

## Climatic controls on the isotopic composition and availability of soil nitrogen across mountainous tropical forest

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**Abstract.** While tropical forests play a critical role in global carbon (C) and nitrogen (N) cycles, how their biogeochemical dynamics will respond to changes in climate, especially warming, is uncertain. To shed light on links between climate and N cycling in tropical forests, we measured bulk surface soil C and N concentrations and isotopic content at 40 forested sites spanning an 1800 m elevation transect in Central America, possessing wide variation in mean annual temperature (MAT; range = 10°C) and precipitation (MAP; range = 1.2 m). Climate and terrain attributes were extracted from gridded data sets and regressed against soil variables, and then, empirical relationships were combined with a mass balance model to scale up to the larger landscape. Across the remote study region, elevation and soil  $\delta^{15}\text{N}$  values displayed a strong negative relationship, while elevation was positively related to percent of soil C, N, and C:N ratios. As elevation was tightly correlated with MAT and MAP, soil chemical and isotopic content varied strongly with climate. For example, for every degree increase in MAT, soil  $\delta^{15}\text{N}$  values—an indicator of relative gaseous N losses—increased by a factor of 0.4, and soil C:N ratios, which affect net N mineralization and N availability, declined by a factor of 1.1. With the 40 sites binned into bioclimatic life zones, montane, premontane, and wet-premontane transition forests showed distinct clustering of soil chemical and isotopic properties, yet forest type alone explained less variation compared to continuous elevation–climate parameters. Results of the spatially applied  $^{15}\text{N}$  mass balance model implied shifts in the contribution of gaseous-to-total N loss, from 10% or less in cool, wet high-elevation forests to upwards of 60% at warmer, drier, low-elevation sites. Climate variation was thus associated with significant shifts in N dynamics across this montane tropical region, yet more work is needed to decouple direct vs. indirect climatic controls. While the mechanisms deserve further study, observed shifts in indicators of N availability and gaseous loss may be useful in managing and modeling tropical forests under climate change.

**Key words:** climate change; Costa Rica; montane tropics; nitrogen cycle; Parque Internacional La Amistad.

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### INTRODUCTION

Despite the significance of tropical forests in global carbon (C) and nitrogen (N) cycles, there is large uncertainty surrounding how their biogeochemical dynamics will respond to

changes in climate (Cramer et al. 2004, Bonan and Levis 2010). This includes shifts in precipitation (Malhi et al. 2009, Cleveland et al. 2010) as well as increases in temperature (Malhi et al. 2010, Cavaleri et al. 2015). The latter is an especially salient research gap because precipitation

change will be spatially heterogeneous in sign and magnitude across the tropics, yet all tropical regions are already experiencing unprecedented heat (Mahlstein et al. 2011) and will see temperature regimes outside their historical range of variation in the near future, sooner in fact than other biomes (Diffenbaugh and Scherer 2011, Mora et al. 2013). Moreover, shifts in tropical tree species distributions are already occurring, likely due to warming (Feeley et al. 2011, 2013). Rapid changes in climate and associated ecological processes underscore the urgent need to elucidate how biogeochemical cycles will respond (Cavaleri et al. 2015).

This research is critical not only because of the onset of climatic change but also because the pools and fluxes of essential elements (i.e., C and N) are vast and present significant potential for further climate feedbacks. For instance, tropical regions are the largest global source of nitrous oxide ( $\text{N}_2\text{O}$ ; Vitousek and Matson 1992, Werner et al. 2007, Tian et al. 2014), the third most important greenhouse gas behind carbon dioxide and methane (Forster et al. 2007). Soil  $\text{N}_2\text{O}$  emissions are affected both by temperature and by soil water content (Smith et al. 1998, Davidson et al. 2000, Werner et al. 2007, Dijkstra et al. 2012), such that warming, alone or in combination with precipitation change, is likely to alter gaseous N loss rates. If tropical N-gas emissions increase with rising temperature (Smith 1997), this could serve as a positive feedback to global warming. Tropical N cycling thus has potential for direct climate feedbacks, but indirect effects via linkages between tropical N and C dynamics are also important to consider (Bonan and Levis 2010). Tropical forests account for approximately 30% of terrestrial net primary production and 25% of total terrestrial C pools (Bonan 2008, Saatchi et al. 2011). This large land carbon sink depends on the availability of nutrients (Cramer et al. 2004, Fernández-Martínez et al. 2014), including nitrogen (Bonan and Levis 2010, Townsend et al. 2011). Observational studies (Marrs et al. 1988, Holtgrieve et al. 2006, Wolf et al. 2011) and manipulative experiments (Rustad et al. 2001) suggest that tropical N availability is linked to climate conditions. Therefore, shifts in N availability in response to changes in temperature and precipitation could have significant indirect effects on the tropical climate–carbon feedback.

Assessing current and future links between climate and tropical N cycling requires a multitude of approaches. Controlled climate manipulations (Cleveland et al. 2010, Cavaleri et al. 2015) and long-term observational studies (Clark et al. 2003, Phillips et al. 2010) are needed to provide detailed, mechanistic insights, but such studies with a focus on biogeochemical processes are still relatively few in tropical regions. To help fill this gap, mountainous tropical ecosystems can provide a useful study system, serving as “natural laboratories” that elucidate links between climate and N dynamics across broad gradients, especially those in temperature (Malhi et al. 2010, Bothwell et al. 2014). Observational studies of this nature can have drawbacks, a major one being concurrent variation in non-climate state factors across climate gradients. Thus, when extrapolating to dynamic forest response to climate change, biogeochemical data taken across such gradients must be approached with caution, given the difficulty in disentangling direct and indirect climate controls. However, when selected with care, transects along forested tropical mountain ranges can provide strong natural experiments, revealing climate-related patterns of tropical biogeochemical heterogeneity and giving insight into potential rates of change in N-cycle processes across relevant climate space.

