopetala* for 1 year (August 2011–July 2012) in 30 palms located inside or within 100 m of the Chorro 1-ha plot. We selected individuals with >10 leaves for which all fully expanded leaves could be tagged from the ground (average height of 4.82 m). We assumed that leaf production of subcanopy palms would be similar to leaf production of taller canopy palms due to the high light availability in the understory of this forest (8–10%), and because the shorter palms measured and adult canopy palms did not differ significantly in their average number of leaves.

In July 2012, untagged leaves were counted to determine annual leaf production. We measured the dry mass of three senescing leaves on one *Colpothrinax* individual harvested for destructive biomass estimation. To estimate annual leaf litterfall biomass for *Colpothrinax* in Chorro, we multiplied senescing leaf dry mass (1.365 kg/leaf) × average annual leaf production (2.6

leaves/yr) × number of individuals *Colpothrinax* recorded in the 2008 census of the Chorro plot (173 trees).

DATA ANALYSIS.—We used repeated-measures ANOVA models to test for a plot × year interaction on annual accumulation of total, leaf, reproductive, and the ratio of reproductive to leaf litterfall in the five 1-ha plots in 2009 and 2010. Because there is considerable spatial variation in canopy litterfall (Burghouts et al. 1998), we used litterfall basket as unit of replication to quantify uncertainty in our estimates of annual litterfall. This approach is consistent with how other studies comparing litterfall across forest types have been performed (e.g., Proctor 1983, Dantas & Phillipson 1989, Dezzio & Chacón 2006).

We tested for seasonality in the monthly accumulation rate of each litterfall component in the 1-ha plots using models including a plot × season interaction, where dry season was defined as 1 January–30 April of each year. We calculated the annual or seasonal accumulation of litter in each basket by summing the dry weight of each litter component across biweekly collection periods for the specified time interval. In each model, litterfall basket was designated as a random effect to reduce the number of degrees of freedom incurred by the repeated measurement of the same locations each year or season. Denominator degrees of freedom used to determine *P* values of fixed effects were calculated using the lmerTest package (Kuznetsova et al. 2014), which applies the Satterthwaite approximation (Satterthwaite 1946) to linear mixed effects models created in the lme4 package (Bates et al. 2014) in R (R Development Core Team 2014).

We tested for the effects of nitrogen addition and year on annual accumulation of the total, leaf, and reproductive litterfall in the NITROF plots for the same time period (2009–2010) using a two-way ANOVA. We do not present the results for the treatment  $\times$  year interaction, as it was not significant in any comparison. Each 40 m  $\times$  40 m plot, including four control and four nitrogen-addition plots, was treated as an independent unit of replication.

## RESULTS

**AMONG SITE VARIATION IN LITTERFALL.**—For total annual litterfall, there were significant differences among the 1 ha plots at Fortuna (Fig. 1A), with mean dry mass ranging from 4.78 Mg/ha/yr to 7.96 Mg/ha/yr ( $F = 9.16$ ,  $df = 4,60$ ,  $P < 0.001$ ), and in leaf litterfall (range 3.00–5.16 Mg/ha/yr;  $F = 14.96$ ,  $df = 4,60$ ,  $P < 0.001$ ). Elemental analysis of litter samples revealed significant variation in leaf litter nitrogen concentration ( $F = 6.31$ ,  $df = 4,11$ ,  $P = 0.070$ ), and C:N ( $F = 5.92$ ,  $df = 4,11$ ,  $P = 0.008$ ). Leaf litter N was lowest on the two rhyolite soils (Chorro and Honda) and highest at Palo Seco and Hornito; variation in N was also reflected in litter C:N (Table 1). Differences in total litterfall and litter chemistry among sites also resulted in significant differences in the amount of nitrogen deposited by litterfall, varying two-fold among plots from 56 kg N/ha/yr to 120 kg N/ha/yr ( $F = 16.19$ ,  $df = 4,60$ ,  $P < 0.001$ ).

Support for our hypothesis that litterfall would correlate with soil nutrient availability was weak. While total litterfall and leaf litterfall tended to increase with soil fertility (Fig. 2A), the second most infertile site, Honda, had the highest litterfall. Similarly, although the total amount of N deposited by litter was highest in

the most fertile site, Hornito, and lowest in the least fertile site, Chorro, in both 2009 and 2010, nitrogen in litterfall did not correspond directly with soil fertility due to the relatively high N production in Honda (Fig. 2A). Variation in litterfall among sites could be explained in part by variation in basal area among sites (Table 1). When total litterfall was expressed on a per unit basal area basis, Honda still had the highest litter production rate during the 2 year collection period (Fig. 1B), but overall variance in total litterfall explained by the site was smaller when litterfall was adjusted by basal area (site effect per land area:  $F = 9.16$ ; plot effect per basal area:  $F = 5.37$ ; Table S1).

The accumulation of total reproductive litterfall differed significantly among sites ( $F = 2.90$ ,  $df = 4,60$ ,  $P = 0.029$ ), as did the ratio of reproductive to leaf litterfall ( $F = 5.80$ ,  $df = 4,60$ ,  $P < 0.001$ ). However, contrary with our prediction, the ratio of reproductive to non-reproductive litter was *highest* at the lowest fertility site, Chorro (Fig. 2B). High proportional allocation to reproduction at Chorro reflected both high reproductive biomass and low leaf and support (*i.e.*, branches, bark, epiphytes) biomass (Fig. 1).

