

# Climate, topography, and canopy chemistry are hierarchical controls of soil N cycling in a Neotropical lowland forest

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**Title:** Climate, topography, and canopy chemistry are hierarchical controls of soil N cycling in a Neotropical lowland forest

**Running title:** Hierarchical controls of tropical forest N status

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\* **Author Contributions:** All authors conceived of or designed the study. BBO, MKN, PGT and CSB performed the research and analyzed the data. All authors contributed to the MS - writing led by BBO and SP.

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**Key words:** <sup>15</sup>N, canopy chemistry, Carnegie Airborne Observatory, climate, imaging  
spectroscopy, LiDAR, nitrogen, soil, topography

**Abstract:** Nutrient availability varies substantially across lowland tropical forests and  
constrains their responses to global change. **However**, interactions among regional,  
landscape, and local controls of nutrient availability are poorly understood. In that  
context, we explored the effects of rainfall, topography, and canopy chemistry on  
nitrogen (N) cycling across the Osa Peninsula (Costa Rica). We sampled soils from  
catenas in regions receiving 3,000 vs. 5,000 mm of rainfall per year. Within the **less**  
**humid** region, we sampled catenas starting on either broad stable terraces or knife-edged  
ridges. On the stable terraces, we sampled soils from 0.25 ha plots with either high or low  
mean canopy N. In all sites, we measured metrics of long- (soil  $\delta^{15}\text{N}$ ) and short-term (net  
nitrification and mineralization, and KCl-extractable N) N availability. Mean soil  $\delta^{15}\text{N}$   
was elevated in the **less humid** region ( $3.8 \pm 0.16\text{‰}$  vs.  $3.1 \pm 0.14\text{‰}$ ;  $P=0.003$ ). Within that  
region, mean  $\delta^{15}\text{N}$  was  $\sim 1\text{‰}$  heavier on stable terraces ( $5.3 \pm 0.14\text{‰}$ ), than nearby knife-  
edged ridges ( $4.0 \pm 0.24\text{‰}$ ;  $P<0.001$ ). Short-term N metrics did not vary with rainfall or  
topography ( $P>0.05$ ). In contrast, short-term soil N metrics did vary **under canopies with**  
**high vs. low canopy N**, but soil  $\delta^{15}\text{N}$  did not. These results illustrate the role of climate  
and topography as dominant drivers of long-term N status on the Osa, as well as the

potential for canopy characteristics, which are likely determined by phylogeny in this system, to impose small-scale heterogeneity within those broader constraints. Overall, our work suggests the use of a hierarchical framework for understanding how diverse drivers of nutrient status interact across space and time in tropical forests.

## INTRODUCTION

Nutrient availability regulates many ecosystem processes in lowland tropical forests, including net primary productivity (Mirmanto and others 1999; Wright and others 2011; Alvarez-Clare and others 2013), decomposition (Cleveland and others 2006), reproductive litter production (Kaspari and others 2008), and trace gas emissions (Hall and Matson 2003). Nutrient status may also influence forest responses to global change (Thornton and others 2007; Bonan and Levis 2010; Townsend and others 2011; Cleveland and others 2013; Wieder and others 2015). In the lowland tropics, a combination of empirical data and theory suggest that many forests are relatively nitrogen (N) rich but phosphorus (P) poor (Vitousek 1984; Martinelli and others 1999; Wang and others 2010; Cleveland and others 2011). However, recent work has highlighted the biogeochemical heterogeneity of these diverse ecosystems and suggested that any biome-wide representation of nutrient status and/or limitation is likely an oversimplification (Townsend and others 2008; Porder and Hilley 2011). While small-scale variations in patterns and rates of many ecosystem processes point to the heterogeneity of tropical forests (Burghouts and others 1998; Dent and others 2006; Xia and others 2015), the

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relative influence of the factors that contribute to that variability across the landscape is not well understood.

Here, we focus on N cycling and availability, which vary widely across tropical systems. For example, many geologically-stable lowland forests cycle N in excess (Vitousek 1984; Martinelli and others 1999; McGroddy and others 2004). In contrast, N availability can be quite low in forests growing where rates of N loss are high, such as rapidly eroding regions or those with especially high rainfall (Houlton and others 2006, 2007; Hilton and others 2013). Examples of such regions include the Central Range of Taiwan (Hilton and others 2013) and the Osa Peninsula of Costa Rica (Bern and others 2005; Wieder and others 2009, 2011). Indeed recent work has highlighted the importance of N in some tropical regions. Nitrogen has been shown to limit and/or co-limit microbial respiration on the Osa (Ilstedt and Singh 2005; Cleveland and Townsend 2006) as well as reproductive litter production and sapling growth in Panama (Kaspari and others 2008; Wright and others 2011) and Indonesia (Mirmanto and others 1999; Adamek and others 2009).

It remains unclear, even in areas where N availability is relatively low and thus may limit important ecosystem properties, how and why N status varies across space and time. To better understand N variability in lowland tropical forests, we examined how three drivers of N cycling (rainfall, topography, and canopy chemistry) influence soil N status in tropical forest across the Osa Peninsula in southwestern Costa Rica. Work in montane tropical forests as well as global meta-analyses indicate that N availability decreases with rainfall in wet tropical forests (Schuur 2003; Houlton and others 2007;

84 Nardoto and others 2008; Craine and others 2009). To our knowledge, this relationship  
85 has not been explicitly tested in wet *lowland* tropical forests, where annual precipitation  
86 ranges widely (Malhi and Wright 2004). However, it is likely that climatic differences  
87 drive differences in N cycling in these regions as well.

88 At the scale of watersheds, topography can drive differences in nutrient  
89 availability by setting the pace of erosion, and thus soil residence time (Jenny 1941;  
90 Vitousek 2004; Porder and Hilley 2011). These effects are most pronounced where  
91 topography creates differences in soil age. For example, in some but not all locations  
92 ridges tend to host relatively older soils than their adjacent slopes due to slower rates of  
93 erosion (Porder and others 2005, 2015). This state of geomorphic disequilibrium is  
94 common where there is rapid or recent tectonic uplift, which isolates upland areas from  
95 being eroded by river channels. Erosion-driven differences in soil age can affect both N  
96 and P (and other rock-derived nutrient) availability (Amundson and others 2003;  
97 Vitousek and others 2003; Hilton and others 2013; Weintraub and others 2015).

98 Finally, plant-soil **interactions** may influence nutrient availability at small spatial  
99 scales (Dent and others 2006; Xia and others 2015). **Nutrient rich soils can promote**  
100 **elevated foliar nutrient concentrations, lower nutrient resorption, rapid decomposition,**  
101 **and thus higher soil fertility (Vitousek 2004). The influence of soil nutrient availability**  
102 **on foliar chemistry among tree species has been observed across montane tropical forests**  
103 **(Hidaka and Kitayama 2011) and demonstrated experimentally within species in a**  
104 **lowland forest (Mayor and others 2014a, 2014b). Similarly, the influence of canopy foliar**  
105 **chemistry on soil is well documented, at least in temperate forests (Binkley and Giardina**

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106 1998; Lovett and others 2004; Hobbie and others 2006; Laughlin and others 2015). Such  
107 effects are more difficult to document in the hyperdiverse tropics. Perhaps as a result,  
108 some tropical forest studies report correlations between foliar chemistry and soil nutrients  
109 (Keller and others 2013), free-living N fixation (Reed and others 2008), litter  
110 decomposition rates (Wieder and others 2008), and carbon dioxide and nitrous oxide gas  
111 fluxes (Van Haren and others 2010; Waring and others 2015), while others suggest that  
112 individual trees have little to no influence in the presence of such high diversity (Powers  
113 and others 2004; John and others 2007). The high phylogenetic and functional diversity  
114 of trees in tropical forests (Townsend and others 2008; Fyllas and others 2009) makes it  
115 difficult to identify places on the forest floor that receive litterfall from a single species or  
116 group with shared functional traits. This may partially explain the lack of consensus in  
117 regards to the role of tropical trees in influencing soil nutrient status.

118 Here, we explore the influence of mean annual precipitation (MAP), topography  
119 and canopy chemistry on N cycling in the lowland tropical forests of the Osa Peninsula,  
120 Costa Rica. We coupled high-resolution LiDAR and image spectrometry with targeted  
121 ground-based soil sampling to test the following three hypotheses. First, we hypothesized  
122 that soil N availability would be lower in the wetter region of the Peninsula. Next, we  
123 hypothesized that in sites receiving similar amounts of rainfall, N availability would be  
124 higher on broad, slowly eroding terraces with functionally older soils, than on narrow  
125 ridges and adjacent slopes with short soil residence times. Finally, in climatically and  
126 topographically similar sites, we hypothesized that soil N availability would be higher

under high N canopies than low N canopies. We explore evidence as to the direction of this relationship (plant effects on soil vs. soil effects on plants) in the discussion.