Climate–nitrogen linkages may be especially pertinent in montane tropical forests. Unlike their mature lowland counterparts, many of which cycle N in relative excess (Vitousek and Farrington 1997, Martinelli et al. 1999, Hedin et al. 2009), montane tropical forests tend to have low N availability relative to demand (Tanner et al. 1998, Arnold et al. 2009). This is due to the predominance of cool, wet conditions that slow decomposition and lower N mineralization rates (Marrs et al. 1988). As a result, montane tropical zones exhibit relatively low  $\text{N}_2\text{O}$  emissions (Purbopuspito et al. 2006, Teh et al. 2014) and have biomass that is more often limited by N (Tanner et al. 1998, Fisher et al. 2013, though see Brookshire et al. 2012). However, both N emissions and limitation are related to nitrogen availability (Wolf et al. 2011), which may increase as the montane tropics warm up and dry out (Marrs et al. 1988). The potential for N-mediated shifts in multiple aspects of montane tropical biogeochemical dynamics means that linkages between

variation in climate, N availability, and gaseous losses there merit further investigation.

While previous findings suggest that climate, gaseous N losses, and N availability are indeed linked, key knowledge gaps remain. For instance, N<sub>2</sub>O emission rates were twofold to eightfold greater in lower montane compared to upper montane forests in southern Ecuador (Wolf et al. 2011) and Peru (Teh et al. 2014), and these gaseous N emissions were correlated with indicators of N availability. Such findings implicate relationships between climate and the availability and gaseous loss rates of N, but as sampling was focused on few sites selected to serve as representative end-members from different bioclimatic life zones (e.g., upper, lower, and premontane forests), it remains difficult to assess the rate of change in N dynamics with variation in climate. A continuous sampling approach, with frequent observations across a wide range of climates, could shed light on this issue. Moreover, recent studies on N cycling across elevation gradients in the montane tropics are clustered in the Western Amazon (Arnold et al. 2009, Wolf et al. 2011, Fisher et al. 2013, Teh et al. 2014), such that observations from other undisturbed regions would help establish the broad applicability of recently described trends. By increasing our fundamental understanding of the controls on N dynamics, such data could enhance our ability to simulate present and future biogeochemical fluxes in tropical regions.

In this study, we utilized a continuous, 1800-m montane tropical forest elevation transect across a remote region in Central America to investigate relationships between elevation, climate, gaseous N losses, and indicators of N availability. We hypothesized that both signatures of gaseous N loss and indicators of N availability would increase with declining elevation, resulting in positive relationships with mean annual temperature (MAT) and negative relationships with mean annual precipitation (MAP). Further, we predicted that these relationships would explain more of the variation in soil N properties than bioclimatic forest type alone. To evaluate these hypotheses, we measured bulk soil C and N concentrations as well as natural abundance isotopic ratios from 40 forested sites that varied widely in elevation and thus mean annual climate. We then combined an observed elevation/climate/soil N

isotope relationship with a steady-state N isotope mass balance model (Amundson et al. 2003, Houlton and Bai 2009, Hilton et al. 2013, Houlton et al. 2015) to estimate relative gaseous N losses across the remote montane study region.

## METHODS

To procure samples from pristine, mountainous tropical forest encompassing wide variation in climate, we leveraged a unique research expedition by the American Climber Science Program (ACSP). In January 2014, ACSP members travelled over 150 km by foot from west to east across the Cordillera Talamanca, the highest non-volcanic mountain range in Central America (maximum elevation = 3800 m; Fig. 1). Their goal was to collect baseline data and make ecological observations across this remote, poorly studied region (Cole et al. 2014). Trails and roads were uncommon, and the team employed indigenous guides to assist with route finding. The route traversed Parque Internacional La Amistad (PILA), a UNESCO biosphere reserve encompassing 401,000 ha of rugged forested mountains in Costa Rica and Panama, the largest contiguous area of tropical forest remaining in Central America (Cole et al. 2014; Fig. 1).

The team collected samples for soil analyses from 40 forested sites, mostly within PILA, ranging in elevation from 2300 to 500 m a.s.l. and separated by 0.5–2 km each. All sites shared a common parent material of Miocene-era, igneous, and intrusive rocks (Morell et al. 2012), soils were classified as Humults, and they had no history of major anthropogenic disturbance or land use change. At each site, four soil samples representative of the area were collected, separated by at least 10 m. Organic horizons, which were substantial (from 8 to 15 cm thick) at the upper end of the transect but disappeared at lower elevations, were removed, and ~0.5 kg of mineral soil was excavated from a small 0- to 10-cm surface pit. The four soil samples were then combined, homogenized, and a 200-g subsample retained.

