

Litterfall mass and nutrient fluxes over an altitudinal gradient in the coastal Atlantic Forest, Brazil

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Abstract: Litterfall is one of the most important pathways through which nutrients are recycled in the terrestrial biosphere. In tropical soils, which are generally low in essential nutrients such as phosphorus and cations, the flux of nutrients through litterfall is particularly important to sustaining CO₂-uptake capacity; however, questions remain over the role of altitude in altering litter nutrient cycling rates among tropical forest ecosystems. Here we examine litterfall, carbon (C), nitrogen (N) and phosphorus (P) fluxes through litterfall over an altitudinal gradient in the coastal Atlantic Forest located on the northern coast of the State of São Paulo, Brazil. Litterfall was collected twice a month for 1 y (April 2007–March 2008) using 30 litter traps placed in four different forest types arrayed by altitude – coastal forest (sea level), lowland forest (50–200 m asl), submontane forest (300–500 m asl) and montane forest (1000 m asl). Litterfall mass-fluxes decreased with increasing altitude, from ~9 Mg ha⁻¹ in lowland forests to 7 Mg ha⁻¹ in higher-altitude ecosystems. Contribution of reproductive organs to litterfall was significantly greater in lower than in higher altitudes. Litterfall N and P fluxes were higher in the lowland forest vs. other forest types, pointing to strong altitudinal controls over nutrient cycling. Furthermore, nitrogen-use efficiency (NUE) was lower and litter δ¹⁵N was higher in the lowland site providing additional evidence for lack of N constraints to productivity in lowland of the south-eastern Atlantic Forest.

Key Words: altitudinal range, Atlantic Forest, Brazil, litterfall, nitrogen, nutrient input, phosphorus

INTRODUCTION

Tropical forests play a disproportionate role in the global carbon cycle as this biome occupies only 14% of the terrestrial Earth surface, but is responsible for over half of the global net primary productivity (NPP) (Melillo *et al.* 1993, Nottingham *et al.* 2015). In the tropics, current estimates suggest that one third of the NPP is allocated to litterfall each year (Aragão *et al.* 2009, Bray & Gorham 1964, Girardin *et al.* 2010, Malhi *et al.* 2011).

Across tropical forests, litterfall rates tend to decrease with increasing altitude (Girardin *et al.* 2010, Proctor 1983, Röderstein *et al.* 2005). Nutrient limitation could

also play a role in patterns of forest productivity and biomass, with lower nutrient fluxes and higher nutrient-use efficiencies observed for montane vs. lowland forest sites (Arnold *et al.* 2009, Corre *et al.* 2010, Unger *et al.* 2010, Vitousek 1984, Wolf *et al.* 2011). However, questions remain over the importance of altitude, seasonality and nutrients in altering patterns of productivity within the diverse tropical forest biome.

The Atlantic Forest, located in south-east Brazil, is one of the most diverse tropical biomes in South America (Myers *et al.* 2000). This forest was estimated to cover an area of *c.* 1.5 million km²; however, only 12–15% of its original area is left (Ribeiro *et al.* 2009). One of the best preserved portions of the Atlantic Forest is located in the Serra do Mar, a coastal mountain chain located on the coastal region of South-east Brazil, where the relief with

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steep scarps protects against substantial agriculture and urbanization (Ranta *et al.* 1998, Ribeiro *et al.* 2009).

This difference in altitude, coupled with changes in climate, induces a series of changes in the composition, structure and functioning of forests along altitudinal ranges. Tree species change (Sanchez *et al.* 2013), and species richness reaches its maximum in the submontane forest (Eisenlohr & De Oliveira-Filho 2015). Structurally, the above-ground biomass (AGB) increases (Alves *et al.* 2010), and foliar specific leaf area decreases at higher altitudes (Rosado *et al.* 2016). Soil concentrations and stocks of C and N also increase with altitude, while decomposition rates and CO₂ and N₂O soil emissions decrease (Sousa Neto *et al.* 2011, Vieira *et al.* 2011).