## METHODS AND MATERIALS

### Site description

We tested these hypotheses in mature lowland tropical forests on the Osa Peninsula in southwestern Costa Rica. Mean annual temperature at the elevation of our sites (100-200 m above sea level) is relatively uniform across the Peninsula ( $\sim 26^{\circ}\text{C}$ ), and rainfall ranges from  $\sim 3,000\text{ mm y}^{-1}$  on the southern end of the Osa up to  $\sim 5,000\text{ mm y}^{-1}$  in the north (Taylor and others 2015). Two of our study sites, Piro North and Piro South, are located near the Piro Biological Station ( $8^{\circ}24'\text{N}$ ,  $83^{\circ}19'\text{W}$ ) in the south and receive  $\sim 3,000\text{ mm MAP}$ . Our third site, Rancho Mariposa near Drake Bay ( $8^{\circ}43'\text{N}$ ,  $83^{\circ}37'\text{W}$ ; hereafter referred to as Drake), receives  $\sim 5,000\text{ mm MAP}$  (Taylor and others 2015; Figure 1). All three sites experience a pronounced dry season from December – April, with heavy rainfall common the rest of the year. The Osa has stratified, closed-canopy forests that include  $\sim 57$  tree families and  $>400$  species with an estimated 100-200 tree species  $\text{ha}^{-1}$  (Kappelle and others 2003).

The Osa Peninsula has experienced recent tectonic uplift and the landscape is being rapidly dissected by downcutting streams (Hauff and others 2000). As in similar geomorphic settings, broad, flat, or gently sloping terraces underlie some portions of the landscape. These slowly-eroding terraces are the highest topographic points locally and are isolated from the steep slopes and rapidly incising streams on their flanks, similar to other terraces on the Pacific Coast of North and Central America (Jenny and others 1969;



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White and others 2009). Such terraces are prominent in Piro South, but largely absent in Piro North and Drake (Figure 1). In the latter two sites, rapid stream incision (3.5-7 m y<sup>-1</sup>) (Hauff and others 2000) has completely dissected these terraces and brought the landscape closer to geomorphic equilibrium, where knife-edged ridges are bound on either side by steep slopes. Thus, we expect both ridges and slopes are eroding at similar rates in these sites (Figure 1).

Soils on the Osa are primarily Ultisols (mostly Typic Tropohumults), however Inceptisols (Typic Humitropepts) can be found in steep areas (Perez and others 1978; Vasquez 1989). Rapid erosion provides sufficient inputs of fresh rock such that soil exchangeable strontium, and by extension nutrient cations, are provided by rock weathering rather than atmospheric deposition in both Drake (Bern and others 2005) and Piro (Osborne, Unpublished Data). Drake is underlain by basalt flows, while Piro North and South are primarily underlain by lithified andesitic and basaltic sediments (e.g. volcaniclastics) that were deposited in a shallow marine environment (Buchs and others 2009).

**Airborne LIDAR and high fidelity imaging**

The Carnegie Airborne Observatory (CAO)'s Airborne Taxonomic Mapping System (AToMS) was used in February of 2012 to complete a series of remote sensing flights over the Osa Peninsula. The AToMS platform combines a high-fidelity imaging spectrometer (HiFIS) with a dual laser, waveform LiDAR scanner (Asner and others 2012). Data were collected at an altitude of 2000 m above ground level at a ground speed of approximately 200 km h<sup>-1</sup>. The LiDAR was operated at a pulse repetition frequency of

50 khz. Beam divergence was set to 0.56 mrad (l/e) for each of the two lasers, providing a total of 1.12 m laser spot spacing and allowing for two laser shots per m<sup>2</sup>. To generate digital elevation models (DEM), such as those included in Figure 1, 10 m x 10 m kernels were passed over georeferenced LiDAR data points. The lowest elevation estimate in each kernel was assumed to be ground. All remaining ground points were identified by iteratively fitting a horizontal plane to each of the ground seed points and selecting the closest point < 5.5° and 1.5 m higher in elevation.

The AToMS HiFIS measures spectral radiance in 5 nm increments (full-width at half-maximum), spanning the visible to shortwave infrared spectrum (380-2510 nm). The raw HiFIS data were made up of 480 contiguous channels, which were resampled to 214 bands at 10 nm increments for analysis. The derived spectral radiance data were atmospherically corrected and converted to brightness-normalized reflectance to minimize the differences in observed brightness due to canopy leaf tissue orientation and depth (Feilhauer and others 2010; Asner and others 2015).

The canopy N mapping data used in our study were derived using a spectral calibration originally developed in Amazonian tropical forests (Asner and others 2015), and previously applied on the Osa Peninsula, Costa Rica (Asner, Unpublished data). However, because the spectral calibration was not specific to the forests of the Osa, we have conservatively chosen to refer to the remotely sensed N values as a “canopy N metric” rather than concentration. Hereafter, we simply refer to the mapped value as “canopy N”. In general, a data-fusion approach combining HiFIS with Partial Least Squares Regression (Haaland and Thomas 1988) and LiDAR data was used to produce 2

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193 m resolution canopy N maps with reduced effects from illumination and viewing angle  
194 variation, crown architecture, inter- and intra- crown shading, forest gaps, and terrain-  
195 related artifacts (Asner and others 2012).

196 **Experimental design, soil collection, and tree species identification**

197 We used MAP records in conjunction with DEMs generated from the LiDAR data  
198 **described** above to identify sites within the CAO flight lines with the desired climatic and  
199 topographic conditions. To evaluate the influence of MAP on N status we compared soils  
200 from Piro North and Drake, which differ in MAP (~3,000 vs. ~5,000 mm MAP,  
201 respectively) but have similar topography. Both sites are dominated by knife-edged  
202 ridges in geomorphic equilibrium with their adjacent slopes (Figure 1). To measure the  
203 effects of topography on N status we compared soils in Piro North and Piro South, which  
204 have similar MAP (~3,000 mm y<sup>-1</sup>) but different geomorphology.

205 In each site, we sampled four catenas (ridge, shoulder, mid slope, and low slope  
206 transects). All of the catenas start on either a broad flat ridge (Piro South) or a narrow  
207 knife-edge ridge (Piro North and Drake), and end on a low portion of the slope  
208 (floodplains are absent from these first order valleys; Figure 1). At each slope position  
209 (ridge, shoulder, mid slope, and low slope), we used a hand auger to extract five 0-10 cm  
210 **samples of mineral soil** located roughly every 5 m along a contour line (e.g. at constant  
211 elevation). These five subsamples were homogenized for a single slope position on a  
212 given catena prior to analysis. **Soils in the Osa typically have minimal O horizons, during**  
213 **the dry season litter builds up directly on the mineral soil and in the wet season the**  
214 **mineral soil is immediately beneath a thin layer of decomposing litter.**

We sampled soils during both the wet (July 2014) and dry (January 2014, February 2015) seasons. We focus on wet season data here because we sampled all of the sites during the July 2014 campaign, while dry season data for Piro North and Drake were collected during a different dry season and year than Piro South. Data from the dry season are included Supplementary Figure 1. We did not expect soil  $\delta^{15}\text{N}$  to vary seasonally, so for this metric we analyzed soils collected in both seasons and averaged our results

In order to explore the influence of canopy chemistry on soil N, we used HiFIS to identify circular 0.25 ha plots with either high or low canopy N, which we defined as having  $>$  or  $<$  0.5 standard deviation of the regional mean canopy N (Figure 2; Table 2). Regional mean canopy N was calculated using all of the data collected along a flightline with a total area of over 56 km<sup>2</sup>. In an effort to hold all other drivers as constant as possible, we selected high and low canopy N plots within 1 km<sup>2</sup> of one another on the same broad flat terrace in Piro South (Figure 1). After preprocessing of the canopy N dataset to remove poorly illuminated and/or non-canopy structures, the number of pixels in the 0.25 ha plots ranged from 218 (0.09 ha) and 443 (0.18 ha; Table 2). On average, canopy N in the high N plots was two standard deviations above the regional mean, while low N plots averaged 0.6 standard deviations below the regional mean. Overall, canopy N values in these plots spanned almost the entire range of canopy N that has been observed among tropical forest ecosystems (Balzotti and others, unpubl. data; Asner and others 2014). We collected three soil samples (0-10 cm) from the inner 10 m of each circular plot using a hand auger in February, May, and August of 2015.