**INTERANNUAL VARIATION IN LITTERFALL.**—The magnitude of interannual variation in total litterfall was highly site specific (range in percent change: 2–29%). Significantly more litter fell in 2009 (the year of a large storm event) than in 2010 in two sites: Honda and Samudio, while total accumulation in Palo Seco, the only site on the Caribbean slope, was greater in 2010 than 2009 (Fig. 1; site  $\times$  year interaction:  $F = 4.30$ ,  $df = 4,60$ ,  $P = 0.004$ ). Across all plots, significantly more leaf litter fell in 2009 than in 2010; however, the magnitude of this difference was small relative to interannual variation in total litterfall (range in percent change

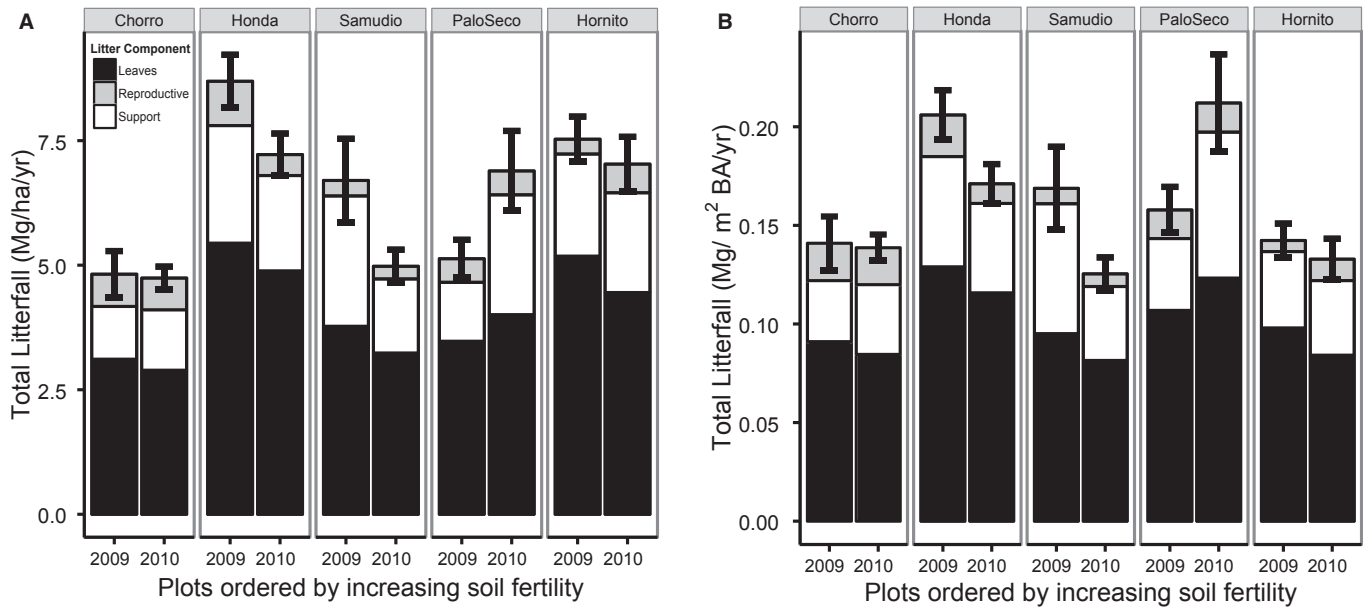


FIGURE 1. (A) Mean annual litterfall (Mg/ha/yr) measured over the calendar years 2009 and 2010 at each of the site ordered by increasing soil fertility. Stacked bars represent the contributions of each litter fraction (support = wood, bark, and epiphytes); error bars are standard errors calculated on total litterfall. (B) Mean annual litterfall adjusted for differences in basal area among plots (Mg/m<sup>2</sup> basal area/yr).

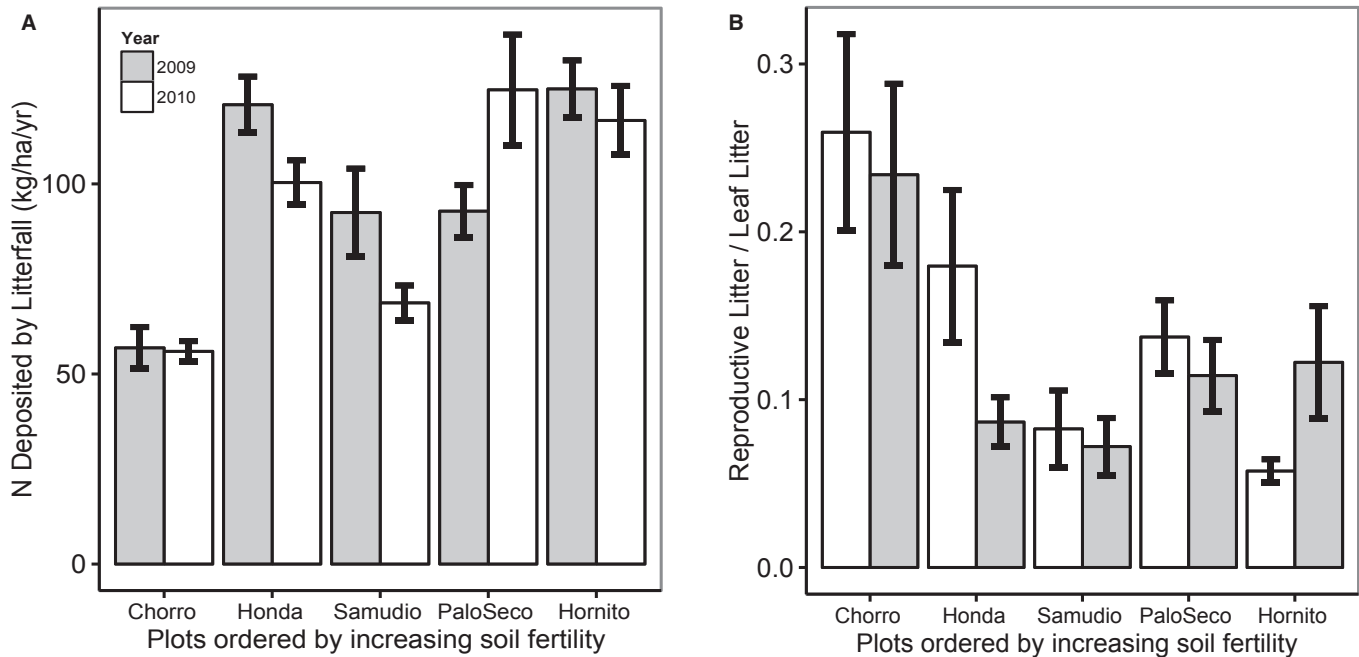


FIGURE 2. (A) Mean annual nitrogen (N) deposited by litterfall (kg/ha/yr) and (B) ratio of reproductive to leaf litter biomass among sites in 2009 and 2010.