Here we examine relationships between litterfall and nutrients flux over an altitudinal gradient in the Atlantic Forest. Based on predictions of the literature, we investigate three core hypotheses: (1) litterfall will be higher in lowland forests than upland forests (Girardin *et al.* 2010, Proctor 1983, Röderstein *et al.* 2005, Walker *et al.* 1996); (2) litterfall will increase during the dry period as a delayed response to drought (Martinelli *et al.* in press, Reich & Borchert 1984, Wright & Cornejo 1990, Zhang *et al.* 2014); and (3) lowland forest will have a higher N-availability than upland forest, leading to higher N losses, and consequently lower NUE and higher foliar $\delta^{15}\text{N}$ in lowland forest (Arnold *et al.* 2009, Corre *et al.* 2010, Unger *et al.* 2010, Vitousek 1984, Wolf *et al.* 2011).

STUDY SITES

The Serra do Mar is a rift system that stretches from south-west to north-east along the Brazilian coast (29°26'S–21°46'S), hosting the highly diverse Atlantic Forest in Brazil (de Almeida 1976, Murray-Smith *et al.* 2009). We measured litterfall in four different forest types distributed over an altitudinal gradient in the Serra do Mar State Park, located on the northern coast of the State of São Paulo, Brazil (Figure 1).

This forest encompasses different physiognomies according to altitude (Oliveira-Filho 2009, Veloso *et al.* 1991). We selected four different sites: coastal sandy evergreen rain forest (coastal forest) occurring at sea level, evergreen rain forest (lowland forest) at 50–300 m asl, evergreen rain forest (submontane forest) at 300–700 m asl, and, finally, upper highland evergreen rain forest (montane forest), at ~1000 m asl (Figure 1).

The mean annual temperature (MAT) is 22°C in lowland areas, and 16°C in the uplands (Alves *et al.* 2010) (Table 1). The mean annual precipitation (MAP) in lowland areas is ~2200 mm y⁻¹, whereas at higher altitudes MAP is around 1970 mm y⁻¹ (www.dae.sp.gov.br). According to the Köppen climate classification, the lowland area is classified as Cfa

(humid subtropical climate) and montane areas as Cwb (subtropical highland climate) (Alvarez *et al.* 2014). The parent material is mostly uniform along the altitudinal range, and composed of Pre-Cambrian granite, gneiss rocks, which leads to the formation of sandy clay soils, acidic and poor Inceptisols in lowland, submontane and montane forests (Martins *et al.* 2015). Coastal forest is the exception in which the parent material is mainly composed of marine sediments, where sandy, acidic and even more nutrient-poor soils are formed (Quartzipsamment).

Most of the species on the coastal Atlantic Forest are evergreen (> 80%) (Morellato *et al.* 2000). The main families in our forest sites are Myrtaceae, Rubiaceae, Fabaceae and Lauraceae (Sanchez *et al.* 2013). Species richness increases with altitude, with the lowest richness in the coastal forest, and reaching the maximum in the submontane forest (Table 1). The average height of the forest for trees with diameter at breast height larger than 10 cm is around 14 m (range = 8.4–39 m), and emergent trees are 25–30 m tall (Scaranello *et al.* 2012); AGB increases with altitude from ~170–280 Mg ha⁻¹ (Alves *et al.* 2010) (Table 1).

METHODS

Sampling

We collected litter in eight 1-ha permanent plots over the altitudinal range under study (Table 1). Fresh fine litter were collected twice a month from April 2007 to March 2008 by placing 30 litter traps of 0.25 m² per plot at 1.0 m from the ground, from which 10 traps were randomly selected for chemical analysis of the litterfall.

The litter samples were dried, leaves were separated from reproductive organs (fruits and flowers), twigs and other organic material, such as bark (miscellaneous). Only twigs with a diameter < 0.5 cm were considered in this study. All tissues were dried at 60°C, ground, sieved and sent for analysis.

Analysis

Approximately 2–3 mg of subsamples of litter were sealed in tin capsules and combusted in a Carlo Erba elemental analyser (Milan, Italy) to determine N and C concentrations. For the determination of total P concentration in the plant material, digestion was carried out with perchloric acid + nitric acid (ratio 5:1), using 0.5 g of sample and 6 ml of a mixture of acids. After digestion, the material was diluted with 50 ml of deionized water. The concentration of P was determined

Table 1. Basic information related to the forests plots along the altitudinal range litterfall in the south-eastern coastal Atlantic Forest. Soil types and composition from Martins *et al.* (2015). Above-ground biomass (AGB) of vegetation from Alves *et al.* (2010).