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237           To compare canopy tree species composition between the high and low N plots,  
238 we identified trees with  $\geq 40$  cm diameter at breast height (DBH). This DBH cut-off has  
239 previously been identified as the inflection point of a height-to-diameter curve of trees on  
240 the peninsula, suggesting that trees of this size are likely to be canopy emergents and thus  
241 visible to our airborne sensors (Taylor and others 2015). In addition, we carried out field  
242 surveys to ascertain which trees in our plots were canopy emergents and found that the 40  
243 cm DBH cutoff was representative. The plots contained an average of 14 individuals with  
244  $\geq 40$  cm DBH, and included 40 different species

245   **Soil analyses**

246 We measured pH in 1:2 soil/deionized water solutions using an InLab 413 glass electrode  
247 (Mettler Toledo, Schwerzenbach, Switzerland). Within three hours of collection, we  
248 extracted  $\text{NO}_3^-$  and  $\text{NH}_4^+$  by shaking 8 g of field moist soil in 30 mL of 2M KCl for one  
249 minute every hour for four hours (Weintraub and others 2015). After four hours, extracts  
250 were filtered through Whatman glass microfiber filters and stored frozen until analysis.  
251 We stored a second soil aliquot at field temperature in the dark for five days and then  
252 extracted with 2M KCl as described above (Weintraub and others 2015). We analyzed  
253  $\text{NO}_3^-$  and  $\text{NH}_4^+$  on a Westco Smartchem 200 discrete element analyzer (Brookfield, CT,  
254 USA). We calculated net nitrification and N mineralization as the difference between  
255 extractable  $\text{NO}_3^-$  and total inorganic N concentrations from the completion of the five-day  
256 incubation and our initial extraction in the field. We measured bulk soil C, N, and  $\delta^{15}\text{N}$   
257 on air dried, ground soils using a Europa 20-20 continuous-flow isotope ratio mass  
258 spectrometer interfaced with a Europa ANCA-SL elemental analyzer (Sercon Ltd.,

Cheshire, UK) at the Marine Biological Station Stable Isotope Laboratory (Woods Hole, Massachusetts). We report all concentrations on a soil dry mass basis (105°C for 48 hours).

### Statistical analyses

We log transformed all data that did not fit the assumptions of normality. To understand the influence of rainfall and slope position, we compared soil N availability in geomorphically similar sites with high MAP (~5,000 mm, Drake) and low MAP (~3,000 mm, Piro North) (Figure 1) using a two-way ANOVA with rainfall and slope position as fixed variables. We then tested the influence of slope position (ridge, shoulder, mid slope, and low slope) on soil N using one-way ANOVAs and Tukey's HSD test separately in each site (Piro South, Piro North, and Drake). To determine the effects of soil residence time we used a t-test to compare N cycling metrics between the ridges of Piro South (broad, flat terrace) and Piro North (knife-edge ridges; Figure 1). We also used a t-test to examine differences in soil N status between the high and low canopy N plots using one-way ANOVA. The analyses described above were all performed using SAS JMP Pro software version 11.2.0 (SAS Institute Inc., Cary, North Carolina) and results are reported as means  $\pm$  standard error. We compared tree species composition in the canopy N plots using nonmetric multidimensional scaling (NMDS). Using the function 'metaMDS' in the R package vegan (Oksanen and others 2016), we generated an ordination plot representing each site based on the total basal area of species with individuals of  $\geq 40$  cm DBH. Data was square root transformed and Bray-Curtis distances were used to create a dissimilarity matrix. The function then used multiple starting

configurations to identify a stable solution, which was ultimately configured to maximize variability along the first NMDS axis.

RESULTS

Rainfall and topographic effects on soil N status

Soil  $\delta^{15}\text{N}$  was lower on Drake **catenas** (5,000 mm MAP;  $3.1 \pm 0.14\text{‰}$ ) than in the less humid Piro North sites (3,000 mm MAP;  $3.8 \pm 0.16\text{‰}$ ;  $N=4$ ;  $P=0.003$ ; Table 1). In both Drake and Piro North, catenas start on knife-edged ridges rather than flat terraces, and soil  $\delta^{15}\text{N}$  did not differ between ridges and slopes ( $P>0.05$ ). However, in Piro South, mean soil  $\delta^{15}\text{N}$  was highest on broad flat terraces ( $5.3 \pm 0.14\text{‰}$ ), intermediate on shoulders ( $4.8 \pm 0.30\text{‰}$ ) and lowest on adjacent mid and low slope positions ( $4.3 \pm 0.13\text{‰}$ ) ( $P=0.005$ ; Figure 3A). The broad flat ridgetops in Piro South were enriched by  $\sim 1\text{‰}$  relative to the knife-edged ridges of nearby Piro North ( $4.0 \pm 0.24\text{‰}$ ;  $P<0.001$ ; Figure 3). Soil  $\delta^{15}\text{N}$  on the shoulder and mid slope positions in Piro South were not significantly different than equivalent topographic positions in Piro North ( $4.1 \pm 0.19\text{‰}$ ;  $P>0.05$ ). The low slope position was significantly lower in Piro North ( $4.2 \pm 0.20\text{‰}$ ) than in Piro South ( $3.0 \pm 0.14\text{‰}$ ,  $P<0.0001$ ), a result driven by two of the four low slope replicates in Piro North. These replicates had  $\delta^{15}\text{N}$  levels  $\geq 1\text{‰}$  lower than any other position in either of the Piro sites (Figure 3). In contrast to soil  $\delta^{15}\text{N}$ , there were no significant differences in **KCl-extractable** inorganic N, net nitrification, or net N mineralization across slope positions or between sites ( $P>0.05$ ) with the exception of  $\text{NO}_3^-$ , which was elevated in Piro North relative to Drake ( $P=0.011$ ; Table 1). Generally, the same was true during the dry season: inorganic nitrogen concentrations, and N cycling rates were unaffected by

slope position (Supplementary Table 2). However, we were unable to interpret the influence of MAP during the dry season because Piro South and Drake were sampled in January 2014, while Piro North was sampled in February 2015.

### Relationship between canopy N and canopy tree species and soil N status

In contrast to topography and rainfall, both of which influenced soil  $\delta^{15}\text{N}$  but not inorganic N or N processing rates, differences in canopy N did not correlate with differences in soil  $\delta^{15}\text{N}$  (soil  $\delta^{15}\text{N}$  below high N canopy =  $4.8 \pm 0.25$ ; soil  $\delta^{15}\text{N}$  below low N canopy =  $4.6 \pm 0.26$ ,  $P > 0.05$ ;  $N=5$ ; Table 2). However mean extractable  $\text{NH}_4^+$  ( $P=0.046$ ),  $\text{NO}_3^-$  ( $P < 0.0001$ ), net nitrification ( $P < 0.0001$ ), and net N mineralization ( $P < 0.0001$ ) were  $\sim 1$  order of magnitude higher in high vs. low N canopy plots in August of 2015 (Figure 4; Table 2). Similar trends were observed during our two additional sampling campaigns (February and May, 2014) (Supplementary Figure 1).

With our tree species data, we produced a two-dimensional NMDS ordination plot with a stress value of 0.15, which represents the correlation between Bray-Curtis distance and the distances in ordination space. The separation of the high and low N plots and their centroids on the plot suggest that canopy species composition of the high N plots differs from that of low N plots (Supplementary Figure 2). Interestingly, only ten individual canopy trees were species that are known to nodulate (Sprent 2009), and there was no difference in their abundance between high and low canopy N plots (data not shown).

## DISCUSSION



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324 Our findings suggest that tropical nutrient dynamics and heterogeneity reflect  
325 interactions among multiple drivers that are spatially nested. On the Osa, annual rainfall  
326 and topographic variability dominantly control long-, but not short-term N availability.  
327 Rainfall varies at the scale of the Peninsula, topography at the smaller spatial scale of the  
328 landscape. Within a given slope position, soil inorganic N cycling is strongly correlated  
329 with local canopy N. Canopy N varies regionally as a result of climate (and likely  
330 phylogenetic sorting; Balzotti and others, Unpublished data). **While the correlation**  
331 **between soil and canopy N could be the result of N rich soils creating N rich canopies or**  
332 **the reverse, we suggest below that in our sites it is likely that variation in canopy**  
333 **communities drive local variability in soil N** (Asner and others 2014; Asner and Martin  
334 2015). This variation likely fluctuates over relatively small spatial scales and short  
335 timescales as trees grow and die, and may be modifying the influence of rainfall and  
336 topography on short-term N status (Figure 5).