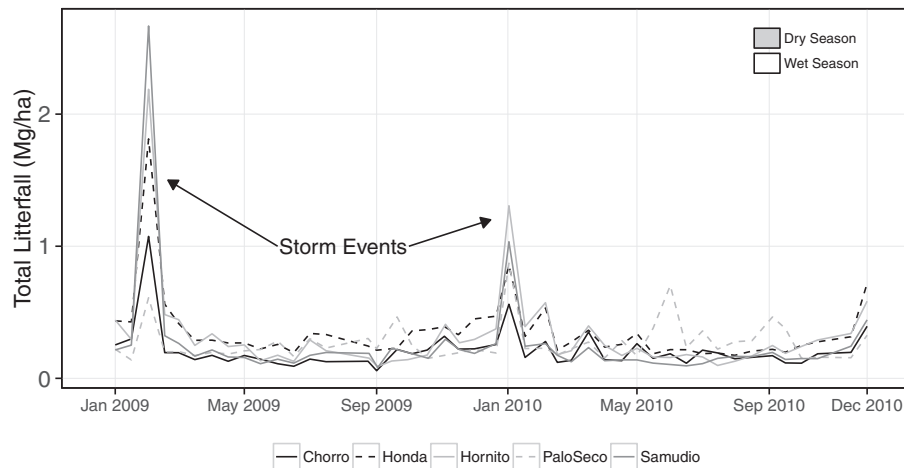


FIGURE 3. Across-site comparison of total litterfall biomass over the 2-year collection period. The litter collected following the severe storm in February 2009 accounted for 25 percent of the litter biomass measured that year.

10–15%; year effect:  $F = 4.06$ ,  $df = 1,60$ ,  $P = 0.048$ ). There was a significant site  $\times$  year interaction in the production of reproductive litterfall: the accumulation of fruits and flowers differed substantially between 2009 and 2010 at Honda and Hornito (Fig 2B), while reproductive litterfall did not differ between years at Palo Seco, Chorro or Samudio (range 0.1–71%; site  $\times$  year interaction  $F = 3.28$ ,  $df = 4,60$ ,  $P = 0.017$ ).

SEASONALITY.—Two large peaks in litterfall were observed over the study period in all the five sites (Fig 3), occurring in the early dry season (February 2009 and January 2010). These peaks

coincided with severe storms and accounted for up to 40 percent of annual litterfall at Samudio in 2009, and 21 percent of annual litterfall at Samudio in 2010. When total litterfall was calculated for the dry and wet seasons there was a significant site  $\times$  season interaction in total litterfall production ( $F = 3.06$ ,  $df = 4,190$ ,  $P < 0.001$ ). With the exception of the aseasonal site of Palo Seco, there was significantly more monthly total, leaf, and support litterfall in the dry season than wet season (Fig. 4A, B and D). In contrast, monthly accumulation of reproductive litterfall was greater in the wet season than the dry season (season effect:  $F = 5.31$ ,  $df = 1,190$ ,  $P = 0.020$ ; Fig. 4C).