In the laboratory, samples were processed for chemical and isotopic analyses. This included removal of roots, drying, grinding, and packing into tin capsules. Capsules were sent to the Center for Stable Isotope Biogeochemistry at University of California Berkeley for continuous

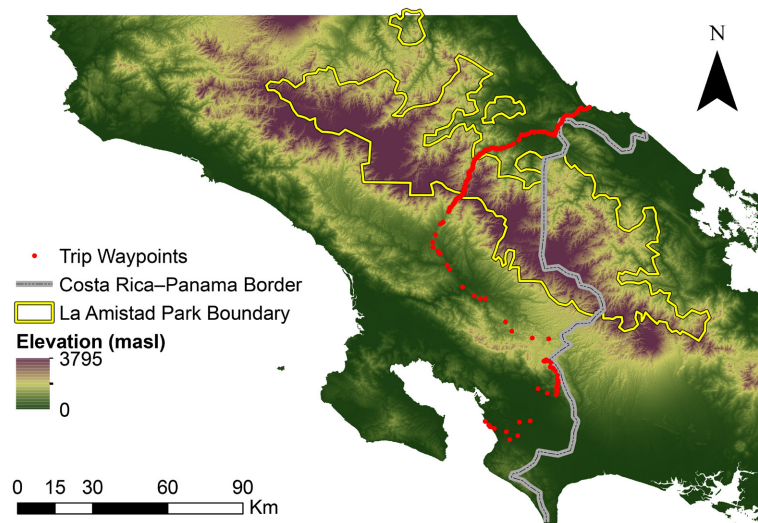


Fig. 1. Elevation map of the study region, with the Cordillera Talamanca in purple, waypoints from the American Climber Science Program expedition marked in red, and the Parque Internacional La Amistad (PILA) boundary in yellow. Ninety-five percent of sites sampled for the elevation transect were within the PILA boundary, with the remaining 5% sitting just outside the park boundary in undisturbed forest on the Caribbean side. The border between Costa Rica and Panama is indicated in gray.

flow dual isotopic and elemental analysis of total soil carbon and nitrogen. Bulk soil chemical and isotopic values integrate the net effects of biogeochemical processing over relatively long (i.e., yearly-to-decadal or longer) timescales, making them useful for detecting broad differences in C and N dynamics between sites that have evolved over time. Natural abundance of soil  $^{15}\text{N}$  and  $^{13}\text{C}$  was calculated as:  $\delta^{15}\text{N}$  or  $^{13}\text{C}$  (‰) =  $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $R$  = the ratio of  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$  of the sample and standard, which were atmospheric  $\text{N}_2$  or VPDB, respectively. Sample reproducibility was 0.06‰ and 0.03‰ for C and N, respectively, while long-term analytical precision for C and N isotope measurements was 0.10‰ and 0.15‰.

The locations of all sampling sites were recorded with a Global Positioning System (GPS) so that coordinates could be used to extract climate and spatial information using a geographic information system (Appendix S1: Table S1). Climate data were taken from the high-resolution, spatially interpolated maps provided by the WORLDCLIM database (Hijmans et al. 2005). Initially, a suite of WORLDCLIM's 19 bioclimatic variables were examined, but as many of these were highly correlated, we decided to

focus on MAT and MAP as the most useful and simple parameters in the context of this study. As WORLDCLIM maps have a spatial resolution of 1 km<sup>2</sup>, some of the adjacent sampling sites fell within the same pixel and thus had equal values for climate data (Appendix S1: Table S1). We note that forests above 1000 m had slightly higher precipitation seasonality (coefficient of variation [CV] = 50–58%) compared to forests below 1000 m (CV = 39–45%), but all sites has seasonal precipitation inputs with wetter and drier periods, and our sampling was conducted during the dry season. Elevation, slope angle, and aspect of the study sites were extracted from NASA's 90-m resolution digital elevation model (DEM) from the Shuttle Radar Topography Mission (Appendix S1: Table S1).

Alongside these continuous climatic and physiographic variables, each site was categorized according to its bioclimatic life zone (Holdridge 1967). To accomplish this, Tosi's 1969 *Republic of Costa Rica: Ecological Map* was digitized and the GPS locations of the sampling sites were overlaid on the digital map. Based on inspection of the resulting layers, each sampling site was assigned to one of three categories: lower montane (2300–1800 m a.s.l.), premontane



(1800–1000 m a.s.l.), and wet-premontane transition (1000–500 m a.s.l.) forests.

We used linear regression models in order to test whether soil chemical and isotopic variables were significantly related to climate, physiography, and each other. Correlations between climatic and physiographic parameters were examined using Pearson correlation tests. To assess whether bioclimatic life zone had an integrated effect on the suite of soil chemical and isotopic data, we used principal components analysis and a PERMANOVA test, including five variables in the multivariate analysis: soil C and N concentrations, soil C:N ratio, and soil  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Examination of statistical model residuals suggested that response variables did not require transformation to meet assumptions of normality and homoskedasticity. All statistical analyses were conducted in R (R Core Team 2015), and alpha was set at 0.01.

To expand upon findings from the environmental transect and explore how they scaled across the landscape, we combined spatial linear regression with a soil N isotope mass balance model. First, a DEM encompassing the forested zone of PILA (i.e., excluding the alpine) was extracted from NASA's 90-m resolution DEM in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA). Given its utility as an integrated metric of forest N status and forms of loss (Martinelli et al. 1999), we estimated and mapped spatial patterns of soil  $\delta^{15}\text{N}$  across PILA, based on a linear regression with elevation derived from our transect data. Further, as soil  $\delta^{15}\text{N}$  values correlate with gaseous N loss rates in montane tropical forests (Purbopuspito et al. 2006, Wolf et al. 2011) and have been used to estimate relative gaseous N losses within the tropics (Brookshire and Thomas 2013, Hilton et al. 2013, Weintraub et al. 2015) and at global scales (Houlton and Bai 2009, Houlton et al. 2015), we applied a  $^{15}\text{N}$  mass balance model to the newly created  $\delta^{15}\text{N}$  layer in order estimate spatial patterns of relative gaseous N loss across PILA. This mass balance modeling approach yielded the proportion of N lost in gaseous form but not gaseous N flux rates.

