Environmental controls on canopy foliar nitrogen distributions in a Neotropical lowland forest

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Abstract. Distributions of foliar nutrients across forest canopies can give insight into their plant functional diversity and improve our understanding of biogeochemical cycling. We used airborne remote sensing and partial least squares regression to quantify canopy foliar nitrogen (foliar N) across ~164 km² of wet lowland tropical forest in the Osa Peninsula, Costa Rica. We determined the relative influence of climate and topography on the observed patterns of foliar N using a gradient boosting model technique. At a local scale, where climate and substrate were constant, we explored the influence of slope position on foliar N by quantifying foliar N on remnant terraces, their adjacent slopes, and knife-edged ridges. In addition, we climbed and sampled 540 trees and analyzed foliar N in order to quantify the role of species identity (phylogeny) and environmental factors in predicting foliar N. Observed foliar N heterogeneity reflected environmental factors working at multiple spatial scales. Across the larger landscape, elevation and precipitation had the highest relative influence on predicting foliar N (30% and 24%), followed by soils (15%), site exposure (9%), compound topographic index (8%), substrate (6%), and landscape dissection (6%). Phylogeny explained ~75% of the variation in the field collected foliar N data, suggesting that phylogeny largely underpins the response to the environmental factors. Taken together, these data suggest that a large fraction of the variance in foliar N across the landscape is proximately driven by species composition, though ultimately this is likely a response to abiotic factors such as climate and topography. Future work should focus on the mechanisms and feedbacks involved, and how shifts in climate may translate to changes in forest function.

Key words: Carnegie Airborne Observatory; gradient boosting; hyperspectral; light detection and ranging; Osa Peninsula, Costa Rica; topography; partial least squares regression.

INTRODUCTION

Nitrogen (N) is an essential element for biological metabolism, and its abundance strongly influences the structure and functioning of ecosystems. Lowland tropical forests often cycle N in excess relative to rock-derived nutrients such as phosphorus (P) and calcium (Ca; Martinelli et al. 1999, Reich and Oleksyn 2004). However, recent work shows tremendous heterogeneity and range in N availability within tropical rainforests at a variety of spatial scales (Townsend et al. 2008). The ecological importance, environmental drivers, and spatial dependencies of canopy foliar N (foliar N) heterogeneity are poorly understood, yet may be critical to resolving the role of N in regulating forest productivity and composition (Adamek et al. 2009, Cleveland et al. 2011, Asner et al. 2014), coupled biogeochemical cycles (Mayor et al. 2015, Nottingham et al. 2015), and watershed biogeochemistry (Brookshire et al. 2012, Taylor et al. 2014).

Foliar N is controlled by multiple factors. Past studies across tropical altitudinal gradients demonstrate that foliar and soil N decreases with elevation, with significant differences among lower elevation tropical forests (typically <1,000 m above sea level) and nearby tropical montane forests (Grubb 1977, Vitousek et al. 1995, Tanner et al. 1998, van de Weg et al. 2009). Elevation does not directly affect N but likely reflects the effects of co-occurring shifts in climate, vegetation, topographic position, parent material, and soil age. With increasing elevation, tropical forests generally experience increased cloud cover, changes in precipitation, and decreasing temperature that can combine to reduce both productivity and decomposition rates, leading to a decrease in rates of N cycling and availability (Grubb and Whitmore 1966, 1967, Schuur and Matson 2001, Kitayama and Aiba 2002). In many tropical regions, greater rates of long-term annual rainfall are linked to declines in both foliar and soil N content, suggesting that moisture driven shifts in plant–soil feedbacks may limit N availability and recycling (Martinelli et al. 1999, Nardoto et al. 2008, Fyllas et al. 2009). Regardless of the mechanism, N cycling varies with
broad climatological patterns, yet much less is known about the effects of finer-scale ecological heterogeneity on N cycling at a given elevation (Reed et al. 2008, Townsend et al. 2008, Weintraub et al. 2015).