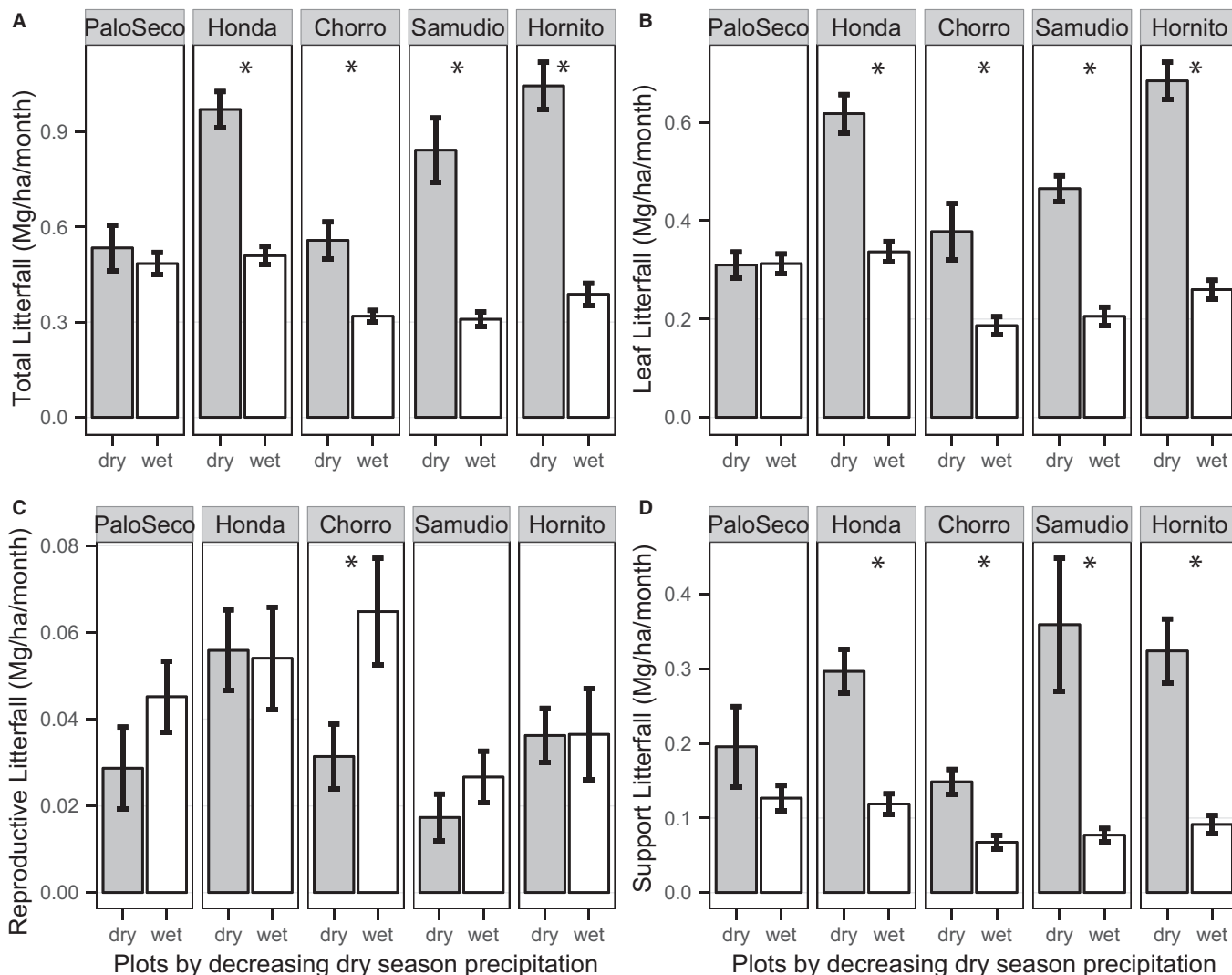


FIGURE 4. Mean dry and wet season total (A), leaf (B), reproductive (C), and support (D) monthly litterfall accumulation  $\pm$  1 SE in each site. “\*” indicates a significant difference in litterfall accumulation between seasons ( $P < 0.05$ ).

**RESPONSE TO NITROGEN ADDITION.**—Over the same period (2009 and 2010), total litterfall ranged from  $6.04 \pm 0.15$  to  $7.95 \pm 1.66$  Mg/ha/yr (mean dry mass  $\pm$  standard deviation) across the eight NITROF plots (Fig. 5). Total litterfall rates at the NITROF plots were therefore comparable to those measured at the nearby site of Honda ( $7.96 \pm 1.04$  Mg/ha/yr). N fertilization resulted in a significant (13%) increase in total litterfall (Fig. 5,  $F = 5.90$ ,  $df = 1,13$ ,  $P = 0.029$ ), and 11 percent increase in leaf litterfall relative to unfertilized controls, which was not statistically significant ( $F = 3.08$ ,  $df = 1,13$ ,  $P = 0.10$ ). Neither reproductive litterfall ( $F = 0.06$ ,  $df = 1,13$ ,  $P = 0.80$ ) nor the ratio of reproductive to leaf litterfall ( $F = 0.41$ ,  $df = 1,13$ ,  $P = 0.53$ ) differed significantly between treatments. No component of litterfall accumulation differed between 2009 and 2010 (Table S3).

**COLPOTHRINAX LEAF PRODUCTION.**—The annual leaf litter accumulation of *Colpotherinax* was estimated as 0.61 Mg/ha/yr when calcu-

lated as a product of the 2012 leaf production rate and species abundance in Chorro plot. Therefore, if litterfall traps failed to collect any *Colpotherinax* leaves, leaf litterfall in Chorro, measured as 3.00 Mg/ha/yr in litterfall traps, would theoretically be underestimated by 16 percent, and total litterfall underestimated by 11 percent. While *Colpotherinax* made up 30 percent of the basal area in Chorro, it contributed at most 20 percent to overall leaf litterfall.

## DISCUSSION

**LITTERFALL RATES IN A LOWER MONTANE FOREST.**—Although total litterfall accumulation ranged widely among permanent plots measured along the Fortuna soil gradient (4.78–7.96 Mg/ha/yr), this variation did not correspond directly with differences soil nutrient availability among sites. At Fortuna, the lowest and highest litterfall rates were recorded at the two sites with the lowest nitrification rate, Mehlich-extractable P and soil pH, and with the

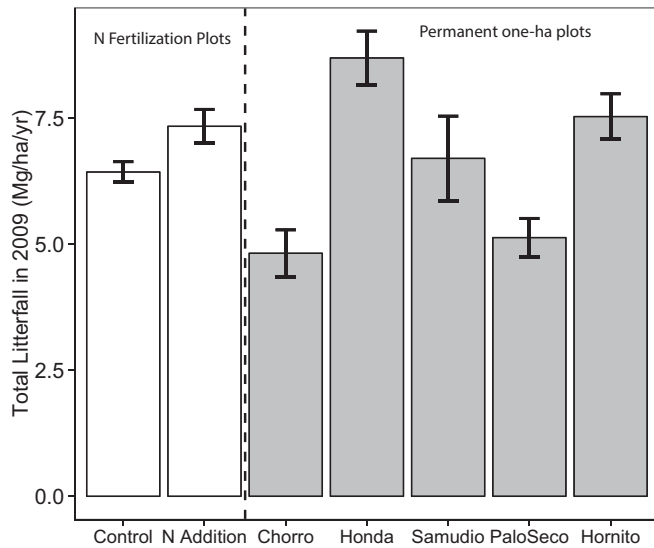


FIGURE 5. Mean total litterfall (Mg/ha/yr) in control and nitrogen-addition plots in the on-going nitrogen addition experiment in fourth year of the experiment (2009) compared to the variation in total litterfall accumulation in the same year among the five permanent 1-ha plots spanning the Fortuna soil fertility gradient.

lowest foliar nitrogen concentrations: Chorro and Honda. The Chorro site, with the lowest litterfall, has developed on a two-meter deep layer of coarse white silica-rich rhyolitic tuff, with a shallow organic horizon <10 cm deep (Table 1; Andersen *et al.* 2009). Although floristically distinct, the Chorro soils are analogous to Amazonian white sand forests and its productivity appears to be comparable; total litterfall at Chorro was within the 95% confidence intervals of six white-sand forests reported by Chave *et al.* (2010). Soils at the Honda site, <1 km from Chorro, are also derived from rhyolite, but are better developed (Table 1) with mineral soil extending 60 cm below the surface. Given the low fertility of the Honda site, its high litterfall compared to forests developed on andesite and dacite likely reflects a compositional difference. A larger fraction of the basal area of Honda consists of ectomycorrhizal (EM) tree species (*Oreomunnea* and *Quercus*) than the other sites (Table 1). EM species are thought to have an advantage over arbuscular mycorrhizal (AM) tree species where nitrogen is limiting, as EM fungi are capable of accessing sources of organic nitrogen unavailable to AM fungi (Hodge *et al.* 2001, Read & Perez-Moreno 2003).