Site parameter	Forest type			
	Coastal	Lowland	Submontane	Montane
Plot code	A	B, E	G, I, J	K, N
Altitude (m asl)	0-50	50-100	200-500	800-1200
Topography	Flat (0-10°)	Gentle (10–30°)	Steep (> 30°)	Steep (> 30°)
Soil type	Quartzipsamment	Inceptisols	Inceptisols	Inceptisols
Air temperature (°C)	20	20	19	16
Soil sand content (%)	88.1	60.4	66.7	57.4
Soil clay content (%)	6.1	31.5	16.4	20.3
Soil pH	3.4	3.6	3.6	3.5
CEC (mmol _c kg ⁻¹)	112	138	193	163
P (mg kg ⁻¹)	11.5	17.6	12.9	21.2
SB (mmol _c kg ⁻¹)	4.2	12.9	22.5	15.8
(AGB) (Mg ha ⁻¹)	154	198	239	263

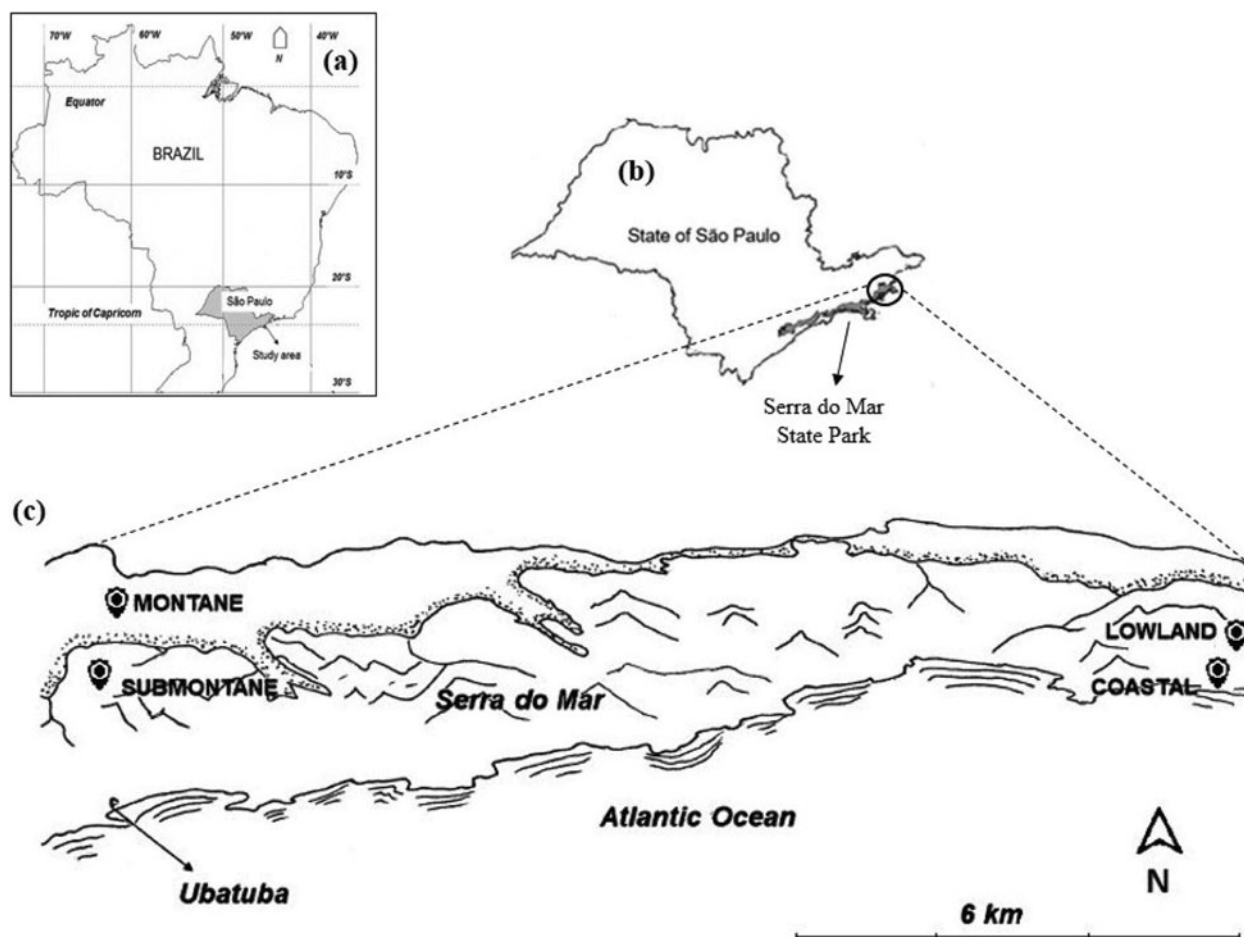


Figure 1. Location of study. Map of Brazil with border of the State of São Paulo (a). Map of the State of São Paulo with limits of the Serra do Mar State Park (b). Sampling sites on the slopes of the Serra do Mar in the north coast of the State of São Paulo (c). Litterfall fluxes were measured in four different forest types distributed over an altitudinal gradient in the Serra do Mar State Park: coastal forest (0–50 m asl), lowland (50–100 m asl), submontane (200–500 m asl) and montante forests (800–1200 m asl).

Table 2. Mean \pm SD of total litterfall expressed in Mg ha⁻¹, and respective fractions: leaves, twigs, reproductive material and miscellaneous organic material in four types of forests along the altitudinal range in the south-eastern coastal Atlantic Forest. Numbers in parentheses represent the relative contribution of litter fractions to total litterfall.

	Coastal	Lowland	Submontane	Montane
Total	8.12 \pm 1.10	9.20 \pm 1.20	7.01 \pm 1.80	6.55 \pm 1.54
Leaves	5.13 \pm 0.90 (0.63)	5.30 \pm 0.80 (0.58)	4.70 \pm 1.19 (0.67)	4.30 \pm 0.92 (0.66)
Twigs	1.50 \pm 0.50 (0.18)	1.94 \pm 0.82 (0.21)	1.07 \pm 0.77 (0.15)	1.18 \pm 0.71 (0.18)
Reproductive	0.94 \pm 0.35 (0.12)	0.94 \pm 0.35 (0.10)	0.45 \pm 0.46 (0.06)	0.36 \pm 0.33 (0.05)
Miscellaneous	0.55 \pm 0.25 (0.07)	1.02 \pm 0.38 (0.11)	0.76 \pm 0.34 (0.11)	0.65 \pm 0.31 (0.10)

Table 3. Above-ground biomass (AGB), litterfall, and respective inputs of carbon, nitrogen, and phosphorus; and nutrient-use efficiency ([NUE]) for nitrogen and phosphorus, C:N and N:P ratios and $\delta^{15}\text{N}$ values in the four types of forests along the altitudinal range in the south-eastern coastal Atlantic Forest.