337 **Regionally, MAP is a dominant control of long-term N cycling**

338 Our **soil**  $\delta^{15}\text{N}$  suggest that, on the Osa, regional variability in MAP creates long-  
339 term differences in N status. At Drake, with high MAP ( $\sim 5,000$  mm rainfall  $\text{y}^{-1}$ ), **soil**  $\delta^{15}\text{N}$   
340 was lower than at Piro South (3,000 mm rainfall  $\text{y}^{-1}$ ). This result is consistent with prior  
341 work in montane (Schuur and Matson 2001) and gradients in lowland-to-montane (Asner  
342 and Martin 2015) tropical forests that show broad rainfall-driven declines in soil  $\delta^{15}\text{N}$ .  
343 **These studies suggest that, over long time scales, there is a net effect of MAP on soil N**  
344 **cycling and availability. The lower  $\delta^{15}\text{N}$  signature of Drake could be the result of several**  
345 **different mechanisms, which are not mutually exclusive: 1) Decomposition, N**

mineralization and nitrification could be inhibited by low oxygen availability in very wet soils and/or 2) denitrification of a large proportion of the  $\text{NO}_3^-$  pool could result in less fractionation during N gas loss (Schuur and others 2001; Houlton and others 2006). We think that the latter explanation may be more probable in the Osa because decomposition rates remain extremely high in the well-drained soils even where rainfall is high and, unlike in poorly-drained montane sites, net primary productivity and above ground biomass are not reduced even at  $5 \text{ m yr}^{-1}$  rainfall.

While we found that MAP influenced soil  $\delta^{15}\text{N}$ , short-term metrics of N cycling and availability (i.e. inorganic N concentrations, net N mineralization, net nitrification) did not vary between geomorphically similar high and low rainfall sites (i.e., Drake vs. Piro North). Although the expectation is that  $\delta^{15}\text{N}$  reflects the net effects of short-term N availability and cycling over time (Handley and others 1999), there are few data from the lowland tropics that explicitly test the influence of annual rainfall on short-term N cycling. However, across a montane climosequence in Maui, Hawai'i (MAP 2,500 to  $>5,000 \text{ mm yr}^{-1}$ ), both long and short-term N metrics are correlated with MAP (Schuur and Matson 2001; Houlton and others 2007). Interestingly, the species composition across the Maui gradient is quite uniform, which makes it ideal as a climosequence but may mask the importance of tree species in creating short term and small spatial scale variation in N availability. In the Osa, where diversity of trees is much higher, greater sampling may be required to see the influence of regional drivers in the face of local variation in the vegetation (see below).

**At the landscape scale, slope position is a dominant driver of long-term N cycling**

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368 Our data suggest that, within a given MAP zone on the Osa, long-term N status is  
369 also driven by soil residence time. We examined the influence of topography on soil N  
370 availability independently of MAP by comparing soil N from catenas in geomorphic  
371 equilibrium (Piro North) and disequilibrium (Piro South) from sites with similar climatic  
372 conditions. Soil  $\delta^{15}\text{N}$  was higher on slowly eroding flat terraces compared to knife-edged  
373 ridges, and similar between knife-edged ridges and their adjacent slopes (Figure 3). We  
374 interpret this as an effect of topographically mediated differences in soil age. Slowly  
375 eroding flat surfaces allow N availability to accumulate over long timescales, resulting in  
376 more open N cycling and the preferential loss of  $^{14}\text{N}$  over time. However, N  
377 accumulation, and thus cycling and  $^{14}\text{N}$  losses, is less on knife-edged ridges due to rapid  
378 erosion. Thus, these sites have effectively younger substrates with relative less N and a  
379 more conservative N cycle. Others have observed comparable trends in soil  $\delta^{15}\text{N}$  along  
380 topographic gradients and proposed a similar mechanism of control (Amundson and  
381 others 2003; Hilton and others 2013).

382 Contrary to what has been found in other parts of the world (Kitayama and others  
383 1997; Martinelli and others 1999), we did not detect significant effects of topography on  
384 short-term N cycling. As with the climate signal, we suggest this may be a result of  
385 species affects on short term N cycling metrics, and the need for more intensive sampling  
386 to document these effects where diversity is high. Previous work on one of the catenas  
387 included in our study was able to demonstrate a link between topography, soil  $\delta^{15}\text{N}$  and  
388 rates of inorganic N cycling (Weintraub and others 2015), but only through intensive

389 sampling of a single catena. It is possible that we did not detect the effects of topography  
390 (and/or climate) because we did not sample each catena sufficiently.

### 391 Plant-soil feedbacks influence local short-term N cycling

392 On the broad flat remnant terrace in Piro South, where MAP and topography  
393 remain constant, we found strong positive correlations between canopy N and soil  $\text{NO}_3^-$   
394 concentrations as well as net nitrification and net N mineralization rates. Under high  
395 canopy N, inorganic N concentrations were more than six times higher than in soils  
396 beneath low N canopies. However, we found no variability in soil  $\delta^{15}\text{N}$ . We also found  
397 evidence that the community of canopy emergent trees differed between plots with high  
398 and low canopy N, although there were very few putative N fixers (Sprent 2009) in any  
399 of the plots.

400 High canopy N can either result from or cause high soil N. However, given the  
401 spatial scale of our canopy analysis, we suggest that our data provide an intriguing hint as  
402 to possible causation. First, different tropical forest trees growing in the same place have  
403 a wide range of canopy N that that been convincingly linked to phylogeny (e.g. Asner  
404 and Martin, 2015). Second, all of the plots included in this study are concentrated in a  
405 small area that does not host known variation in many other factors that drive differences  
406 in soil N (e.g. climate, parent material, topography, soil age). Third, our analysis of the  
407 species composition data suggests these remotely-identified sites that differ in canopy N  
408 also differ in the community of canopy emergent species (Supplementary Figure 2).  
409 Lastly, if soil nutrients were the root cause of heterogeneity in foliar N, we might expect  
410 to see differences in soil  $\delta^{15}\text{N}$  as a reflection of sustained variability in N status. Instead,

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411 we observed no differences in soil  $\delta^{15}\text{N}$  between high and low canopy N plots. While this  
412 line of reasoning is not a smoking gun - *a priori* differences in soil N could set the stage  
413 for the success of different tree communities, which then participate in a positive  
414 feedback with soil fertility. However, we believe that given the available evidence, it is  
415 more likely that the stochastic distribution of trees across this small, relatively  
416 homogenous portion of the Osa landscape gives rise to patches of particularly high and  
417 low canopy and soil N.

418 **Hierarchical controls of N status on the Osa Peninsula**

419 The climatic, geomorphic, and biological heterogeneity of the Osa informs a  
420 conceptual framework through which to view our original hypotheses and the data that  
421 support (or do not support) them. Our first hypothesis, that N availability would be lower  
422 in Drake (5,000 mm  $\text{y}^{-1}$ ) than Piro North (3,000 mm  $\text{y}^{-1}$ ) was supported by differences in  
423 soil  $\delta^{15}\text{N}$ , but not by inorganic N concentrations, net nitrification or net N mineralization  
424 data. Similarly, our soil  $\delta^{15}\text{N}$  data suggested higher long term N availability, and thus  
425 more fractionating N losses, from broad, flat, slowly eroding terraces (Piro South ridge)  
426 compared with more rapidly eroding surfaces (Piro South slopes and all of Piro North).  
427 However, contrary to our hypothesis, we saw no differences in shorter-timescale N  
428 cycling metrics across sites with varying topography (Table 1).

429 Overall, our data indicate that a spatially and temporally nested set of controls  
430 drive N cycling patterns across the Osa Peninsula (Figure 5). In this conceptual model,  
431 long-term integrative N cycling metrics (such as soil  $\delta^{15}\text{N}$ ) measured in a particular place  
432 are influenced by factors that change over long timescales (i.e. topography, climate, and

parent material). In contrast, both long-term drivers and processes that fluctuate on shorter timescales (i.e. local tree assemblage, seasonality, and weather) influence metrics of short-term N availability (i.e. net nitrification and mineralization).

This conceptual model helps us understand the lack of correlation between soil  $\delta^{15}\text{N}$  and inorganic N availability on the Osa. Soil  $\delta^{15}\text{N}$  integrates short-term N dynamics because dominant N loss pathways favor  $^{14}\text{N}$  (Handley and others 1999). Thus, soil  $\delta^{15}\text{N}$  increases as a result of higher  $\text{NO}_3^-$  losses. Such concordance is observed in some systems, including the aforementioned Maui climate gradient (Schuur and Matson 2001; Houlton and others 2007). The climosequence in Maui is in a montane system with plots located on virtually uneroded, gently sloping surfaces (<5% relief) that are ~400,000 year old and dominated by a single tree species (Schuur and others 2001). Weather at each site is also relatively stable, because the climate gradient is driven by plot position relative to the windward-leeward transition across the Haleakala Volcano. Because these other factors are relatively constant, we would expect all N cycling metrics to reflect the influence of rainfall (Figure 5). Indeed, the hallmark of a well-chosen climosequence is lack of variation in other factors that might obscure the signal of climate on the process of interest.