In addition to climate, soil N availability increases as soils age and bedrock-derived nutrients become relatively scarce (Walker and Syers 1976, Crews et al. 1995, Vitousek 2004). While such soil differences are paralleled by changes in foliar N in low diversity tropical sites such as Hawai‘i (Vitousek 2004), it is unclear how tight the link between soil and foliar N is in diverse tropical forests. Recent field-based efforts across a wide diversity of tropical forest ecosystems have shown that foliar N (more than other nutrients such as P or Ca) is influenced by species identity more than by site (Asner et al. 2014, Asner and Martin 2016). However, these effects can be difficult to tease apart because changes in soils and nutrient cycling are often paralleled by shifts in forest composition. For example, sandy soils can have lower N availability than adjacent clay-rich soils, and this difference is reflected in the presence of different species, with higher or lower foliar N, on the two substrates (e.g., Livingston et al. 1988, Luizão et al. 2004).

Soil nutrients are also influenced by topographic variation that creates differences in hydrology, erosion rates, and thus, soil residence time (Raghunathan 1992, Amundson et al. 2003, Vitousek et al. 2003, Porder et al. 2005, 2007, 2015, Hilton et al. 2013). In our study area, the Osa Peninsula, Costa Rica, a variety of sedimentary deposits have recently been uplifted, leaving a landscape with abundant marine terraces that are being rapidly incised by the region’s rivers. The broad, flat terraces are eroding more slowly than slopes or narrow ridges in this landscape, and thus have longer soil residence times and increased N availability (Hilton et al. 2013, Taylor et al. 2014, Weintraub et al. 2015). How these soil differences are reflected in the canopy is one focus of the work described here.

The major goal of this work was to understand, in this diverse lowland forest, how abiotic and biotic characteristics influence foliar N. There is reason to think the biotic factor will be important, at least as a proximate control. Recent floristic analyses across gradients in state factor variation indicate that shifts in plant and soil N abundance are mediated by forest composition and species identity (Aiba and Kitayama 1999, Fyllas et al. 2009, Homeier et al. 2010, Asner and Martin 2016). Foliar N concentration is especially constrained by species, whereas other foliar nutrients, particularly bedrock-derived Ca and P, are controlled more so by underlying soil conditions (Asner et al. 2014, Asner and Martin 2016). Altogether, recent findings suggest that while species identity is a strong proximate driver of foliar N variation, state factors ultimately organize the spatial distribution of foliar N by governing the longer-term dynamics of phylogenetic adaptation, community assembly, and functional diversity (Asner et al. 2014, Asner and Martin 2016).

In this context, we combined foliar chemistry from a tree-climbing campaign with high fidelity remote sensing of canopy chemistry across the Osa Peninsula, Costa Rica. The latter has been made possible by rapid advances in the science of remote sensing, making it a powerful ecological tool (Chambers et al. 2007). Improved remote sensing platforms, better pre-processing algorithms, and additional computational power have made it possible to convert high fidelity hyperspectral data into accurate foliar chemistry maps (e.g., Asner et al. 2015a, b). These foliar chemistry maps can be generated at a fine resolution (map units <1 ha) across large areas (>100 km) and can be collected at multiple temporal scales. Remotely sensed foliar nutrient maps improve our ability to test current hypotheses about canopy foliar nutrient distributions within individual plants (Yu et al. 2014) and across landscapes (Asner et al. 2015b) and can be valuable in the discovery of new spatial patterns and ecosystem processes (Asner et al. 2015a).

We had three objectives to this study. First, we examine the influence of elevation, climate, parent material, and topography on patterns of tropical forest foliar N concentration. Many field studies have shown the effect of individual state factors on forest foliar chemistry, but comparatively little research has explored the relative strength of each factor in complex lowland tropical terrain. Our second objective was to examine the local influence of slope position on foliar N patterns. Recent research in the Osa Peninsula has demonstrated soil N accumulation on relatively slowly eroding terraces and lower N availability in portions of the landscape (narrow ridges, steep slopes) that are rapidly eroding (Weintraub et al. 2015). We explored how these geomorphic differences influenced foliar N concentration. Finally, we examined species-specific foliar chemical data to determine the influence of phylogeny on foliar N concentration in the region.

**METHODS**

**Region of study**

The Osa Peninsula is a biologically rich, geologically complex, lowland tropical forest located on the pacific slopes of southwestern Costa Rica (Fig. 1). The Osa
Peninsula has been identified as the largest remaining, intact, Pacific lowland tropical forest in Central America (Barrantes et al. 1999). Despite past selective logging in the region (Lobo et al. 2007), large areas dominated by mature tropical forests remain, with canopy trees reaching heights >60 m. These canopy trees help to make the forests of the Osa Peninsula some of the most carbon-rich in the Neotropics (Taylor et al. 2015). The peninsula is also home to high species diversity and endemism (Barrantes et al. 1999, Wanek et al. 2008, Cornejo et al. 2012). The flora of the Osa Peninsula has a strong affinity with flora of northwestern South American and Central American species (Cornejo et al. 2012). This overlap of flora, and associated fauna, along with the size of the remaining intact forest, make the Osa Peninsula an important refuge for the survival of many Central American plant and animal species (Cornejo et al. 2012).