Following Houlton and Bai (2009) and Brookshire and Thomas (2013), we calculated the fraction of N lost as a gas for each pixel of the PILA DEM according to the following equation:

$$f_{\text{gas}} = \delta^{15}\text{N}_{\text{soil}} - \delta^{15}\text{N}_{\text{input}} + \epsilon_{\text{non-gas}} / (\epsilon_{\text{non-gas}} - \epsilon_{\text{gas}}). \quad (1)$$

Soil  $\delta^{15}\text{N}$  values ( $\delta^{15}\text{N}_{\text{soil}}$ ) were derived from the modeled  $\delta^{15}\text{N}$  layer.  $\delta^{15}\text{N}$  values of inputs ( $\delta^{15}\text{N}_{\text{input}}$ ) were estimated at  $-1\text{‰}$ , isotope effects of gaseous losses ( $\epsilon_{\text{gas}}$ ) were assumed to be  $-11\text{‰}$ , and isotope effects of non-gaseous losses ( $\epsilon_{\text{non-gas}}$ ) were assumed to be  $-0.5\text{‰}$ , based on published values from an area near the study region (Brookshire et al. 2012). To explore how variation in isotope effect parameters could affect proportional gas loss estimates (Houlton and Bai 2009), we calculated steady-state solutions over a realistic spread of isotope effect values, using the mean observed  $\delta^{15}\text{N}$  from the three forest types that were the focus of our study. These analyses were conducted in R.

## RESULTS

Soil chemical and isotopic values displayed significant variation, highlighting key shifts in N dynamics, across the environmental transect. First, a strong negative linear relationship was observed between soil  $\delta^{15}\text{N}$  values and elevation ( $\delta^{15}\text{N} [\text{‰}] = \text{Elevation [m a.s.l.]} \times -0.0026 + 6.49$ ;  $R^2 = 0.61$ ,  $F_{1,38} = 60.61$ ,  $P < 0.001$ ; Fig. 2A). As elevation was tightly correlated with MAT (Pearson's  $r = -0.98$ , range =  $14.5\text{--}23.5^\circ\text{C}$ ) and MAP (Pearson's  $r = 0.91$ , range =  $3.7\text{--}2.8\text{ m}$ ),  $\delta^{15}\text{N}$  values increased with temperature ( $\delta^{15}\text{N} [\text{‰}] = \text{MAT } [^\circ\text{C}] \times 0.44\text{--}5.59$ ;  $R^2 = 0.59$ ,  $F_{1,38} = 54.85$ ,  $P < 0.001$ ; Fig. 2B) and decreased with precipitation ( $\delta^{15}\text{N} [\text{‰}] = \text{MAP [m]} \times -3.78 + 15.04$ ;  $R^2 = 0.60$ ,  $F_{1,38} = 56.35$ ,  $P < 0.001$ ). Unlike prior studies in montane tropical forests, which detected strong links between slope angle and soil  $\delta^{15}\text{N}$  values (Hilton et al. 2013), effects of slope angle (mean =  $16.9^\circ$ , range from  $5^\circ$  to  $38^\circ$ ) were much weaker than those of elevation and climate in the forests examined here ( $\delta^{15}\text{N} [\text{‰}] = \text{Slope angle } [^\circ] \times 0.09 + 1.06$ ;  $R^2 = 0.17$ ,  $F_{1,38} = 8.1$ ,  $P = 0.007$ ). Elevation also exhibited significant positive relationships with concentrations of soil C (%C =  $\text{Elevation [m a.s.l.]} \times 0.0186\text{--}4.73$ ;  $R^2 = 0.40$ ,  $F_{1,38} = 26.91$ ,  $P < 0.001$ ) and N (%N =  $\text{Elevation [m a.s.l.]} \times 0.0006 + 0.35$ ;  $R^2 = 0.32$ ,  $F_{1,38} = 19.69$ ,  $P < 0.001$ ). As the increase in soil N content was weaker than that of soil C,

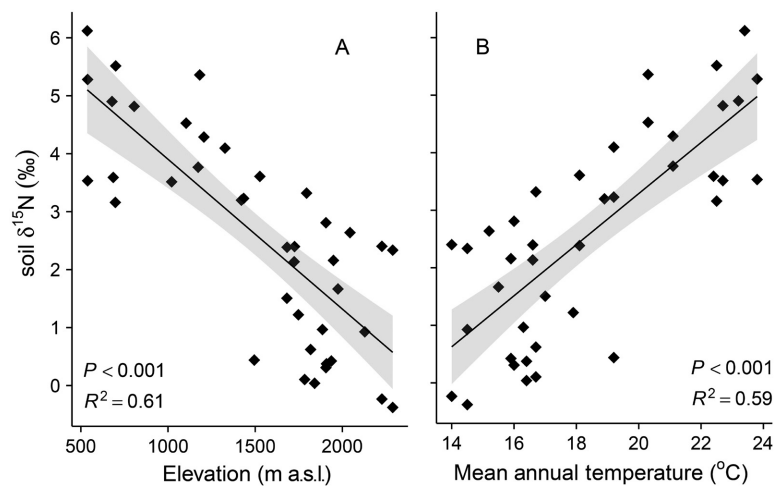


Fig. 2. Relationship between elevation (A) and mean annual temperature (B) with surface soil (0–10 cm)  $\delta^{15}\text{N}$  values (‰) across the tropical montane transect.

soil C:N ratios also increased significantly with elevation ( $\text{C:N} = \text{Elevation} \times 0.0066 + 6.55$ ;  $R^2 = 0.48$ ,  $F_{1,38} = 37.03$ ,  $P < 0.001$ ), leading to a negative linear relationship between soil C:N and MAT ( $\text{C:N} = \text{MAT } [^{\circ}\text{C}] \times -1.1004 + 36.82$ ;  $R^2 = 0.44$ ,  $F_{1,38} = 30.38$ ,  $P < 0.001$ ) and a positive linear relationship with C:N and MAP ( $\text{C:N} = \text{MAP [m]} \times 7.89 - 9.173$ ;  $R^2 = 0.31$ ,  $F_{1,38} = 17.24$ ,  $P < 0.001$ ).