In contrast to Maui, our sites on the Osa Peninsula differ in both long- and short-term drivers of N cycling. Of the metrics we measured, only soil  $\delta^{15}\text{N}$  is influenced predominantly by long-term drivers such as MAP and topography (Figure 5). Shorter-term N cycling metrics are influenced by those factors as well, but their signal may be obscured by differences in other controls (e.g., tree species and weather) that vary over

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455 smaller spatial scales and shorter timescales. The strong correlations between canopy and  
456  $\text{NO}_3^-$ , net nitrification, and net N mineralization suggest that species, and their associated  
457 functional diversity, may have a particularly strong influence over local variability in  
458 nutrient availability on the Osa (Figure 5).

459 **Conclusions**

460 It has long been recognized that the conception of tropical forests, even lowland  
461 tropical forests, as uniformly N rich and P-poor is an oversimplification (Vitousek 1984;  
462 Townsend and others 2008; Porder and Hilley 2011). In particular, the variation in  
463 multiple drivers across tropical landscapes has presented a challenge to biogeochemists  
464 and ecosystem ecologists seeking to understand tropical forest properties at large spatial  
465 and temporal scales. Our work suggests a hierarchical framework for considering this  
466 biogeochemical diversity. We highlight the role of just a few factors (parent material,  
467 climate, topography) in driving the long-term nutrient status of landscapes, a result that  
468 has been born out in other systems (Porder and others 2015). However, shorter-term  
469 nutrient dynamics on the Osa are also influenced by canopy characteristics, which are  
470 likely the result of small-scale tree aggregations and the phylogenetic signal they impart  
471 to the canopy. If our results from the Osa are representative, community shifts that result  
472 from climate change may play a key role in driving the biogeochemical responses of  
473 tropical forests.

474  
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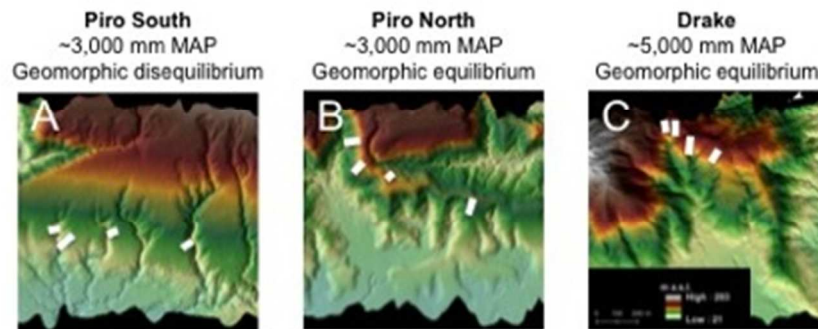


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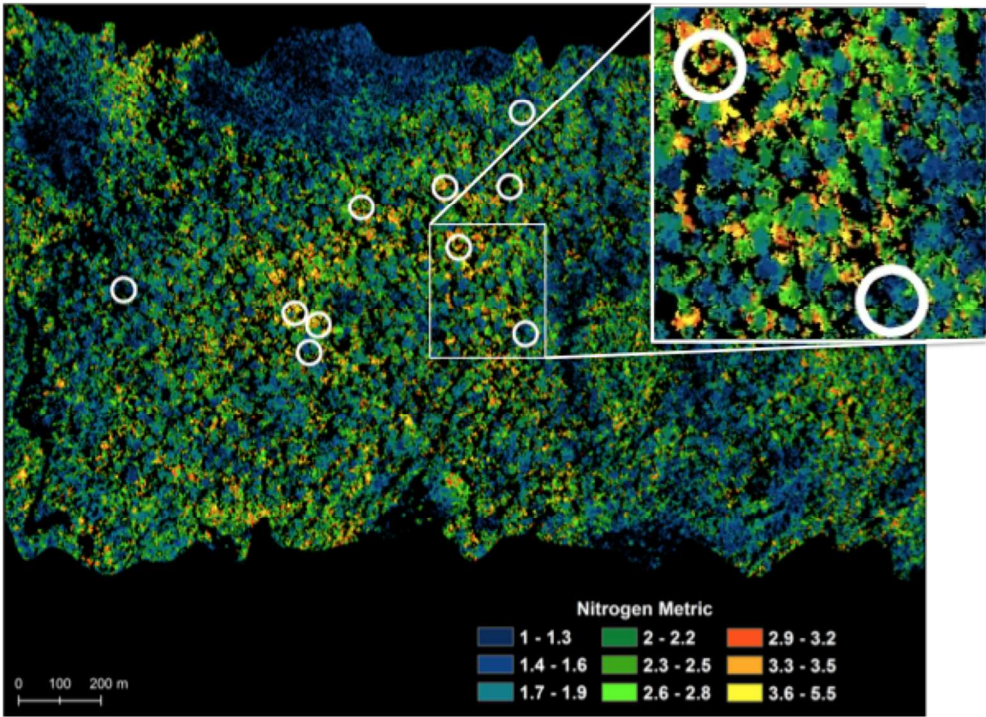
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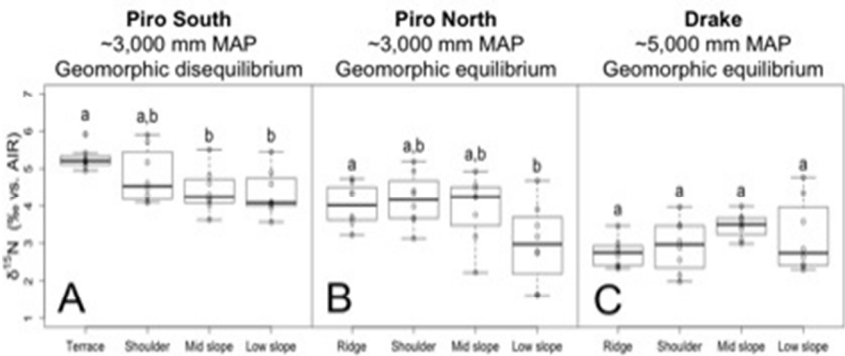
Airborne LiDAR-based digital elevation models of the three landscapes a) Piro South, b) Piro North, and c) Drake. White lines on the elevation maps indicate catena locations in each site. Note that catenas in Piro South start on broad, flat, slowly eroding terraces and cross a break in slope (knickpoint) to steep, rapidly eroding portions of the landscape. In contrast, catenas in Piro North and Drake Bay start on knife-edged ridges with similar erosion rates and soil residence times to their adjacent slopes. MAP is mean annual precipitation.

152x59mm (72 x 72 DPI)



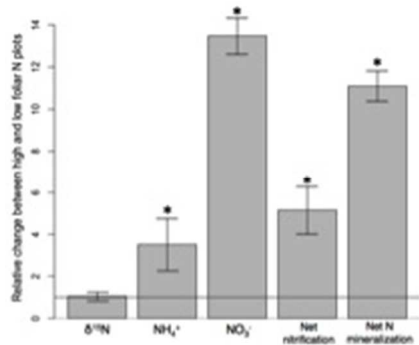


Map of the canopy nitrogen metric generated via imaging spectroscopy from the Carnegie Airborne Observatory along a flight line in Piro South. The white circles highlight the 0.25 ha high and low canopy nitrogen plots (ten total). The inset shows variability in canopy nitrogen between one high and one low plot.