The geologic history of the Osa Peninsula has been described and mapped in detail by Buchs et al. (2009) and summarized by Taylor et al. (2015). The dominant geologic substrates that make up the peninsula vary by age and type, with older basalts to the north, Pliocene sediments in the central portions of the peninsula, and Quaternary alluvium in the flood plains. The Osa Peninsula is further shaped by high uplift rates (2.5–6.5 m/kyr) and rapid erosion. This has created a highly dissected topography across much of the peninsula, but in some areas, remnant flat terraces remain isolated from the rapid river incision and erosion that dominates slopes and narrow ridges. Rainfall rates, calculated over the last five years from field stations on the peninsula, ranged from 3,000 to 7,000 mm/yr, and mean annual temperature (MAT) ranged from 24.5° to 26.5°C (Taylor et al. 2015). The topographic diversity and geologic history make the Osa Peninsula an ideal location to investigate the influence of topographic heterogeneity and patterns in foliar N. For the regional assessment, four flight paths (~1.2 km wide) were used to sample the landscape (Fig. 1). The flight paths covered 10 geologic substrates and five soil orders, varied in precipitation, and ranged in elevation from sea level to 745 m above sea level.

**Remotely sensed data**

In 2012, remotely sensed data were collected at an elevation of 2,000 m above ground level, across the study region, with the Carnegie Airborne Observatory Airborne Taxonomic Mapping System (CAO-AToMs; Asner et al. 2012; hereafter referred to as CAO), onboard a Dornier 228 Aircraft. The sensor configuration used for the 2012 campaign consisted of a high-fidelity imaging spectrometer (HiFIS) and a dual laser, waveform light detection and ranging (LiDAR) sensor.

The CAO HiFIS sensor measured spectral radiance in 5-nm increments, with nominally 6-nm spectral response function (full-width at half-maximum), spanning the visible to shortwave infrared spectrum (380–2,510 nm). The raw output of the HiFIS was 427 contiguous spectral bands at a resolution of 2 m. Prior to analysis, the HiFIS data were converted from raw digital numbers to atmospherically corrected reflectance in ENVI version 4.8 (Exelis Visual Information Solutions, Boulder, Colorado, USA) following Asner et al. (2015b). First, the data were converted to radiance (W·sr⁻¹·m⁻²) with a flat-field correction. Atmospheric correction was done using the ACORN-5 model (Inspec, Glendale, California, USA). Following conversion, the original 427 HiFIS bands were resampled to 214 bands at 10 nm increments. The number of bands was further reduced for analysis by removing the bands in the range of atmospheric water absorption (1,350–1,480; 1,780–2,032 nm) and bands in the far ends of the spectra (<410 nm, >2,450 nm). The data were then converted to brightness normalized reflectance (Feilhauer et al. 2010). Brightness normalization was used to minimize the differences in observed brightness in the data, due to canopy leaf tissue orientation and depth (Feilhauer et al. 2010; Appendix S1: Fig. S1). The spectral data were further filtered, using a LiDAR HiFIS fusion technique, to remove bare-ground and canopy shading (Asner et al. 2007). In short, the LiDAR data were used to create a ray tracing model that incorporates solar viewing geometry, to mask out canopy pixels that were in shade at the time of the flight. Finally, any pixels with NDVI <0.8 were masked to remove non-photosynthetic vegetation and areas with low leaf area.