With study sites binned into bioclimatic life zones, soil chemical and isotopic variables displayed significant clustering by forest type (PERMANOVA:  $R^2 = 0.36$ ,  $F_{2,37} = 10.40$ ,  $P = 0.001$ ; Fig. 3). The first principal component was driven by percent soil C and C:N ratios and the second by soil  $\delta^{15}\text{N}$  values. Further, a strong negative linear relationship was observed between soil C:N ratios and  $\delta^{15}\text{N}$  values ( $R^2 = 0.66$ ,  $F_{1,38} = 73.92$ ,  $P < 0.001$ ), with forest types plotting at discrete locations along the regression line (Fig. 4). Unlike N isotope data, soil  $\delta^{13}\text{C}$  values did not vary systematically across the transect and were not related to climatic or physiographic variables.

Utilizing the observed regression equation between elevation and soil  $\delta^{15}\text{N}$  values to scale to the larger landscape, lowest values of soil  $\delta^{15}\text{N}$  (near 0‰) were mapped to the high-elevation forests near the crest of the Talamanca, and highest  $\delta^{15}\text{N}$  values (upwards of 7‰) were modeled for forests

on the Caribbean slopes and foothills (Fig. 5). Using these continuous  $\delta^{15}\text{N}$  values as inputs, the  $^{15}\text{N}$  mass balance model calculated a six-fold increase in the proportion of N lost by gaseous pathways, from relatively low values near the crest of the Talamanca (~10% or less) to upwards of 60% in the lower forested zones

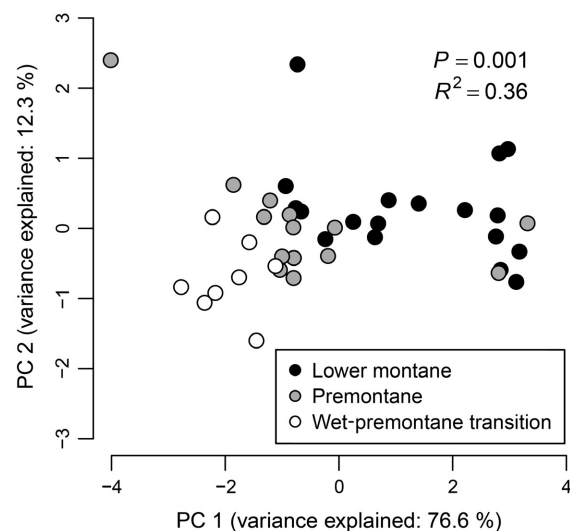


Fig. 3. Principal components analysis and PERMANOVA results, with sites grouped by forest type, including five surface soil variables: C and N concentrations (%), C:N ratios,  $\delta^{15}\text{N}$ , and  $\delta^{13}\text{C}$  values (‰).

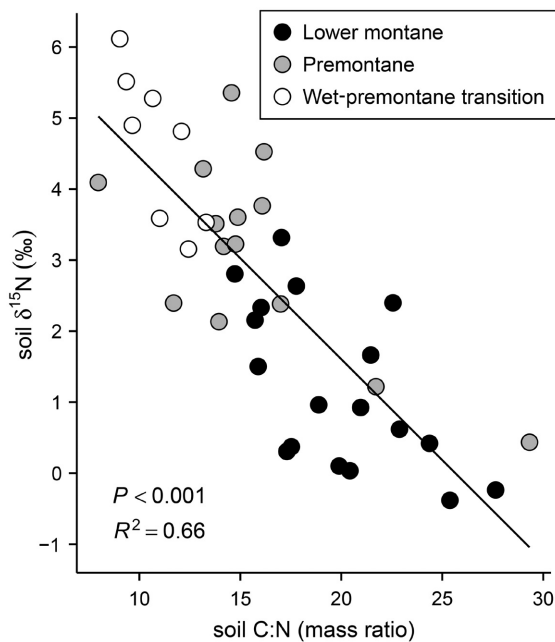


Fig. 4. Relationship between surface soil C:N ratios and  $\delta^{15}\text{N}$  values (‰) across the tropical montane transect.

(Fig. 5). When isotope effect parameters varied but  $\delta^{15}\text{N}$  values of inputs and bulk soil were held constant, a ~20% range was observed for relative gas loss estimates (Fig. 6).

## DISCUSSION

The relationships between elevation, soil N isotopes, and soil C and N contents across this pristine, continuous transect highlight links between climate and N cycling in mountainous tropical forests. These findings align with and expand upon previous results from the montane tropics, which have documented shifts in N availability and gaseous emissions across elevation–climate gradients at few but intensively studied sites (Purbopuspito et al. 2006, Arnold et al. 2009, Wolf et al. 2011, Teh et al. 2014). That we observed higher  $\delta^{15}\text{N}$  values at lower elevations also aligns with global-scale observations, where  $\delta^{15}\text{N}$  values increase with temperature and decrease with precipitation (Amundson et al. 2003, Craine et al. 2015). It thus appears that climatic controls on N availability and forms of loss operate within heterogeneous tropical ecosystems as much as observed across other biomes.