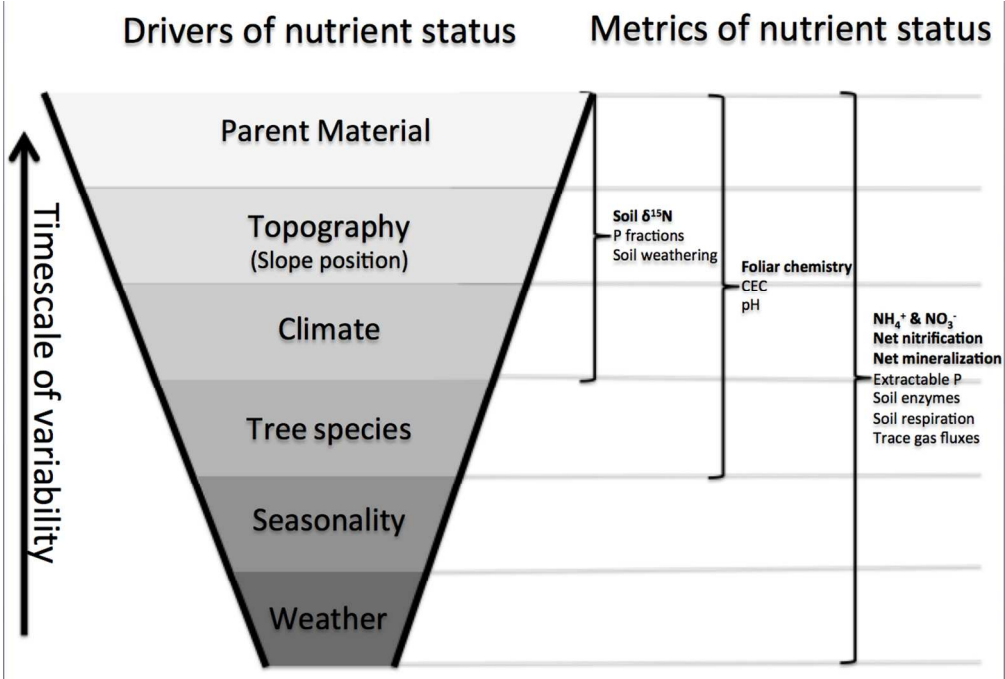


Mean soil  $\delta^{15}\text{N}$  ( $\pm 1$  SE) of soils by site and slope position (0–10 cm soil,  $N = 8$ ). Different letters denote significant ( $P < 0.05$ ) differences between slope positions within A) Piro South, B) Piro North, and C) Drake. The “terrace” position in Piro North refers to the broad flat terrace in Piro North, while the “ridge” positions in Piro South and Drake are knife-edged ridges in those regions.

152x70mm (72 x 72 DPI)



The relative difference in soil nitrogen concentrations (0 – 10 cm) beneath 0.25 ha plots with high (N=5) and low (N=5) canopy nitrogen. Values above one show the factor by which each metric is elevated in high vs. low canopy nitrogen plots. Asterisks denote significant ( $P < 0.05$ ) differences between high and low plots. 76x62mm (72 x 72 DPI)



A conceptual model for understanding which drivers may exert influence on commonly used metrics of nutrient status in the Osa Peninsula. While the influence of these drivers varies over different spatial scales, this diagram focuses on the plot (sub hectare) scale. For example, parent material, climate, and topography influence soil  $\delta^{15}\text{N}$  and potentially other metrics of long-term nutrient availability. However, processes that vary over shorter timescales, such as weather, do not. In contrast, short-term metrics, such as nitrification, are potentially influenced by all of the drivers included in this diagram. Metrics measured in this study are bolded.

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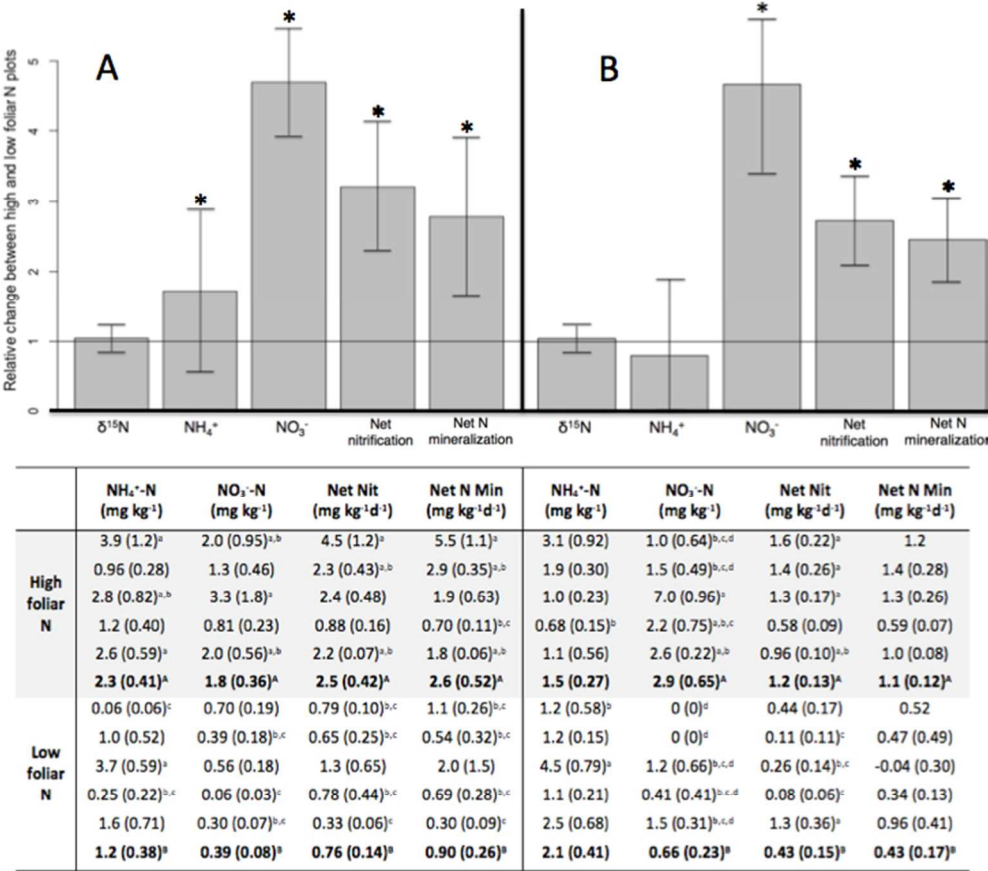
| Site<br>(MAP)                           | Slope<br>Position | pH                         | C (g kg <sup>-1</sup> ) | N (g kg <sup>-1</sup> )   | δ <sup>15</sup> N<br>(‰ vs. AIR) | NH <sub>4</sub> <sup>+</sup> -N<br>(mg kg <sup>-1</sup> ) | NO <sub>3</sub> <sup>-</sup> -N<br>(mg kg <sup>-1</sup> ) | Net Nit<br>(mg kg <sup>-2</sup> d <sup>-1</sup> ) | Net N Min<br>(mg kg <sup>-2</sup> d <sup>-1</sup> ) |
|-----------------------------------------|-------------------|----------------------------|-------------------------|---------------------------|----------------------------------|-----------------------------------------------------------|-----------------------------------------------------------|---------------------------------------------------|-----------------------------------------------------|
| Piro<br>South<br>(3 m y <sup>-1</sup> ) | Terrace           | 5.6 (5.6-5.8)              | 53 (2.2) <sup>a</sup>   | 4.6 (0.28) <sup>a</sup>   | 5.3 (0.14) <sup>a</sup>          | 1.3 (0.11)                                                | 0.45 (0.16)                                               | -0.08 (0.02)                                      | -0.20 (0.02)                                        |
|                                         | Shoulder          | 5.7 (5.6-5.7)              | 47 (4.5) <sup>a</sup>   | 3.9 (0.35) <sup>a</sup>   | 4.8 (0.15)                       | 1.5 (0.21)                                                | 0.38 (0.10)                                               | -0.06 (0.01)                                      | -0.19 (0.02)                                        |
|                                         | Mid-slope         | 5.5 (5.3-5.7)              | 44 (6.7) <sup>a,b</sup> | 3.7 (0.54) <sup>a,b</sup> | 4.4 (0.19) <sup>b</sup>          | 1.3 (0.28)                                                | 0.44 (0.14)                                               | 0.06 (0.03)                                       | -0.22 (0.10)                                        |
|                                         | Low slope         | 5.6 (5.5-5.7)              | 36 (5.3) <sup>b</sup>   | 3.1 (0.45) <sup>b</sup>   | 4.3 (0.20) <sup>b</sup>          | 0.83 (0.11)                                               | 0.38 (0.18)                                               | -0.08 (0.04)                                      | -0.13 (0.07)                                        |
|                                         | Mean              | 5.6 (5.3-5.8) <sup>a</sup> | 45 (2.7) <sup>a</sup>   | 3.8 (0.23) <sup>a</sup>   | 4.7 (0.13) <sup>a</sup>          | 1.2 ± 0.11                                                | 0.41 (0.07)                                               | -0.07 (0.01)                                      | -0.18 (0.02)                                        |
| Piro<br>North<br>(3 m y <sup>-1</sup> ) | Ridge             | 5.2 (4.9-5.6)              | 37 (3.7)                | 3.3 (0.39)                | 4.0 (0.24) <sup>a</sup>          | 2.1 (0.47)                                                | 0.26 (0.08)                                               | -0.03 (0.03)                                      | -0.05 (0.22)                                        |
|                                         | Shoulder          | 5.1 (4.6-5.9)              | 35 (5.3)                | 3.3 (0.49)                | 4.2 (0.15)                       | 2.7 (0.94)                                                | 0.68 (0.17)                                               | -0.11 (0.04)                                      | -0.38 (0.25)                                        |
|                                         | Mid-slope         | 5.4 (5.0-6.0)              | 36 (7.6)                | 3.2 (0.42)                | 4.0 (0.38)                       | 1.1 (0.14)                                                | 0.95 (0.70)                                               | -0.12 (0.08)                                      | -0.13 (0.10)                                        |
|                                         | Low slope         | 5.6 (5.3-6.0)              | 34 (4.0)                | 3.2 (0.24)                | 3.0 (0.14) <sup>b</sup>          | 1.6 (0.19)                                                | 1.3 (0.59)                                                | -0.09 (0.13)                                      | -0.40 (0.04)                                        |
|                                         | Mean              | 5.3 (4.6-6.0) <sup>b</sup> | 35 (2.4) <sup>b</sup>   | 3.2 (0.18) <sup>b</sup>   | 3.8 (0.16) <sup>b</sup>          | 1.8 (0.26)                                                | 0.83 (0.26) <sup>a</sup>                                  | -0.09 (0.04)                                      | -0.22 (0.07)                                        |
| Drake<br>(5 m y <sup>-1</sup> )         | Ridge             | 4.8 (4.7-5.1)              | 56 (6.0)                | 4.3 (0.32)                | 2.8 (0.18)                       | 1.7 (0.61)                                                | 0.16 (0.09)                                               | 0.01 (0.02)                                       | 0.24 (0.10)                                         |
|                                         | Shoulder          | 4.7 (4.5-5.1)              | 57 (9.1)                | 4.4 (0.54)                | 2.9 (0.33)                       | 1.3 (0.26)                                                | 0.41 (0.09)                                               | 0.01 (0.05)                                       | 0.40 (0.47)                                         |
|                                         | Mid-slope         | 4.8 (4.7-5.1)              | 46 (3.7)                | 3.8 (0.33)                | 3.5 (0.08)                       | 1.9 (0.60)                                                | 0.26 (0.12)                                               | 0.00 (0.03)                                       | 0.16 (0.23)                                         |
|                                         | Low slope         | 4.8 (4.7-5.2)              | 52 (6.9)                | 4.2 (0.46)                | 3.2 (0.42)                       | 2.3 (0.09)                                                | 0.20 (0.10)                                               | -0.05 (0.01)                                      | -0.24 (0.06)                                        |
|                                         | Mean              | 4.8 (4.5-5.2) <sup>c</sup> | 53 (3.2) <sup>a</sup>   | 4.2 (0.19) <sup>a</sup>   | 3.1 (0.14) <sup>c</sup>          | 1.7 (0.24)                                                | 0.23 (0.05) <sup>b</sup>                                  | -0.01 (0.01)                                      | 0.13 (0.11)                                         |