After this extensive pre-screening process, the remaining reflectance data were more representative of unshaded canopy vegetation, often referred to as sunlit canopy foliage (Asner et al. 2015a). Clouds, cloud shadows, and areas without forest were manually masked in ENVI. For the regional model, 1-ha cells with a mean top of canopy height <5 m were also masked to avoid the influence of secondary forests. The preprocessed HiFIS spectral data were used to estimate canopy foliar N (%) concentration, by mass, across the study region. The foliar N map was created at the same map unit resolution as the HiFIS data (2 m) and at 1 ha, using partial least squares regression (PLSR; Haaland and Thomas 1988). PLSR is a linear regression method that was chosen due to its ability to deal with the large numbers of correlated spectral variables (bands) generated from the CAO HiFIS data, and its past use in estimating leaf traits and biochemical compounds from vegetation with spectroscopy (Feilhauer et al. 2010, Asner et al. 2011, 2015b, Serbin et al. 2014, Chadwick and Asner 2016, Chavana-Bryant et al. 2016). Similar to principal components analysis, PLSR converts the highly correlated spectral bands (predictor variables) into uncorrelated variables (latent vectors). These latent vectors are created by an optimization process that involves a dimensionality reduction and cross-validated linear regression (Feilhauer et al. 2010). To avoid statistical overfitting, the number of vectors used in the PLSR analysis was determined by minimizing the predicted residual error sum of squares (PRESS) statistic (Chen et al. 2004). A leave one out cross-validation procedure was used. The precision (coefficient of determination) and accuracy (root mean square error; RMSE) were assessed between the
The final geomorphometric models used in the regional assessment.

<table>
<thead>
<tr>
<th>DEM derived variables</th>
<th>Description</th>
<th>Formula</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compound topographic index (CTI)</td>
<td>wetness index</td>
<td>( CTI = \ln\left(\frac{a}{\tan\theta}\right) )</td>
<td>Moore et al. (1993)</td>
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<tr>
<td></td>
<td></td>
<td>( a = \text{catchment area} \times (\text{pixel area in m}^2) )</td>
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<td></td>
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<td>( \theta = \text{slope angle in radians} )</td>
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<tr>
<td>Site exposure index (SEI)</td>
<td>relative exposure to solar radiation</td>
<td>( \text{SEI} = \text{slope} \times \cos \left(\frac{\text{aspect} - 180}{180}\right) )</td>
<td>Balice et al. (2000)</td>
</tr>
<tr>
<td>Dissection</td>
<td>measure of surface texture</td>
<td>( \text{Dissection} = \frac{z_{\text{max}} - z_{\text{min}}}{z_{\text{max}} - z_{\text{avg}}} )</td>
<td>Evans (1972)</td>
</tr>
</tbody>
</table>

remotely sensed and field measured N (Asner and Martin 2011, Chavana-Bryant et al. 2016). The model was first built and validated using 22 tropical forest types across a 3,500 m elevation gradient throughout Peru (Asner et al. 2014, 2015b). It was then applied to the Osa Peninsula. Independent validation of the PLSR was done using field collected foliar N (see Methods: Foliar N field data) averaged within 1-ha grids on three separate flight lines across the Osa peninsula (n = 21).

The CAO dual laser LiDAR (1,064 nm), flown at 2,000 m above ground level, at a ground speed ≤204 km/h with a 34° field of view, pulse repetition frequency of 100 kHz, and a beam divergence set to 0.56 mrad (1/e) for each of the two lasers, allowed for 1.6 pulses/m² for each laser (Asner et al. 2012, Asner and Mascaro 2014). The discrete return LiDAR data were used to create 2-m resolution digital elevation models (DEMs). The georeferenced LiDAR data point cloud was processed into DEMs using the LAStools software suite (Gilching, Germany), by first identifying the lowest point in 10 × 10 m grids. The lowest point estimate in each grid was assumed to be ground. The remaining ground points in each grid were determined by an iterative process of fitting a horizontal plane and selecting the nearest point that was <5.5° and <1.5 m higher in elevation. This method has been successfully used in creating accurate DEMs across a wide variety of terrains and forest types (Asner and Mascaro 2014), including the study area (Taylor et al. 2015).

In addition to the DEMs, geomorphometric models were generated from the DEMs (e.g., slope curvature and aspect). The DEM generated models were created with the Geomorphometric and Gradient Metrics Toolbox (Evans et al. 2014) and the Land Facet Corridor Designer Toolbox (Jenness et al. 2013) and implemented with ESRI software (ArcMap, ESRI, Redlands, California, USA). Over 13 DEM derived geomorphometric models were calculated based on use in past studies; however, only three were used in the regional gradient boosting model (GBM), due to high collinearity (\( r^2 > 0.7 \); Dormann et al. 2013). If two variables were found to have \( r^2 > 0.7 \), the variable least correlated with foliar N was removed. The final geomorphometric models used to represent topography in the study were compound topographic index (CTI), site exposure index (SEI), and dissection (Table 1). The CTI, also known as the wetness index, is a function of slope and upstream contributing area (Moisen et al. 1993). High CTI values indicate zones of higher potential soil moisture due to topography. The SEI represents relative solar exposure and is a function of aspect and slope (Balice et al. 2000). Higher SEI values represent greater exposure. Landscape dissection was evaluated using relative changes in elevation (Table 1).