While previous studies have observed increased N availability and gaseous loss in lower compared to upper montane tropical forests (and hypothesized that climate played a role), our sampling approach allowed us to demonstrate that temperature and precipitation were indeed linearly and continuously related to

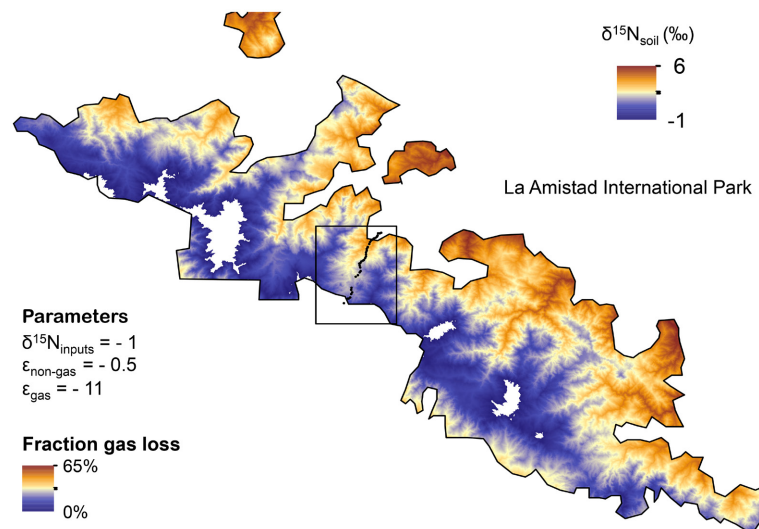


Fig. 5. Map of modeled values of  $\delta^{15}\text{N}_{\text{soil}}$  (‰) and fraction gas losses (%) across Parque Internacional La Amistad.  $\delta^{15}\text{N}$  values were estimated from the regression:  $\delta^{15}\text{N}_{\text{soil}}$  (‰) = Elevation (m a.s.l.)  $\times$   $-0.002586 + 6.490389$ . The regression equation was derived from sampling the region within the black rectangle (black dots = sampling sites;  $n = 40$ ). Fraction gas losses were calculated using the mass balance equation and parameters detailed in the text.

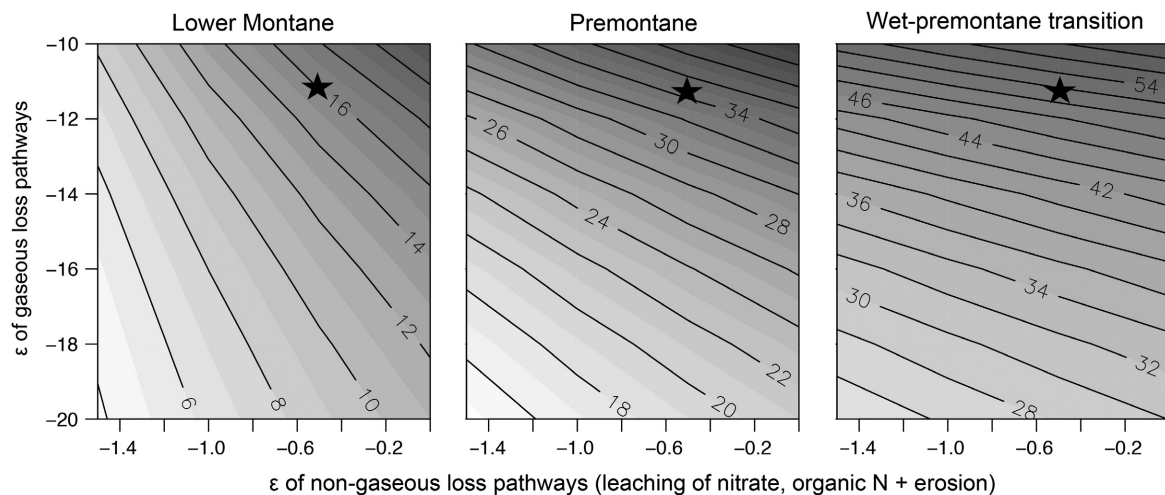


Fig. 6. Estimates for the proportion of N lost as a gas (expressed as % of total N losses) across a range of isotope effect values ( $\epsilon$ , ‰) for gaseous and non-gaseous loss mechanisms. Estimates are derived using the  $^{15}\text{N}$  mass balance model detailed in the text. Black stars indicate our estimates for fraction gas losses from each forest type, using mean soil  $\delta^{15}\text{N}$  values for all sites in that life zone and the parameters:  $\epsilon_{\text{gas}} = -11\text{‰}$  and  $\epsilon_{\text{non-gas}} = -0.5\text{‰}$ .

key N-cycle parameters. For example, for every  $^{\circ}\text{C}$  increase in MAT,  $\delta^{15}\text{N}$  values increased by a factor of 0.4, and C:N ratios declined by a factor of 1.1. Similarly, for every 1-m increase in MAP,  $\delta^{15}\text{N}$  values decreased by a factor of  $-3.8$  and C:N ratios increased by a factor of 7.9. As these shifts were linear and continuous, climate—or proxies for climate, such as elevation—did a better job of explaining variation in bulk soil metrics than forest type alone. For instance, elevation, which was tightly correlated with MAT and MAP, explained  $\sim 60\%$  of the variance in soil  $\delta^{15}\text{N}$  values and  $48\%$  of the variation in soil C-to-N ratios, whereas forest type only accounted for  $36\%$  of the variance in the suite of soil chemical and isotopic variables. Accordingly, the use of climate data may enable more accurate spatial extrapolation and modeling of tropical forest N dynamics compared to approaches that depend on bioclimatic life zone or forest functional types.