The range of annual litterfall we observed ( $6.37 \pm 1.25$ ) falls below the mean litterfall rate of  $8.61 \pm 1.91$  Mg/ha/yr recorded for 81 mostly lowland sites (Chave *et al.* 2010), but is comparable to five montane sites ranging from 1890 to 3370 m elevation ( $7.06 \pm 3.72$  Mg/ha/yr) included in the same paper and 13 montane sites 1000–2500 m elevation listed in Vitousek (1984) ( $7.43 \pm 2.29$  Mg/ha/yr). Whereas the Fortuna sites had slightly lower total litter accumulation on average than previously measured montane sites, the 1-ha plots measured here had greater total litter N production (ranging from 56 to 124 kg/ha/yr) compared to the Vitousek (1984) sites, which ranged from 31 to

90 kg/ha/yr. This difference between our data and previous results was driven by low dry mass:N ratios (high litter N concentrations), ranging from 55 to 84 at Fortuna compared to 80–180 in Vitousek (1984), indicating that the Fortuna sites as a whole have lower within-stand nitrogen use efficiency. In contrast with Vitousek (1984), dry mass:N ratio did not correlate with total N production for the five Fortuna plots, due in part to high productivity, but poor litter quality at the low fertility, EM-dominated Honda site.

The increased forest nitrogen use efficiency of EM-dominated Honda compared to the other AM-dominated sites at Fortuna is consistent with the mycorrhizal-associated nutrient economy (MANE) hypothesis outlined by Phillips *et al.* (2013). This hypothesis states that forests containing AM-associated species produce high quality litter with a relatively fast decomposition rate because nutrient uptake by AM fungi relies on scavenging for nutrients mineralized by saprophytic fungi. In contrast, EM fungi, while more costly in terms of plant carbon investment, are capable of metabolizing nitrogen from organic material directly (Chalot & Brun 1998), and are therefore advantageous relative to AM-fungi where N is limiting to plant growth. If EM-associated stands produce nutrient poor, slowly decomposing litter, then these stands should retain a larger proportion of mineralized inorganic N within the ecosystem. Consistent with this pattern, the EM-dominated site, Honda, returned a relatively large amount of N to the ground via recalcitrant litterfall with high C:N ratios. Differences in nutrient cycling pathways among AM, EM, and mixed forest stands constitute one avenue by which compositional change may complicate the relationship between nutrient availability and canopy productivity and should be further evaluated in lower montane forests where both associations are abundant.

Analyses of canopy productivity, however, should keep in mind that litterfall is not a direct measure of the production of leaves, reproductive tissues, wood, bark, and epiphytes. Plant material consumed by herbivores or decomposed in the canopy does not fall into litter baskets and, therefore, could result in underestimation in canopy NPP estimates (Clark *et al.* 2001). Furthermore, the loss of plant material from the canopy is not necessarily synchronous with production of new biomass during the year it is measured, especially in the case of coarse woody structural material (Chambers *et al.* 2001). However, given that the aim of this study is compare litter production among sites and treatments rather than construct quantitatively precise carbon budgets, the strength of these sources of uncertainty would have to be highly variable across space to qualitatively influence our results.

LITTERFALL RESPONSE TO NITROGEN FERTILIZATION.—This study provided an opportunity to evaluate the magnitude of nitrogen-limitation to canopy litterfall in a mixed EM-AM community through an on-going nitrogen fertilization (NITROF) experiment alongside the Honda plot. N fertilization effects on litterfall were assessed for the same two-year period as our other five sites, and were measured 3 years after fertilization treatments were initiated.

While a previous N fertilization experiment in a montane forest in Venezuela did not observe significant effects on litterfall until the fourth year after first fertilization (Tanner *et al.* 1992), at Fortuna fertilization effects were observed in the first 2 years of fertilization (2006–2007), with on average 11 percent higher total litterfall and 17 percent higher leaf litterfall in the nitrogen addition treatment relative to control (Adamek *et al.* 2009). In 2009–2010 total litterfall was 13 percent higher in the treatment plots, while leaf litter mass was 11 percent above controls. These differences after heavy nitrogen addition remain relatively small compared to landscape-scale variation among our other sites (Fig. 5). Excluding Chorro, total litterfall and leaf litterfall at Honda was 31 percent and 38 percent higher, respectively, than the nearby site of Samudio (Fig. 5). These results suggest that compositional differences, or nutrient limitation by elements other than nitrogen, notably phosphorus, likely account for variation in productivity at Fortuna.

Further evidence of P limitation at Fortuna can be seen in the foliar chemistry of the plant community: 77 of 91 species sampled across the Fortuna soil gradient had foliar N:P ratios >16 (J. Dalling, unpublished data), which is the empirically derived threshold for discerning plant P limitation (Koerselman & Meuleman 1996). P has been found to be co-limit litterfall production in fertilization experiments in tropical montane forests in Venezuela (Tanner *et al.* 1992) and Ecuador (Homeier *et al.* 2012). However, P availability alone cannot explain the difference in litterfall among sites, given that Hornito and Honda vary 10-fold in Mehlich P, but do not differ significantly in total litterfall accumulation.