**Additional environmental data**

Three additional variables (not generated from the CAO LiDAR and HiFIS sensors) were also used in the regional 1-ha predictive N model: mean annual precipitation (MAP), geologic substrate, and soils. The MAP (~1950–2000) data were obtained from WorldClim (data available online). Although mean annual temperature (MAT) was also obtained for the same time period, it was not included in the final model due to high correlation with elevation (\( r^2 = -0.9 \)) and precipitation (\( r^2 = 0.8 \); Appendix S1: Fig. S2). Therefore, elevation was used as a proxy for temperature. As elevation increases, MAT decreases at a rate of 1°C for approximately every 220 m (Appendix S1: Fig. S2). A geologic substrate layer was digitized from Buchs et al. (2009). The geologic substrate layer has previously been implemented in Taylor et al. (2015). There were ten substrate types defined by Buchs et al. (2009): Golfito basalts, Esquinas basalt, Vaquedano basalt, Fan Delta, Miocene Melange, Miocene sediments, Volcanic sediment, Pleistocene sediments, Pliocene sediments, and Quaternary alluvium. A recently generated soil order layer was obtained from the Agronomy Research Center, University of Costa Rica (Mata et al. 2013). The soil orders found in the study region included Entisols, Histosols, Fluvial Entisol/Inceptisol, Inceptisols, and Ultisols.

**Analytical approach**

We used a GBM (Friedman 2001) to determine the influence of environmental factors on foliar N distribution patterns across the study region. The GBM was chosen for its ability to fit complex, nonlinear ecological interactions, its resistance to outlier influence (via loss functions), its tolerance of collinear predictor variables, and its ability to cope with categorical and missing data (Moisen et al. 2006, Elith et al. 2008, Dormann et al. 2007). GBMs are based on regression trees, with the splitting rules automatically selected. In a GBM, the basic regression tree is modeled using a gradient descent algorithm, which results in a model by minimizing a loss function. The loss function is the mean squared error (MSE) for continuous response variables, and the deviance for binary classification. In this application, the response variable was foliar N, and the independent variables were the CTI, SEI, dissection, and regional elevation gradient.

The CTI, SEI, dissection, and elevation gradient were used as independent variables in the PLSR model. The original PLSR model was limited to three independent variables (CTI, SEI, and dissection) to reduce the influence of collinearity on model performance. To determine the importance of collinearity, the PLSR model was analyzed using a single regression tree with a random forest (RF) algorithm. The RF algorithm was used to determine the importance of each independent variable (CTI, SEI, and dissection) and the relative importance of the regional elevation gradient.

To validate the PLSR model, we used a cross-validation method with 10-folds. The cross-validation method was used to determine the importance of each independent variable (CTI, SEI, and dissection) and the relative importance of the regional elevation gradient.

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GBMs are tolerant of predictor (independent) variables that are collinear. However, only predictor variables with a correlation of $|r^2| < 0.7$ with other predictor variables and a variable inflation factor (VIF) <5 were included in the final model (Dormann et al. 2013; Appendix S1: Fig. S2). The GBMs produce a series of individual regression trees that sequentially decrease the model bias. Because each iteration of the GBM affects the model bias, the model requires proper selection of metaparameters to prevent overfitting (Hastie et al. 2009). We selected tuning parameters, by first excluding 10-fold cross-validation on a grid of all possible tuning parameter combinations. The R package gbm (Ridgeway 1999) and the Python package scikit-learn (Pedregosa and Varoquaux 2011) were used to implement the GBM. Tuning parameters to increase performance and reduce overfitting include the number of trees (860), interaction depth (16), learning rate or shrinkage (0.02), and the loss function (laplace). The loss function was weighted by the inverse histogram of N distribution, in order to fully represent the entire range of N. The response (dependent) variable was foliar N, generated directly from the canopy, with the CAO HiFIS (described previously). The predictor (independent) variables used were elevation, CTI, SEI, dissection, precipitation, geologic substrate, and soil order. Model performance was evaluated by using a 10
fold cross-validation. The influence of each predictor variable on the model was evaluated using relative influence and partial dependency plots. Relative influence is a measure of how well each variable improves the model, averaged across all trees (Friedman and Meulman 2003). Partial dependency plots show the effect of each predictor variable on the response variable, after accounting for the average effects of the other variables in the model (Hastie et al. 2009).