Title: Mean soil chemical characteristics of catena soils.  
Legend: Soil samples (0-10 cm) were collected from four catenas in each site during the wet season (July 2014). Along each catena we sampled in four slope positions. Values are arithmetic means (± SE), with the exception of the pH column, which contains true means (range). Lowercase letters indicate significant differences (P<0.05) between slope positions at each site. Capital letters indicate significant differences (P<0.05) between site means. MAP is mean annual precipitation.  
427x201mm (72 x 72 DPI)

|               | Plot # | Relative Canopy N         | Pixel Count | pH                             | C (g kg <sup>-1</sup> ) | N (g kg <sup>-1</sup> ) | $\delta^{15}\text{N}$ (‰ vs. AIR) | NH <sub>4</sub> <sup>+</sup> -N (mg kg <sup>-1</sup> ) | NO <sub>3</sub> <sup>-</sup> -N (mg kg <sup>-1</sup> ) | Net Nit (mg kg <sup>-1</sup> d <sup>-1</sup> ) | Net N Min (mg kg <sup>-1</sup> d <sup>-1</sup> ) |
|---------------|--------|---------------------------|-------------|--------------------------------|-------------------------|-------------------------|-----------------------------------|--------------------------------------------------------|--------------------------------------------------------|------------------------------------------------|--------------------------------------------------|
| High canopy N | 1      | +1.6                      | 361         | 5.7 (5.6-5.8) <sup>a,b,c</sup> | 59 (13)                 | 5.7 (1.1)               | 4.8 (0.37)                        | 0.71 (0.27)                                            | 1.5 (0.5) <sup>b,c</sup>                               | 6.2 (1.1) <sup>a,b</sup>                       | 5.7 (1.2)                                        |
|               | 2      | +2.2                      | 299         | 5.9 (5.8-6.0) <sup>a</sup>     | 49 (9.5)                | 4.3 (0.85)              | 5.3 (0.12)                        | 0.72 (0.06)                                            | 2.6 (0.42) <sup>a,b</sup>                              | 7.6 (1.9) <sup>a,b</sup>                       | 6.9 (1.8)                                        |
|               | 3      | +1.5                      | 321         | 5.9 (5.8-6.0) <sup>a</sup>     | 50 (4.2)                | 4.6 (0.37)              | 4.7 (0.20)                        | 0.65 (0.42)                                            | 5.2 (0.53) <sup>a</sup>                                | 6.5 (0.66) <sup>a,b</sup>                      | 5.9 (0.88)                                       |
|               | 4      | +1.7                      | 421         | 5.1 (5.1) <sup>d</sup>         | 32 (0.6)                | 3.3 (0.08)              | 5.8 (0.50) <sup>a</sup>           | 6.1 (2.9) <sup>a</sup>                                 | 1.9 (0.32) <sup>b</sup>                                | 9.2 (1.6) <sup>a</sup>                         | 7.4 (1.6)                                        |
|               | 5      | +2.8                      | 374         | 5.7 (5.6-5.8) <sup>a,b</sup>   | 60 (5.7)                | 5.0 (0.32)              | 3.5 (0.46) <sup>b</sup>           | 3.0 (1.1)                                              | 2.6 (0.58) <sup>a,b</sup>                              | 9.5 (1.1) <sup>a</sup>                         | 6.6 (1.5)                                        |
|               | Mean   | +2.0 (0.24) <sup>A</sup>  | 355 (21)    | 5.6 (5.1-6.0) <sup>A</sup>     | 50 (4.0)                | 4.6 (0.33)              | 4.8 (0.25)                        | 2.2 (0.77) <sup>A</sup>                                | 2.7 (0.39) <sup>A</sup>                                | 7.8 (0.62) <sup>A</sup>                        | 6.4 (0.55) <sup>A</sup>                          |
| Low canopy N  | 1      | +0.48                     | 219         | 5.4 (5.3-5.5) <sup>b,c,d</sup> | 45 (2.9)                | 4.1 (0.32)              | 4.7 (0.45)                        | 0.42 (0.05)                                            | 0.42 (0.11) <sup>c,d</sup>                             | 1.8 (0.12)                                     | 0.93 (0.48)                                      |
|               | 2      | -0.56                     | 443         | 5.1 (5.1) <sup>c,d</sup>       | 51 (4.1)                | 4.6 (0.38)              | 4.1 (0.45)                        | 0.55 (0.55) <sup>b</sup>                               | 0 (0) <sup>d</sup>                                     | 0.39 (0.39) <sup>c</sup>                       | -0.14 (0.83)                                     |
|               | 3      | -1.4                      | 218         | 5.7 (5.5-5.8) <sup>a,b,c</sup> | 67 (12)                 | 5.1 (0.79)              | 3.7 (0.41) <sup>b</sup>           | 1.7 (0.44)                                             | 0.17 (0.14) <sup>d</sup>                               | 2.9 (1.1)                                      | 1.4 (1.3)                                        |
|               | 4      | -1.1                      | 386         | 5.6 (5.4-5.7)                  | 60 (2.7)                | 5.2 (0.21)              | 4.5 (0.24)                        | 0.46 (0.14) <sup>b</sup>                               | 0.10 (0.08) <sup>d</sup>                               | 0.09 (0.05) <sup>c</sup>                       | -0.20 (0.11)                                     |
|               | 5      | -0.38                     | 325         | 5.2 (5.2) <sup>d</sup>         | 37 (4.0)                | 3.7 (0.31)              | 6.0 (0.50) <sup>a</sup>           | 0 (0) <sup>b</sup>                                     | 0.33 (0.05) <sup>c,d</sup>                             | 2.4 (2.0) <sup>b,c</sup>                       | 0.91 (0.48)                                      |
|               | Mean   | -0.58 (0.32) <sup>B</sup> | 318 (45)    | 5.4 (5.1-5.8) <sup>B</sup>     | 52 (3.6)                | 4.6 (0.23)              | 4.6 (0.26)                        | 0.70 (0.20) <sup>B</sup>                               | 0.19 (0.05) <sup>B</sup>                               | 1.4 (0.50) <sup>B</sup>                        | 0.56 (0.34) <sup>B</sup>                         |