The nature of this study prevented us from making direct measurements of N mineralization or gaseous fluxes, yet bulk soil chemical and isotopic values likely reflected biologically meaningful changes in relative N availability and forms of loss. At steady state, soil  $\delta^{15}\text{N}$  values are a function of the isotopic composition of inputs and relative magnitudes of different forms of loss (Brenner et al. 2001). In pristine ecosystems with

little variation in input isotopic values, higher soil  $\delta^{15}\text{N}$  generally indicates greater importance of loss pathways involving isotope discrimination (Austin and Vitousek 1998, Amundson et al. 2003). Both nitrate leaching and denitrification can cause ecosystem  $\delta^{15}\text{N}$  enrichment via preferential loss of  $^{14}\text{N}$ , but the former has a notably smaller isotope effect than the latter (Houlton and Bai 2009). As such, enriched  $\delta^{15}\text{N}$  values at steady state are most parsimoniously explained by higher relative rates of gaseous loss. Moreover, high  $\delta^{15}\text{N}$  values are frequently associated with overall N-rich conditions in the ecosystem (Martinelli et al. 1999, Brookshire and Thomas 2013). Conversely, low soil  $\delta^{15}\text{N}$  values imply the dominance of losses with lower isotope discrimination, sensu dissolved N leaching and/or erosion (Hilton et al. 2013), and may indicate N-poor conditions at the ecosystem scale (Austin and Vitousek 1998, Weintraub et al. 2015). Shifts in soil organic matter C:N ratios also tend to reflect variation in forest N status. High soil C:N ratios promote net microbial N assimilation over N mineralization, thus lowering soil N availability (Mooshammer et al. 2014). These patterns can be further reinforced by plant–soil feedbacks promoting low N litter (Cusack et al. 2009, Werner and Homeier 2015). In our study, high-elevation, cool/wet forests had high soil C:N



ratios and low soil  $\delta^{15}\text{N}$  values and that trend reversed along the transition to low-elevation, warmer/drier forests. This implied significant changes in N availability and forms of loss across the elevation–climate transect.

Specifically, steady-state  $^{15}\text{N}$  mass balance modeling using bulk soil  $\delta^{15}\text{N}$  values suggested that non-discriminating losses dominated in the cool, wet montane zone of PILA, while gaseous (i.e., highly discriminating) losses accounted for over half of total N losses in warmer, drier sites (Fig. 5). Using observed mean soil  $\delta^{15}\text{N}$  values from the three bioclimatic life zones (1.2‰, 3.2‰, and 4.6‰ for lower montane, premontane, and wet-premontane transition forests, respectively), the  $^{15}\text{N}$  mass balance model calculated mean gas loss fractions of 16%, 35%, and 49%, respectively, with a ~20% range depending on isotope effect assumptions (Fig. 6). These life zone averaged values overestimate gaseous N losses at the highest elevations and underestimate them at the lowest elevations, which is why continuous climate (or climate proxy) data may be more useful in modeling efforts. Relative gaseous losses can be converted to N-gas fluxes if other, non-gaseous N loss magnitudes are known. Neither aqueous nor erosive N exports in PILA have been documented, but it is reasonable to expect stream N losses are similar to those reported by Brookshire et al. (2012) for undisturbed montane forests elsewhere in Costa Rica, namely 6–10 kg·N·ha<sup>-1</sup>·yr<sup>-1</sup>. If this estimate is correct, then lower-elevation forests in the vicinity of PILA emit several kilograms of gaseous N per hectare per year. While these gaseous losses will be a mix of denitrification products, N<sub>2</sub>O is likely to be an important component, given high measured N<sub>2</sub>O emission rates in primary forests of the Caribbean lowlands (Keller and Reiners 1994, Weintraub et al. 2014).

The results presented here have two potentially important implications for montane tropical forests in a warming climate: (1) nitrogen availability may increase, and therefore, N limitation may decline, as forests warm up and dry out (Marrs et al. 1988, Bothwell et al. 2014), but (2) gaseous N emissions, including those of N<sub>2</sub>O, may increase substantially in parallel. At present, there is uncertainty surrounding the net climate effect of these two changes. This topic is deserving of further study, as it will contribute to whether montane

tropical forests catalyze positive or negative feedbacks to global climate change.

In this study, we observed shifts in indicators of N availability and forms of loss across long-established bioclimatic gradients, but this is not the same as predicting dynamic change in forest biogeochemical cycling under future climate. Other factors, which indirectly mediate climate effects, will be important to consider, such as turnover in the composition and traits of species and species assemblages along elevation gradients. Although we did not rigorously monitor forest structural and compositional change along the study transect, significant variation in both was likely (Lieberman et al. 1996, Feeley et al. 2013). In turn, changes in community composition and resultant forest structural/functional attributes may have mediated some of the observed N biogeochemical shifts, for instance, variation in stand growth rates, foliar resorption, leaf litter quality, and relative importance of symbiotic microbes (such as N<sub>2</sub>-fixers and mycorrhizae) for nutrient acquisition. These plant-mediated, stand-level traits are likely to respond to climatic change more slowly than N-cycle processes catalyzed by free-living soil microbes (though see Feeley et al. 2011, 2013 documenting shifts in tropical montane species composition in response to recent warming). This may slow the trajectory of N-cycle response to climate change in montane tropical zones, causing a lag between shifting temperature and precipitation regimes and biogeochemical response.