While GBM was used to analyze regional controls on foliar N patterns, a different approach was needed to investigate the influence of finer-scale slope position of foliar N content. The CAO-generated high resolution DEM was used to identify an area within the Osa Peninsula that contained adjacent landscapes in different stages of geomorphic development (Los Patos; Figs. 1B1, 2). In the Los Patos region, levels of foliar N between the terraces and the other slope positions (ravines, steep slopes >10°, and ridges) were tested for statistically significant differences in foliar N. We used a Kolmogorov–Smirnov test (KS test) from a random subsample of 1,000 foliar N samples, from each location, repeated 1,000 times, using the software package R (R Core Development Team 2011).

Foliar N field data

Two field campaigns were conducted on the Osa Peninsula to collect mature top of canopy leaf samples for chemical analysis (Asner & Martin 2016; Taylor et al., unpublished data). The first campaign (2011) sampled 374 tree crowns, representing 269 species found throughout the region. Reference vouchers and photos for the first campaign are located at the Carnegie Institution Department of Global Ecology, Stanford, California, USA. The second campaign took place in 2014, after the CAO flight, and focused on replications of dominant canopy species (10 species, 166 mature crowns). Trained tree climbers collected mature leaves from fully sunlit branches at the top of the canopy. Frozen leaf disks were sent to the Carnegie Spectranomics Laboratory, Stanford, California, USA, for drying and chemical analysis. Total N (%) concentration was determined on oven-dried, ground samples using a combustion-reduction elemental analyzer (Costec Analytical Technologies, Valencia, California, USA). See Asner et al. (2011) and the Spectranomics Project website for further details of the laboratory protocols used.8

For this study, we did not integrate phylogenetic identity into the spatial analyses of foliar N variation because we currently lack sufficient information on species identity, canopy foliar chemistry, and individual location. For now, we use field data from 269 species, represented by 196 genera and 70 families, to examine how phylogeny explains variation in foliar N concentration. In order to determine the phylogenetic partitioning of foliar N within the region, a nested ANOVA model with random effects was used on the field collected data. The nested ANOVA model was implemented using the lme4 package in R. The phylogenetic levels included are family, genus nested within family, and species nested with genus within family. All effects were treated as random. This method has been used successfully to compare phylogenetic partitioning and foliar chemistry in other tropical studies (e.g., Fyllas et al. 2009, Asner and Martin 2016).

RESULTS

Model validations

Independent validations of the PLSR model applied to the CAO HiFIS data in the Osa Peninsula had $R^2$ values of 0.55, 0.59, and 0.28 and RMSE values of 0.07, 0.11, and 0.2, for flightpaths one, two, and three (Appendix S1: Fig. S3). These results were similar to validation plots reported from Peru ($R^2 = 0.48$, RMSE = 0.31; Asner et al. 2015b). This validation suggests that the Peru PLSR foliar N model is robust and may be applied to other Neotropical forests. Similar to Peru, there remains unresolved variation which may be due to a number of factors including a mismatch in the remotely sensed and field data, temporal differences between remotely sensed acquisition and field data, and processing of the field and HiFIS data. Foliar N, predicted from the environmental variables, using the GBM, had a cross-validated $R^2$ of 0.68 and a RMSE of 0.19, compared to the foliar N concentration derived from the tree canopies using the CAO HiFIS data (Appendix S1: Fig. S4).

Landscape controls on foliar N patterns

Elevation had the greatest relative influence on the GBM model (30%), followed by precipitation (24%), soil type (15%), SEI (9%), CTI (8%), geologic substrate (6%), and landscape dissection (6%; Fig. 3). The partial responses from the dependency plots indicated that the