**SEASONAL AND ANNUAL VARIATION IN LITTERFALL.**—We predicted that while annual litterfall would respond to soil fertility, the seasonality of litterfall would be associated with rainfall regime. Although the five sites are separated by a linear distance of <14 km, the proportion of annual rainfall that occurs during the 3-month dry season ranges between 15 and 29 percent (Table 1). Large differences in the seasonality of total and leaf litterfall were observed among sites. With the exception of the most aseasonal site, Palo Seco, significantly more litter fell per month in the dry season than in the wet season, and, in the three most seasonal sites, the majority of annual leaf litter fell in the 4-month dry season. These results are therefore consistent with a more general, but weak relationship between litter and rainfall seasonality for tropical South America (Chave *et al.* 2010), though that study noted that litter seasonality was weakest for montane sites.

Most litterfall datasets for tropical forests are based on a single year of sampling. For lowland tropical forest this appears to provide an adequate estimation of litter production, with interannual variation <10 percent of mean litterfall (Chave *et al.* 2010). However, in this study, interannual variation in total litterfall was higher than 10 percent for three of the five sites, with a maximum difference of 30 percent between 2009 and 2010. Yearly leaf litterfall accumulation was more constrained, as no site differed more than 15 percent between years. Reproductive tissues showed extremely high variation (71%) between years in Honda,

the site dominated by *Oreomunnea mexicana*, supporting the notion that masting is an important component of the success of monodominant ectomycorrhizal forests (*e.g.*, Green & Newbery 2002, Henkel *et al.* 2005). However, because reproductive litter only accounted for an average of 8 percent of annual litterfall across sites, interannual differences in total litterfall were primarily driven by fallen support tissue (branches, twigs) and epiphytes during severe wind disturbance events. In both 2009 and 2010, a large fraction of litterfall occurred in one 2-week census period associated with high dry season winds. Therefore, more than 1 year of litterfall collection may be necessary to quantify litterfall accumulation in montane forests where wind disturbance plays a larger role in forest dynamics than in lowland forest.

**VARIATION IN COMPONENTS OF CANOPY LITTERFALL.**—In addition to influencing the annual accumulation and seasonality of litterfall, we also expected the variability among sites in precipitation and fertility to influence the relative proportion of canopy productivity allocated to leaves, structural support, reproductive organs, and epiphytes. Epiphytes can account for up to 40 percent of total litterfall in montane forest (Hölscher *et al.* 2005), with abundance increasing with forest age and rainfall (Wolf 1993, Köhler *et al.* 2007). At Fortuna, the litterfall fraction consisting of epiphytes and canopy soil was remarkably consistent (range 18–25%) across sites with varying total rainfall. Differences in epiphyte production therefore do not account for differences in litterfall rates among sites. One other possibility is that variation in litter production among sites simply reflects differences in aboveground biomass rather than differences in productivity. While differences among sites in basal area are substantial, litterfall per unit basal area remained significantly higher at Honda than at remaining sites except Palo Seco in 2010.

Given the potentially confounding effect of epiphyte biomass, leaf litter production may be a better metric for comparison among tropical forests (Röderstein *et al.* 2005). At Fortuna, rank order in annual leaf litterfall accumulation among sites closely paralleled rank order in total litterfall accumulation (Fig. 2). Overall, mean leaf litterfall at the five Fortuna sites ( $4.04 \pm 0.91$  Mg/ha/yr) was comparable to values for 19 other montane sites reported in Röderstein *et al.* (2005) ( $4.87 \pm 1.55$  Mg/ha/yr), and with a subset of seven lower montane forests ranging from 1000 to 1550 m elevation ( $4.82 \pm 1.12$  Mg/ha/yr). The exception in this study of significantly lower leaf litter at Chorro (3.00 Mg/ha/yr), when compared to the other Fortuna sites, may be a consequence of the dominance of canopy palms. At Chorro three palm species, *Wettinia quinaria*, *Euterpe precatoria*, and *Colpothrinax aphanopetala* accounted for 42 percent of the basal area of the plot. Adequately sampling leaf litter production in palm-dominated forest is a recognized challenge (Chave *et al.* 2010), as intact falling palm fronds are unlikely to be captured in our traps. Calculation of *Colpothrinax* leaf litterfall, based on a 1-year leaf production census, revealed that if no *Colpothrinax* frond fell in our litter baskets, leaf litter production would have been underestimated by 0.61 Mg/ha/yr. However, even with a 0.61 Mg/ha/yr increase in canopy litterfall, Chorro would remain the least



productive of our study sites. If the leaf production rate represents a reliable estimate of litterfall rates for palms, then the potential contribution of *Colpothrinax* to canopy productivity appears to be quite small. While *Colpothrinax* accounts for 30 percent of basal area in the Chorro plot, its litterfall accounts for up to 16 percent of leaf litter (if no palm fronds were captured in baskets) or 20 percent (if baskets accurately sampled palm litterfall). Slow leaf turnover may be an important functional trait allowing canopy palms to reach high abundance relative to woody dicots on this extremely infertile rhyolitic soil because increased leaf longevity provides a key mechanism by which plants increase nutrient use efficiency (Escudero *et al.* 1992, Cordell *et al.* 2001).

**LITTERFALL AS A METRIC OF REPRODUCTIVE RESOURCE ALLOCATION.**— We predicted that proportional investment in flowers and fruits would increase with soil fertility if nutrients are preferentially allocated to leaves over support tissues in low fertility sites (van Schaik & Mirmanto 1985, Chave *et al.* 2010). In this study, we observed significantly *higher* allocation to reproduction at Chorro than the remaining sites. However, this may be the result of either underestimating leaf litter production, or overestimating reproductive production if the dominant palm species at this site engage in mast fruiting. More generally, Chave *et al.* (2010) have argued that lower investment in reproduction occurs in low phosphorus eastern Amazonian forests, and that mast fruiting may be more frequent in low fertility sites (see also Ichie & Nakagawa 2013). Low-diversity forest stands, or stands where a few species attain high relative abundance may require many years of litterfall collection to accurately characterize reproductive investment.