Forest	AGB (Mg ha ⁻¹)	N (kg y ⁻¹)	P (kg y ⁻¹)	Litterfall (kg ha ⁻¹ y ⁻¹)	C (kg ha ⁻¹ y ⁻¹)	N (kg ha ⁻¹ y ⁻¹)	P (kg ha ⁻¹ y ⁻¹)	[NUE] _N	[NUE] _P	C:N	N:P	$\delta^{15}\text{N}$ (‰)
Coastal	166	14.0	0.55	8121	3883	110	4.5	74	1805	36.2	27.8	-1.2
Lowland	209	20.7	0.64	9169	4367	189	6.0	49	1528	24.3	32.2	2.6
Submontane	254	16.0	0.53	6534	3003	105	3.8	62	1719	29.2	32.0	0.9
Montane	283	17.2	0.52	6549	3141	116	3.4	56	1926	28.2	36.7	1.1

by spectrophotometry using the reactive ammonium metavanadate + ammonium molybdate method.

Statistics and data analysis

In order to test for differences over the altitudinal range, we used general linear mixing models (GLMM). We first grouped litterfall by plots of the same altitude and then grouped the data by month of collection. Nutrient fluxes were estimated by multiplying mean monthly litterfall for each plot by mean monthly nutrient concentrations. For P, only six estimates were available per altitude, since P concentrations were determined every other month. We consider these as categorical factors in the GLMM forest types (lowland, submontane and montane) and time (months). Dependent variables were total litterfall, leaf, reproductive organs and twigs and nutrient fluxes. In order to test for seasonality, we also used GLMM by grouping litterfall and nutrient flux data based on the mean monthly rainfall. April to September was denominated the dry season, and October to March, the wet season. We used precipitation data from the Water and Energy Department of the State do São Paulo. Coastal forest – station Ubatuba (code: E2-052, altitude 10 m asl); lowland forest – station Mato Dentro (code: E2-009, altitude 200 m asl); submontane and montane forests – station Briet (code E2-135, 815 m). In this case, we consider as categorical factors forest types and seasons (dry vs. wet) in a full factorial design. In lowland areas, the precipitation of the driest months is near 100 mm, therefore there is not a true dry season. However, for sake of simplicity we adopted here the term dry season to refer