That said, our estimated rate of change in N-gas losses across the climate gradient was in line with previous work. According to the N isotope mass balance equation, we modeled a 4% increase in fraction gas loss per °C increase in MAT. This equates to a  $Q_{10}$  of ~4 if we assume no change in total N losses across the elevation gradient, that is, only the partitioning between gaseous and erosional/hydrologic losses changes. However, as Brookshire et al. (2012) found no change in hydrologic N exports with elevation across montane forests in Costa Rica, total N losses may in fact increase across the transect as fraction gas loss increases. Under this assumption, modeled  $Q_{10}$  is closer to 8. In either case, values of 4–8 align with  $Q_{10}$  values reported for N-gas emissions under field conditions, summarized in Smith (1997). Importantly, these field-based

$Q_{10}$  estimates, which tend to be higher than  $Q_{10}$  values measured in the laboratory due to intact soil structure, seem to hold even when warming is accompanied by soil drying, as may be the case for montane tropical forests. Thus, while established variation in forest composition and functional traits will likely influence the N-cycle response to climate change, it is notable that inferred rates of change in gaseous N emissions across the bioclimatic gradient are consistent with reported gaseous N loss kinetics.

In this study, we used bulk soil  $\delta^{15}\text{N}$  values to estimate steady-state gaseous N losses, in line with other efforts to partition N loss forms across large scales (Bai et al. 2011, Hilton et al. 2013, Houlton et al. 2015). However, bulk soil values may not always tell the full story, and our conclusions would be strengthened by information on the isotopic composition of other relevant N pools. For example, in montane forests in Hawaii, Houlton et al. (2006) observed a similar trend of decreased bulk soil  $\delta^{15}\text{N}$  values with increased MAP, but did not conclude that gaseous losses declined. Instead, the authors used differences in the  $\delta^{15}\text{N}$  of bulk soil and streams compared to dissolved N in soil water to argue for under-expression of the denitrification isotope effect at the ecosystem scale. When soil water  $\delta^{15}\text{N}$  values were used as inputs, steady-state models actually calculated an increase in gaseous N flux with MAP. It is difficult to assess whether similar isotope effect under-expression plays a role in our system as we lack soil water isotope measurements. Accordingly, our model results may underestimate denitrification in high-elevation forests and should be interpreted with care. That said, in the Houlton et al. (2006) study, temperature was constant across the precipitation gradient, whereas in our study, temperature and precipitation were strongly, negatively correlated. The wetter forests studied here may thus have had lower rates of gas loss if temperature constrained rates of microbial metabolism. While studies in other cool/wet montane forests found low  $\text{N}_2\text{O}$  emission rates that tracked  $\delta^{15}\text{N}$  values and N availability (Purbopuspito et al. 2006, Wolf et al. 2011, Teh et al. 2014), suggesting soil  $\delta^{15}\text{N}$  may be a reasonable proxy to model spatial patterns of gaseous N emission, these studies did not measure  $\text{N}_2$ . This remains a key uncertainty in gaseous N loss studies, in tropical biomes and beyond (Groffman et al. 2006).

It is also possible that shifts in organic matter decomposition contributed to observed  $\delta^{15}\text{N}$  patterns across the elevation–climate gradient. Increases in temperature drive faster rates of decomposition across montane tropical forests (Bothwell et al. 2014). In turn, soil  $\delta^{15}\text{N}$  values generally increase in soil organic matter of a more advanced stage of decomposition (Kramer et al. 2003, Craine et al. 2015). If an alternative mechanism for soil  $\delta^{15}\text{N}$  enrichment, related to decomposition and not forms of N loss, is invoked to explain elevation- $\delta^{15}\text{N}$  linkages (Craine et al. 2015), then forests growing under warmer conditions may have experienced higher rates of decomposition, increased N availability, and higher  $\delta^{15}\text{N}$  values without a concomitant increase in gaseous loss. However, while it may have played a role, the decomposition-based mechanism alone cannot explain stable isotope patterns. At steady state, isotope mass balance dictates that elevated ecosystem  $\delta^{15}\text{N}$  values must be linked to increased relative rates of discriminating losses, most likely via denitrification (as discussed above). It is in fact quite possible that both mechanisms operate in synergy, such that fractionating gaseous losses increase with more microbial processing during decomposition. This is an interesting and relevant topic that merits consideration when assessing the net climate effects of warming in montane tropical forests.

Finally, the availability of other limiting nutrients may underpin some of the variation in N dynamics across climate gradients and play important roles in future forest dynamics. Upper elevation montane forests may have relatively high P availability due to wet, anaerobic conditions that enhance soil P mobilization (Liptzin and Silver 2009). High P availability might thus play a role in promoting relative N constraints. If these cool, moist forests become warmer and drier, phosphorus availability could decline, and P may, over time, become limiting to forest C cycling in the montane zone, mirroring dynamics in many lowland tropical forests (Cleveland et al. 2011). Recent work suggests nutrient limitation in tropical forests in fact often involves multiple elements (Kaspari et al. 2008, Wright et al. 2011); this increases the complexity of predicting carbon-nutrient dynamics under changing climates (Townsend et al. 2011).

All of the above factors merit consideration when interpreting and modeling relationships between

elevation, climate, and indicators of N availability and loss in tropical forests, especially in projecting to forests of the future. Moreover, the direct vs. indirect mechanisms responsible for elevation-driven biogeochemical shifts deserve further study. And yet, the notable soil N isotopic and chemical variation documented here suggests changing tropical climates may have significant implications for relative N availability and gaseous losses in tropical zones. Such findings underscore the need for studies examining C and nutrient dynamics with tropical climate change, especially warming (Wood et al. 2012, Cavaleri et al. 2015). In parallel, baseline data on soil C and nutrient dynamics from remote, heterogeneous landscapes can help provide the information needed to deal with rapid environmental change in diverse tropical regions.

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