The NITROF experiment also provides an additional opportunity to examine whether nitrogen addition impacts reproductive resource allocation. In 2006–2007 there was on average 31 percent higher reproductive litterfall in the nitrogen addition than control treatments (Adamek *et al.* 2009); however, by 2009–2010 reproductive litterfall was 6 percent lower in the nitrogen addition treatment. Since reproductive tissues tend to have high concentrations of nitrogen and other potentially limiting elements relative to vegetative tissue (Kuo *et al.* 1982, Grubb *et al.* 1998), declining reproductive resource allocation in the N addition plots might represent progressive P or K limitation. Consistent with this result, foliar P concentrations have significantly decreased in the nitrogen addition relative to control plots from 2006 to 2013, while foliar N concentrations have remained unchanged in both treatments (A. Hathcock, unpubl. data).

In conclusion, our results provide additional support for reduced litterfall in mid-elevational forests, but in contrast with earlier studies, our results highlight the importance of forest composition, rather than soil fertility, as a determinant of canopy productivity. Although relatively short-term measurements of litterfall may be adequate to characterize leaf litter production rates, measurement of reproductive litterfall may require longer sampling periods to account for mast flowering and fruiting, especially in forests where one tree species achieves high relative abundance.

## ACKNOWLEDGMENTS

We thank the Government of Panama's Secretaría Nacional de Ciencia, Tecnología e Innovación (SENACYT) for providing financial support for this project through the international research collaboration grant COLO08. The NITROF experiment was funded by the Robert Bosch Foundation (Germany) and the Deutsche Forschungsgemeinschaft (German Research Foundation, Co 749/1-1). ENEL Greenpower and the Smithsonian Tropical Research Institute provided logistic support and housing at Fortuna and the Autoridad Nacional del Ambiente (ANAM) provided research permits to undertake the study.

## SUPPORTING INFORMATION

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

TABLE S1. ANOVA table from repeated measures mixed effects models testing if the components annual litterfall accumulation differed among 1-ha plots and between the 2 years of the study.

TABLE S2. ANOVA table from repeated measures mixed-effects models testing if components of monthly litterfall accumulation differed between the dry and wet season in the 5 1-ha plots examined at Fortuna Forest Reserve.

TABLE S3. ANOVA table from the two-way Anova testing the effects of treatment and year on annual litterfall accumulation in the NITROF plots at Fortuna Forest Reserve.

FIGURE S1. Study sites in the Fortuna Forest Reserve and adjacent Palo Seco reserve in western Panama.

## LITERATURE CITED

- ADAMEK, M., M. D. CORRE, AND D. HÖLSCHER. 2009. Early effect of elevated nitrogen input on above-ground net primary production of a lower montane rain forest, Panama. *J. Trop. Ecol.* 25: 637–647.
- ANDERSEN, K., M. J. ENDARA, B. L. TURNER, AND J. W. DALLING. 2012. Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. *Oecologia* 168: 519–531.
- ANDERSEN, K., B. L. TURNER, AND J. W. DALLING. 2009. Soil based habitat partitioning in understory palms in lower montane tropical forests. *J. Biogeogr.* 37: 278–292.
- ARAGÃO, L. E. O. C., Y. MALHI, D. B. METCALFE, J. E. SILVA-ESPEJO, E. JIMÉNEZ, D. NAVARRETE, S. ALMEIDA, A. C. COSTA, N. SALINAS, O. L. PHILLIPS, L. O. ANDERSON, E. ALVAREZ, T. R. BAKER, P. H. GONCALVES, J. HUAMÁN-OVALLE, M. MAMANI-SOLÓRZANO, P. MEIR, A. MONTEAGUDO, S. PATIÑO, M. C. PEÑUELA, A. PRIETO, C. A. QUESADA, A. ROZAS-DÁVILA, A. RUDAS, J. A. SILVA, JR, AND R. VÁSQUEZ. 2009. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* 6: 2759–2778.
- BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. <http://CRAN.R-project.org/package=lme4>
- BURGHOUTS, T. B. A., N. M. VAN STRAALLEN, AND L. A. BRUIJNZEEL. 1998. Spatial heterogeneity of element and litter turnover in a Bornean rain forest. *J. Trop. Ecol.* 14: 477–506.
- CHALOT, M., AND A. BRUN. 1998. Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiol. Rev.* 22: 21–44.