to the less-wet period of the year. In the highlands, at least during 3 mo precipitation is lower than 100 mm, characterizing a true dry season. Statistical differences at the 0.05 level of probability were reported as significant. Statistical analyses were performed by Statistica 13.0 software (Stat Soft, Inc., Tulsa, OK, USA).

RESULTS

Litterfall and nutrient fluxes over the altitudinal range

Litterfall decreased with increasing altitude ($F_{(2,22)} = 6.33$, $P < 0.01$), consistent with the trend observed for leaf mass ($F_{(2,22)} = 2.65$, $P = 0.09$), twigs ($F_{(2,22)} = 5.54$, $P = 0.01$) and amount of reproductive material ($F_{(2,22)} = 18.5$, $P < 0.01$) (Table 2). The proportion of leaves in relation to total litterfall increased with increasing altitude ($F_{(2,22)} = 6.23$, $P < 0.01$), while the proportion of reproductive material showed the opposite trend ($F_{(2,22)} = 10.1$, $P < 0.01$) (Table 2).

Although C fluxes were higher in the lowland forest compared with higher-altitude and coastal forest sites, such differences were not statistically significant (Table 3). Fluxes of N were similar among coastal forest, submontane and montane, but distinctively higher in the lowland forest ($F_{(3,42)} = 3.42$, $P = 0.03$). Higher N fluxes in lowland forest were not only a product of higher litterfall production rates, but also the higher N concentration of litterfall in the lowland site ($F_{(3,41)} = 55.8$, $P < 0.01$) (Table 3). The C:N ratio of litterfall followed a similar pattern with lowest values observed for lowland forest and highest C:N ratios in the coastal forest

($F_{(3,38)} = 43.1$, $P < 0.01$); submontane and montane forests displayed similar C:N ratios. The highest $\delta^{15}\text{N}$ average of litterfall was observed in the lowland forest, while a negative average value was observed in the coastal forest ($F_{(3,38)} = 227$, $P < 0.01$). The submontane and montane forests had intermediate values between these two extremes (Table 3). As a consequence, there was a strong inverse correlation between $[\text{NUE}]_{\text{N}}$ and $\delta^{15}\text{N}$; meaning that higher use efficiency was associated with lower $\delta^{15}\text{N}$ across sites ($r^2 = 0.95$, $F_{(1,2)} = 56.2$, $P = 0.02$).

Litterfall P was also higher in the lowland forest; however, owing to higher variability in P concentrations and lower number of samples, this difference was not significant ($F_{(3,19)} = 2.38$, $P = 0.10$). Higher P cycling rates in the lowland forest were due to the higher litterfall production in this forest, since the P concentration in the litter was not different among forest types (Table 3). On the other hand, $[\text{NUE}]_{\text{P}}$ and N:P ratio did not differ substantially across forest types.

Seasonal changes in litterfall and nutrient fluxes

Considering the interaction between season and forest type, there was no difference in the litter fall between wet and dry season (Figure 2). However, considering only differences between seasons, litterfall ($F_{(1,3)} = 4.98$, $P = 0.03$), leaf mass ($F_{(1,3)} = 15.4$, $P < 0.01$) and amount of reproductive material ($F_{(1,3)} = 9.10$, $P < 0.01$) were higher during the wet than during the dry season. There were no differences in nutrient fluxes between seasons, nor in the C:N, C:P and N:P ratios of litterfall.

DISCUSSION

Litterfall and nutrient flux along the altitudinal range

Our findings support the overarching hypothesis that altitude is a principal determinant of many aspects of ecosystem structure and functioning in the Atlantic Forest Region of Brazil (hypothesis 1) (Table 2). Specifically, litter-mass flux, litterfall composition and key indicators of N cycling rates varied over the altitudinal range. Phosphorus also changed from lowland to upland forest sites; however, substantial site-specific variation in P reduced our ability to draw statistical inferences for this nutrient.