Title: Mean canopy N and soil chemical characteristics of high and low canopy N plots.  
 Legend: Soil samples (0-10 cm) were collected from ten circular 0.25 ha plots with either high or low canopy N (N=5). All plots were located on the broad flat terrace in Piro North and sampled during the wet season (August 2015). Lowercase letters indicate significant differences ( $P < 0.05$ ) among all plots. Capital letters indicate significant differences ( $P < 0.05$ ) between high and low canopy N plot means. The Foliar N column includes the standard deviations of remotely sensed foliar N in each plot relative to the flight line mean.  
 473x161mm (72 x 72 DPI)

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The top panels show relative differences in soil chemical characteristics (0 – 10 cm) beneath 0.25 ha plots with relatively high (N=5) and low (N=5) canopy nitrogen. Data in Panel A and B are from samples collected in February and May 2015, respectively. Values greater than one represent the factor by which each soil characteristic was elevated in high vs. low canopy nitrogen plots. Asterisks denote significant ( $P < 0.05$ ) differences between high and low plots. The table contains arithmetic means ( $\pm$  SE) from each of the canopy N plots. Lowercase letters indicate significant differences ( $P < 0.05$ ) among all plots. Capital letters indicate significant differences ( $P < 0.05$ ) between high and low canopy N plot means.

259x231mm (72 x 72 DPI)

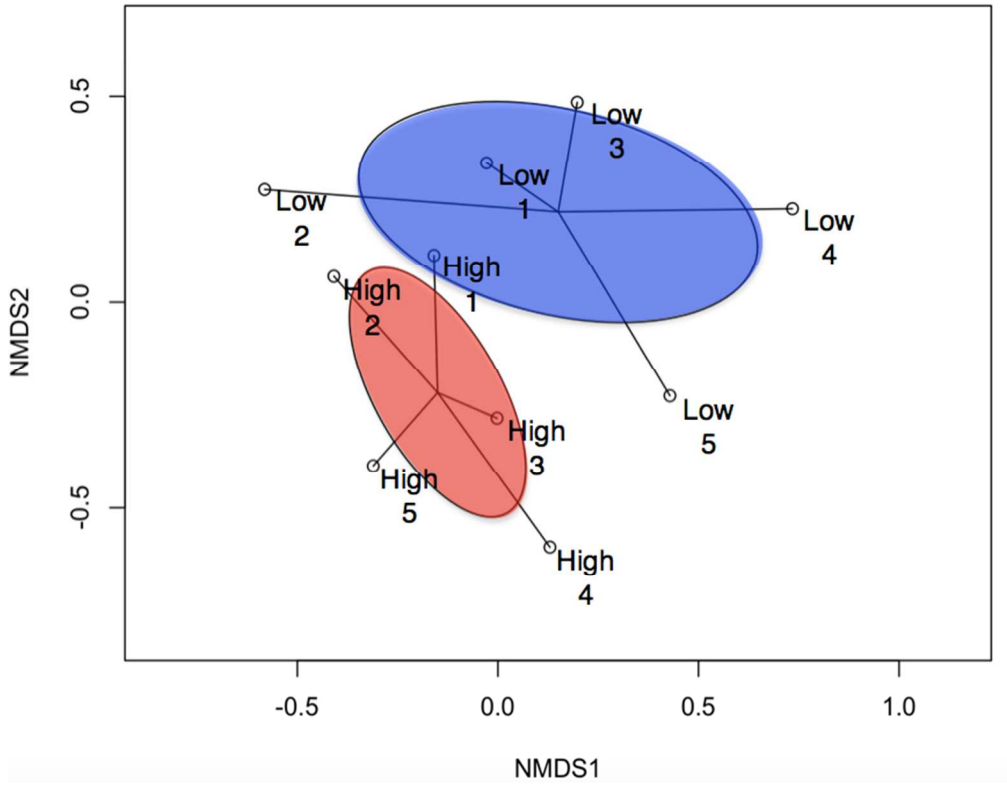


| Site<br>(MAP)                                  | Slope<br>Position | NH <sub>4</sub> <sup>+</sup> -N<br>(mg kg <sup>-1</sup> ) | NO <sub>3</sub> <sup>-</sup> -N<br>(mg kg <sup>-1</sup> ) | Net Nit<br>(mg kg <sup>-1</sup> d <sup>-1</sup> ) | Net N Min<br>(mg kg <sup>-1</sup> d <sup>-1</sup> ) |
|------------------------------------------------|-------------------|-----------------------------------------------------------|-----------------------------------------------------------|---------------------------------------------------|-----------------------------------------------------|
| <b>Piro<br/>South<br/>(3 m y<sup>-1</sup>)</b> | <b>Terrace</b>    | 4.2 (0.96)                                                | 1.3 (0.49)                                                | 0.47 (0.32)                                       | 1.8 (0.26)                                          |
|                                                | <b>Shoulder</b>   | 4.6 (2.0)                                                 | 1.7 (0.82)                                                | -0.08 (0.08)                                      | 1.7 (0.91)                                          |
|                                                | <b>Mid-slope</b>  | 2.1 (0.10)                                                | 1.9 (1.1)                                                 | -0.17 (0.23)                                      | 1.7 (1.1)                                           |
|                                                | <b>Low slope</b>  | 4.5 (0.73)                                                | 1.8 (0.37)                                                | -0.12 (0.20)                                      | 1.7 (0.17)                                          |
|                                                | <b>Mean</b>       | <b>3.9 (0.56)<sup>A</sup></b>                             | <b>1.7 (0.35)<sup>A</sup></b>                             | <b>0.03 (0.12)<sup>B</sup></b>                    | <b>1.7 (0.31)<sup>A</sup></b>                       |
| <b>Piro<br/>North<br/>(3 m y<sup>-1</sup>)</b> | <b>Ridge</b>      | 2.2 (0.75)                                                | 0.10 (0.05)                                               | 0.48 (0.09)                                       | 1.8 (0.91)                                          |
|                                                | <b>Shoulder</b>   | 1.6 (0.66)                                                | 0.25 (0.11)                                               | 0.41 (0.13)                                       | 2.0 (1.3)                                           |
|                                                | <b>Mid-slope</b>  | 2.8 (0.71)                                                | 0.22 (0.07)                                               | 0.88 (0.12)                                       | 5.6 (3.9)                                           |
|                                                | <b>Low slope</b>  | 1.2 (0.04)                                                | 0.19 (0.15)                                               | 0.54 (0.16)                                       | 4.1 (1.8)                                           |
|                                                | <b>Mean</b>       | <b>2.0 (0.32)<sup>B</sup></b>                             | <b>0.19 (0.05)<sup>B</sup></b>                            | <b>0.57 (0.07)<sup>A</sup></b>                    | <b>3.5 (1.1)<sup>A</sup></b>                        |
| <b>Drake<br/>(5 m y<sup>-1</sup>)</b>          | <b>Ridge</b>      | 3.5 (0.81)                                                | 0.07 (0.04)                                               | 0.19 (0.05)                                       | 0.26 (0.09)                                         |
|                                                | <b>Shoulder</b>   | 2.4 (0.40)                                                | 0.32 (0.12)                                               | 0.36 (0.20)                                       | 0.68 (0.32)                                         |
|                                                | <b>Mid-slope</b>  | 1.3 (0.29)                                                | 0.24 (0.11)                                               | 0.09 (0.08)                                       | 0.34 (0.13)                                         |

Soil samples (0-10 cm) were collected from four catenas in each site during the dry season. Piro South and Drake were sampled in January 2014 and Piro North was sampled in February 2015. Along each catena we sampled in four slope positions. Values are arithmetic means ( $\pm$  SE). Lowercase letters indicate significant differences ( $P < 0.05$ ) between slope positions at sd. Capital letters indicate significant differences ( $P < 0.05$ ) between site means. MAP is mean annual precipitation.

248x173mm (72 x 72 DPI)





A two-dimensional nonmetric multidimensional scaling (NMDS) ordination plot representing Bray-Curtis dissimilarities between high (red) and low (blue) foliar N plots (N= 5; Stress=0.15). Ellipses represent standard deviations. Lines connect each plot point to the group centroid.

304x251mm (72 x 72 DPI)