- CHAMBERS, J. Q., J. D. SANTOS, R. J. RIBEIRO, AND N. HIGUCHI. 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecol. Manag.* 152: 73–84.
- CHAVE, J., D. NAVARRETE, S. ALMEIDA, E. ÁLVAREZ, L. E. O. C. ARAGÃO, D. BONAL, P. CHATELET, J. E. SILVA-ESPEJO, J.-Y. GORET, P. VON HILDEBRAND, E. JIMÉNEZ, S. PATIÑO, M. C. PEÑUELA, O. L. PHILLIPS, P. STEVENSON, AND Y. MAHLI. 2010. Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences* 7: 43–55.
- CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, J. NI, AND E. A. HOLLAND. 2001. Net primary production in tropical forests: An evaluation and synthesis of existing field data. *Ecol. Appl.* 11: 371–384.
- CORDELL, S., G. GOLDSTEIN, F. C. MEINZER, AND P. M. VITOUSEK. 2001. Regulation of leaf life-span and nutrient use efficiency of *Metrosideros polymorpha* trees at two extremes of a long chronosequence in Hawaii. *Oecologia* 127: 198–206.
- DANTAS, M., AND J. PHILLIPSON. 1989. Litterfall and litter nutrient content in primary and secondary Amazonian 'terra firme' rain forest. *J. Trop. Ecol.* 5: 27–36.
- DEZZEO, N., AND N. CHACÓN. 2006. Litterfall and nutrient input in undisturbed and adjacent fire disturbed forests of the Gran Sabana, Southern Venezuela. *Interciencia-Caracas* 31: 894.
- ESCUDEIRO, A., J. M. del ARCO, I. C. SANZ, AND J. AYALA. 1992. Effects of leaf longevity and retranslocation efficiency on the retention of nutrients in leaf biomass of different woody species. *Oecologia* 90: 80–87.
- GIRARDIN, C. A. J., Y. MAHLI, L. E. O. C. ARAGÃO, M. MAMANI, W. HUARACA HUASCO, L. DURAND, K. J. FEELEY, J. RAPP, J. E. SILVA-ESPEJO, M. SILMAN, N. SALINAS, AND R. J. WHITTAKER. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Glob. Chang. Biol.* 16: 3176–3192.
- GREEN, J. J., AND D. M. NEWBERY. 2002. Reproductive investment and seedling survival of the mast fruiting rain forest tree *Microberlinia bisulcata* A. chev. *Plant Ecol.* 162: 169–183.
- GRUBB, P. J., D. J. METCALF, E. A. A. GRUBB, AND G. D. JONES. 1998. Nitrogen richness and protection of seeds in Australian tropical rainforests: A test of plant defense theory. *Oikos* 82: 467–482.
- HENKEL, T. W., J. R. MAYOR, AND L. P. WOOLLEY. 2005. Mast fruiting and seedling survival of the ectomycorrhizal monodominant, *Dicymbe corymbosa* (Caesalpinaceae) in Guyana. *New Phytol.* 167: 543–556.
- HODGE, A., C. D. CAMPBELL, AND A. H. FITTER. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* 413: 297–299.
- HÖLSCHER, D., J. MACKENSEN, AND J. M. ROBERTS. 2005. Forest recovery in the humid tropics: Changes in vegetation structure, nutrient pools and the hydrological cycle. *In* M. Bonnell, and L. A. Bruijnzeel (Eds.). *Forests-water-people in the humid tropics*, pp. 598–621. Cambridge University Press, Cambridge, UK.
- HOMER, J., D. HERTEL, T. CAMENZIND, N. L. CUMBICUS, M. MARAUN, G. O. MARTINSON, AND C. LEUSCHNER. 2012. Tropical Andean forests are highly susceptible to nutrient inputs—Rapid effects of experimental N and P addition to an Ecuadorian montane forest. *PLoS ONE* 7: e47128.
- ICHIE, T., AND M. NAKAGAWA. 2013. Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Drybalanops aromatica*. *Ecol. Res.* 29: 151–158.
- KITAYAMA, K., AND S. I. AIBA. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *J. Ecol.* 90: 37–51.
- KOERSELMAN, W., AND A. F. MEULEMAN. 1996. The vegetation N: P ratio: A new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* 33: 1441–1450.
- KÖHLER, L. C., TOBÓN, K. A., FRUMAU, AND L. S. BRUIJNZEEL. 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecol.* 193: 171–184.
- KUO, J., P. J. HOCKING, AND J. S. PATE. 1982. Nutrient reserves in seeds of selected proteaceous species from southwestern Australia. *Aust. J. Bot.* 30: 231–249.
- KUZNETSOVA, A., P. B. BROCKHOFF, AND R. CHRISTENSEN. 2014. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-6. <http://CRAN.R-project.org/package=lmerTest>
- LEIGH, JR., E. G. 1999. *Tropical forest ecology: A view from Barro Colorado Island*. Oxford University Press, New York, NY.
- MOSER, G., C. LEUSCHNER, D. HERTEL, S. GRAEFE, N. SOETHE, AND S. IOST. 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the belowground compartment. *Glob. Chang. Biol.* 17: 2211–2226.
- PHILLIPS, R. P., E. BRZOSTEK, AND M. G. MIDGLEY. 2013. The mycorrhizal-associated nutrient economy: A new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytol.* 199: 41–51.
- PROCTOR, J. 1983. Tropical forest litterfall: Problems of litter comparison. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). *Tropical rain forest: Ecology and management*, pp. 267–273. Blackwell, Oxford, UK.
- R DEVELOPMENT CORE TEAM. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- RAICH, J. W., A. E. RUSSELL, AND P. M. VITOUSEK. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology* 78: 707–721.
- READ, D. J., AND J. PEREZ-MORENO. 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? *New Phytol.* 157: 475–492.
- RÖDERSTEIN, M., D. HERTEL, AND C. LEUSCHNER. 2005. Above- and below-ground litter production in three tropical montane forests in Southern Ecuador. *J. Trop. Ecol.* 21: 483–492.
- SATTERTHWAITE, F. E. 1946. An approximate distribution of estimates of variance components. *Biometrics Bull.* 2: 110–114.
- SAYER, E. J., J. S. POWERS, AND E. V. J. TANNER. 2012. Increased litterfall in tropical forests boosts the transfer of soil CO<sub>2</sub> to the atmosphere. *PLoS ONE* 2: e1299. doi:10.1371/journal.pone.0001299.
- VAN SCHAIK, C. P., AND E. MIRMANTO. 1985. Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica* 17: 196–205.
- SILVER, W. L. 1994. Is nutrient availability related to plant nutrient use in humid tropical forests? *Oecologia* 98: 336–343.
- TANNER, E. V. J., V. KAPO, AND W. FRANCO. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73: 78–86.
- VENEKLAAS, E. J. 1991. Litterfall and nutrient fluxes in two montane tropical rain forests, Colombia. *J. Trop. Ecol.* 7: 319–336.
- VILLELA, D. M., AND J. PROCTOR. 1999. Litterfall mass, chemistry, and nutrient retranslocation in a monodominant forest on Maraca Island, Roraima, Brazil. *Biotropica* 31: 198–211.
- VITOUSEK, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285–298.
- WOLF, J. H. D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Mo. Bot. Gard.* 80: 928–960.
- WRIGHT, S. J., J. B. YAVITT, N. WURZBURGER, B. L. TURNER, E. V. J. TANNER, E. J. SAYER, L. S. SANTIAGO, M. KASPARI, L. O. HEDIN, K. E. HARMS, M. N. GARCIA, AND M. D. CORRE. 2011. Potassium, phosphorus or nitrogen limit root allocation, tree growth and litter production in a lowland tropical forest. *Ecology* 92: 1616–1625.