One of the key observations of our study is the change in litter composition across sites, particularly the tendency for reproductive materials to contribute less to overall litter production at high compared with low-elevation forests. This pattern has been tied to soil fertility in the past, with higher rates of N cycling resulting in greater

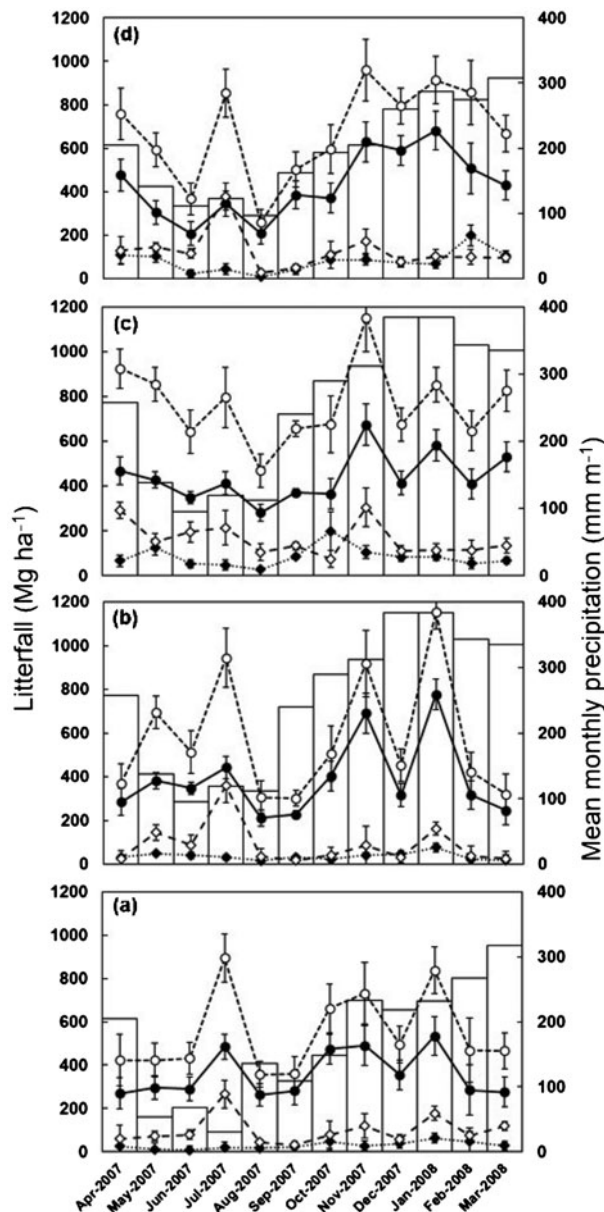


Figure 2. Monthly variation in litterfall and its fractions (left y-axis), and mean monthly precipitation (right axis) in the coastal (a), lowland (b), submontane (c) and montane (d) plots. Total litterfall indicated by open circle, leaves by closed circle, twigs by open diamonds, and reproductive organs by closed diamonds. Months and years are indicated on the x axis.

photosynthetic C investments (Castro *et al.* 2007, Chave *et al.* 2010). However, while our lowland soils are richer in nutrients (particularly N) than soils of the coastal forest (Martins *et al.* 2015), the proportion of reproductive organs is similar across these systems; hence nutrients do not appear to explain the pattern in litterfall composition we observed (Table 2).

An alternative factor could be climate, particularly higher evaporative water losses in the montane forests

causing plants to invest more of their photosynthate into structurally robust leaves to cope with stress (Rosado *et al.* 2016). This in turn would lead to less energy for reproductive organs, thus explaining the litterfall composition pattern across our altitudinal gradient. Additionally, Brito & Sazima (2012) found higher biomass of fruit per individual of *Tibouchina pulchra* in the lowland forest than in the montane forest owing to fewer pollinators at higher altitude. If this pattern holds for other species, it is reasonable to speculate that a change in pollinators could have altered litterfall composition across our sites. In any case, both hypotheses (high energy cost for leaf construction and lack of pollinators) are not mutually exclusive and deserve future attention.