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8 http://spectranomics.ciw.edu
Fig. 4. Partial dependence plots that represent the effect of each predictor variable on the 1-ha canopy foliar nitrogen (percent nitrogen concentration by mass, N) model, after accounting for the average effects of the other variables. For panel (C), numbers correspond to soil types: (6) Entisols, (9) Histosols, (10) Fluvial Entisol/Inceptisol, (13) Inceptisols, and (18) Ultisols. For panel (F), numbers correspond to geologic substrate: (1) Golfito basalts, (2) Esquinas basalt, (3) Vaquedano basalt, (4) Fan Delta, (5) Miocene Melange, (6) Miocene sediments, (7) Volcanic sediment, (8) Pleistocene sediments, (9) Pliocene sediments, and (10) Quaternary alluvium.
forests with the highest foliar N were found at mid elevations (~50–300 m above sea level) with relatively lower precipitation (<3,200 mm), on Inceptisol or Ultisol soils, and on slopes with relatively higher exposure to solar radiation and lower flow accumulation (Fig. 4). After accounting for the average effects of the other predictor variables, landscape dissection and substrate did not contribute to a large range in foliar N (Fig. 4).

A closer look at slope position revealed moderate correlation with regional foliar N distribution, with relatively lower foliar N concentrations in higher elevation hillcrests, lowland mangrove dominated forests, and river valleys (Figs. 1, 5). Foliar N concentration was similar across substrates with the exception of the Quaternary alluvium (Appendix S1: Fig. S5). The Quaternary alluvium contained the forests with the lowest foliar N and showed the greatest range in foliar N and was the only geologic substrate where foliar N was significantly different from foliar N from all other substrates (post-hoc Tukey test).

Phylogenetic control on foliar N patterns

Our regional field sampling of foliar chemistry revealed that phylogenetic partitioning of foliar N in the Osa Peninsula explained ~75% of the variance found in the foliar N data set (n = 540; Fig. 7). The overall variance explained is similar to results from an elevation gradient in the Western Amazon (Asner et al. 2014) and in tropical forests around the world (Asner et al. 2015a, b). In the Osa, species-level differences explained the most variation (39%), followed by family (25%) and genus (13%). These results indicate that phylogenetic adaptations are strong drivers of foliar N distributions across the Osa Peninsula and elsewhere.

Discussion

Patterns of foliar N were correlated with environmental factors at multiple spatial scales. At the regional scale, elevation and mean annual precipitation rates had the strongest influence on spatial patterns in foliar N. At finer spatial scales (<1 km), slope position helped further explain foliar N concentrations. Foliar N concentrations on flat, remnant, marine terraces were significantly higher than concentrations on adjacent hillslopes, which corroborates recent research demonstrating an erosional influence on soil N cycling (Hilton et al. 2013, Taylor et al. 2015, Weintraub et al. 2015). Furthermore, we found that field collected foliar N concentrations were strongly phylogenetically constrained, similar to tropical forests elsewhere (Asner and Martin 2011, 2016, Asner et al. 2014). The joint influence of environment and phylogeny on foliar N patterns suggests that abiotic controls on foliar N are mediated in part by shifts in forest composition.
cloud cover and perhaps even subtle declines in temperature may be responsible for shifts in forest composition that result in lower overall foliar N concentration.

Precipitation can also influence foliar N concentration, which varies widely (3,000–7,000 mm/yr) across the peninsula. High levels of precipitation can drive a decline in foliar N concentration, which arises from long-term plant–soil nutrient feedbacks, derived from low evapotranspiration, water-saturated forest soil, reduced decomposition rates, and in turn, slow rates of N recycling between microbial and plant systems (Schuur and Matson 2001, Schuur 2003). The Osa Peninsula is very wet with average rainfalls ranging from 3,000 to 7,000 mm/yr across the region, and past work implies that foliar N concentration should be negatively correlated with MAP (Schuur and Matson 2001). However, our results suggest that foliar N is not negatively correlated with MAP in the Osa Peninsula. Unlike ecosystems where the decrease in N availability with increased precipitation were noted, the forest soils of the Osa Peninsula are generally well-drained, even in the wettest locations, with a much greater MAT (~23–26°C compared to 16°C; Schuur and Matson 2001). The biogeochemical mechanisms underpinning the relationship between rainfall and foliar N warrant further research, though may stem from rainfall-driven increases in nutrient demand and recycling (Wieder et al. 2011) to support high primary productivity and soil decomposition in wet tropical forests (Cleveland et al. 2006, Hofhansl et al. 2014, Taylor et al. 2015). Thus, the relative and possible interactive role of cloud cover and high rainfall in lowering foliar N concentration in upper elevations warrants more research.