In addition to changes in litterfall composition, results from our study build on evidence for differences in NUE among diverse tropical forests (Vitousek 1984). NUE of the lowland tropical site was lower than the coastal site; that N appears to be in excess in the lowland site, which is consistent with past literature showing excess N cycling in such ecosystems (Hedin *et al.* 2009). The coastal site experiences waterlogging, which reduces nutrient mineralization rates, in coastal vs. other tropical forest sites (Mardegan 2013). Lower rates of N mineralization would impede the availability of this nutrient to growing vegetation thus resulting in nutrient conservation (and a higher NUE) in the coastal site.

In terms of elevation, higher NUEs in montane/submontane compared with lowland forests has been attributed to decreasing temperatures with altitude, which reduces microbial activity and rates of nutrient cycling (Vitousek 1984). This observation – low N availability in submontane/montane vs. lowland sites – is consistent with higher foliar and litter N concentrations (Table 2); soil N₂O emissions (Sousa Neto *et al.* 2011); and riverine inorganic N concentrations (Andrade *et al.* 2011, Groppo 2010, Ravagnani 2015) in our lowland vs. montane sites. Moreover, lower nutrient availability in montane forests has been reported by several other authors in the past (Arnold *et al.* 2009, Corre *et al.* 2010, Edwards 1977, Grubb 1971, Unger *et al.* 2010, Wolf *et al.* 2011).

Furthermore, $\delta^{15}\text{N}$ has been used as a proxy of N availability, partly because systems with high N losses tend to have soil and vegetation enriched in ^{15}N in relation to ^{14}N (Högberg 1997). Consequently, systems with excess N availability and high N losses tend to gravitate toward higher $\delta^{15}\text{N}$ in plants and soils (Craine *et al.* 2009, Houlton *et al.* 2006, Martinelli *et al.* 1999, Pardo *et al.* 2006, Posada & Schuur 2011, Vitousek *et al.* 1989), including patterns of decreasing N availability with increasing altitude (Corre *et al.* 2010, Wolf *et al.* 2011). Hence, the highly significant correlation between $[\text{NUE}]_{\text{N}}$ and litter $\delta^{15}\text{N}$ reinforces our argument for highest N availability in the lowland site; intermediate amounts

of N in submontane and montane forests; and lowest amounts of N in the coastal forest.

Seasonal changes in litterfall and nutrient fluxes

Our findings reveal patterns of litterfall and nutrient cycling that changed throughout the season, pointing to additional interactions between climate, weather and altitude in our forest sites. Interestingly, litterfall was higher during the wet than dry season, a pattern that appears to contradict expectations for a green-up as observed in central Amazon forests during the dry season (Huete *et al.* 2006). Such green-up is associated with the production of new leaves, the effect of which occurs just after leaf abscission in drier months (Wu *et al.* 2016). New leaves are associated with high photosynthetic capacity, which, in turn, allows forest vegetation to take advantage of higher solar radiation fluxes during dry season when cloud cover is reduced (Wagner *et al.* 2016, Wu *et al.* 2016).

Guan *et al.* (2015) proposed that MAP of 2000 mm is a threshold that would allow water to be stored in deep soil layers during the rainy season and used by trees during the dry season. The MAP in our study sites is roughly near the threshold proposed by Guan *et al.* (2015). However, substantial storage of rainy-season moisture is constrained by the occurrence of shallow (1 m) and young soils (Inceptisols), reflecting hilly terrain and landslides in the Serra do Mar (Furian *et al.* 2002, Pinto *et al.* 2016, Salemi *et al.* 2013). Therefore, it seems that the Atlantic Forest is potentially more water- than light-limited. This supposition has been confirmed by Rosado *et al.* (2016) who, based on leaf traits, concluded that water limitation occurs year-round in the montane forest, whereas such moisture constraints are relegated to the dry season in the lowland forest.

CONCLUSION

Seasonal and spatial (altitudinal) patterns of litterfall and nutrient fluxes identified for the Atlantic Forest provide new insights into the functioning of this diverse and rapidly disappearing biome. First, our findings confirm the trend of a decrease in litterfall with increasing altitude, despite the observation of increase in above-ground biomass found by Alves *et al.* (2010). Second, plants invest more in reproduction at lower than at higher altitudes, a trend that is likely to reflect a combination of lack of pollinators, lower temperatures and energy expenditure to reduce water loss in montane tropical forest. Finally, several lines of evidence support the hypothesis that lowland forests are largely N-rich, with lower NUE, higher

N losses and higher $^{15}\text{N}/^{14}\text{N}$ composition compared with other forests in our region of study.

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