To a lesser extent than climate factors, soil type also influenced regional foliar N patterns. For example, foliar N concentrations in forests on Quaternary alluvium were generally lower than in upland forests; however, foliar N within these lower foliar N forests varied. Forests on Quaternary alluvium had foliar N ~10% higher on Fluvial Inceptisols and Entisols, compared to forests on Histosols. The low foliar N found on Histosols was dominated by mangrove ecosystems, where the prevalence of saturated soils and lower mineralization of N limits forest growth (e.g., Komiyama et al. 2008). Entisols and Fluvial Inceptisols, which are located along river ways and on Quaternary alluvium (i.e., erosional outwash from upland regions), are typically dominated by sand, are structurally poor and prone to nutrient leaching (Quesada et al. 2011). Relatively high foliar N, found on the Inceptisols and Ultisols in upland soils on sedimentary and basaltic substrates, is due to the mineral soils that harbor nutrient-rich forests of greater productivity and higher flows of nutrient recycling (Wanek et al. 2008, Taylor et al. 2015). While geologic substrate alone showed no consistent influence on regional N patterns, a role for parent material variation was indirectly witnessed as the primary driver of soil formation.
Topographic variation was also correlated with patterns of foliar N. These findings are consistent with prior research demonstrating relationships between topography and forest structure (e.g., de Castilho et al. 2006, Taylor et al. 2015), turnover rates (e.g., Gale 2000, de Lima and de Moura 2008), N availability (e.g., Weintraub et al. 2015), and canopy nutrient distribution (Asner et al. 2015a). Foliar N levels were positively correlated with increasing site exposure and watershed dissection. This relationship may be the result of more frequent disturbances on exposed ridges, causing gap formation and successional recovery in such areas. Field research in the region indicates that forests on exposed ridges often have greater stem density and high turnover rates (Wanek et al. 2008) composed of successional species with higher levels of foliar N to support fast-growth life-history strategy.

Fine scale slope position controls on foliar N patterns

In the Los Patos region, geomorphic disequilibrium influenced the distribution of foliar N (Fig. 2) at fine spatial scales (<1 km). The flat areas on top of the marine terraces support tree canopies that are more N-rich than the surrounding topographic areas of greater dissection. Field and modeling studies suggest that slower erosion rates on the flat terraces allows for accumulation of N, whereas N availability is constrained by erosional rates in areas of hydrologic dissection (Hilton et al. 2013, Weintraub et al. 2015). The mechanistic linkages between plants and soils on these terraces are currently being investigated (Osborne et al., unpublished manuscript).

Phylogenetic controls on foliar N

Field foliar sampling suggests that phylogeny explains ~75% of the variation in foliar N concentrations across the Osa Peninsula. Such strong phylogenetic constraints on foliar N imply that environmental factors influence the spatial patterns of foliar N by influencing the distribution of taxa with specific foliar N values. Environmental factors appear to filter phylogeny in the Osa Peninsula through the creation of conditions that favor specialized species and their traits (e.g., foliar N) in a particular area (e.g., waterlogged mangroves vs. well-drained terraces vs. steep slopes). Future work, to determine the temporal scales at which environmental factors influence compositional changes of tropical forests, will further our understanding of nutrient cycling in tropical forests. Furthermore, the influence of phylogeny was not evaluated using crown-level delineations of foliar N concentration in the HiFIS data because of insufficient spatial mapping of individual species locations across the study region. Integrating phylogenetic composition into future spatial models would allow us to determine the influence of spatial patterns of species composition on foliar nutrients, which is part of our ongoing research program in the region.

Conclusions

A combination of remote sensing and targeted field work has allowed us to explore controls on regional and local patterns of foliar N across the Osa Peninsula landscape. We discovered high heterogeneity of foliar N across the Osa Peninsula, which is partially organized by underlying environmental conditions, particularly climatic conditions, soil type, and geomorphic development. Field data on foliar N concentration was strongly determined by phylogenetic identity at the species level, suggesting that the influences of environmental factors on foliar N patterns are mediated by forest composition. However, it remains unclear the degree to which foliar chemistry is environmentally filtered and phylogenetically partitioned, and how patterns of community composition are organized by shifts in environmental control factors. Further investigation of these relationships is important for resolving linkages between the functional and biological diversity of rainforests, and consequently for understanding the behavior of tropical forests in the Earth system now and into the future.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1408/full

**Data Availability**

Data associated with this paper are available in Dryad: http://datadryad.org/resource/doi:10.5061/dryad.ck585.