

Trait-based signatures of cloud base height in a tropical cloud forest

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PREMISE: Clouds have profound consequences for ecosystem structure and function. Yet, the direct monitoring of clouds and their effects on biota is challenging especially in remote and topographically complex tropical cloud forests. We argue that known relationships between climate and the taxonomic and functional composition of plant communities may provide a fingerprint of cloud base height, thus providing a rapid and cost-effective assessment in remote tropical cloud forests.

METHODS: To detect cloud base height, we compared species turnover and functional trait values among herbaceous and woody plant communities in an ecosystem dominated by cloud formation. We measured soil and air temperature, soil nutrient concentrations, and extracellular enzyme activity. We hypothesized that woody and herbaceous plants would provide signatures of cloud base height, as evidenced by abrupt shifts in both taxonomic composition and plant function.

RESULTS: We demonstrated abrupt changes in taxonomic composition and the community-weighted mean of a key functional trait, specific leaf area, across elevation for both woody and herbaceous species, consistent with our predictions. However, abrupt taxonomic and functional changes occurred 100 m higher in elevation for herbaceous plants compared to woody ones. Soil temperature abruptly decreased where herbaceous taxonomic and functional turnover was high. Other environmental variables including soil biogeochemistry did not explain the abrupt change observed for woody plant communities.

CONCLUSIONS: We provide evidence that a trait-based approach can be used to estimate cloud base height. We outline how rises in cloud base height and differential environmental requirements between growth forms can be distinguished using this approach.

KEY WORDS climate; Costa Rica; edaphic; elevation; functional; herbaceous; montane; mountain; serpentine; soil enzyme; ultramafic.

Clouds play an important role in the global climate system and are key parameters in global climate models (Sherwood et al., 2014). Indeed, the wide range of uncertainty among climate models is dominated by uncertainties about how clouds respond to global warming (Bony et al., 2015). Cloud immersion of forests strongly reduces solar radiation and outgoing longwave radiation, increases humidity and water inputs, and reduces transpiration (Brujinzeel and Proctor, 1995). The effects of cloud immersion extend to soil structure, nutrient cycling, and plant composition (Still et al., 1999). In particular, cloud base height is a key characteristic for quantifying the influence of clouds on the abiotic and biotic structure of ecosystems.

Tropical cloud forests exemplify the profound consequences of cloud base height on ecosystem structure and function. Tropical cloud forests are species-rich and biogeographically diverse owing to their geographic isolation and persistent cloud immersion (Brujinzeel et al., 2011). Because future and ongoing climate change directly affect cloud formation, cloud forests are considered one of the most threatened ecosystems in the world. Tropical cloud forest climates are predicted to disappear by 2100 (Williams et al., 2007). Yet monitoring and measuring cloud base height and its effects on organisms within tropical cloud forests is challenging because long-term biological sampling and meteorological stations are scarce

(Lawrimore et al., 2011), satellite data are of limited duration and not well resolved for cloudy regions (Qin et al., 2009), and global climate models are too coarse to detect small-scale cloud formation due to the extreme topographical complexity that characterizes montane areas (Lawton et al., 2001). The estimation of cloud base height using ground-based instrumentation (e.g., ceilometers), satellite-based observations, and meteorological model simulations (e.g., Miller et al., 2018) has been important for understanding the effects of climate change for cloud-immersed forests in the Canary Islands (Sperling et al., 2004), Hawaii (Diaz et al., 2011; Zhang et al., 2012), and the eastern United States (Richardson et al., 2003). However, most of the world's tropical cloud forests are inaccessible and studying cloud base height and its effects on organisms remains challenging.

Given the paucity of climate data and long-term monitoring in tropical cloud forests, we propose a trait-based approach to detect cloud base height. Plant traits, like specific leaf area, vary with environmental variables at local to global scales (e.g., Reich et al., 1999; Niinemets, 2001; Wright et al., 2004). For example, in broad-leaved trees, specific leaf area increases with decreasing temperature and increasing precipitation, soil fertility, and elevation (Niinemets, 2001; Wright et al., 2004; Ordoñez et al., 2009). Abrupt changes in temperature, precipitation, soil nutrients and biogeochemical cycles above and below cloud base height lead to high species turnover (Gentry, 1988) and, likely, high functional turnover, too.

We expected that the steep topography that characterizes cloud forests should result in functional trait changes across elevation, as shown for elevational gradients around the world (Reich et al., 1999; Wright et al., 2002). Unlike other studies reporting trait changes across elevation, however, we expected cloud formation to cause an abrupt functional turnover, indicating the location of cloud base height. On the other hand, the structure and functioning of tropical cloud forests is not solely dependent on climatic factors. A dense cloud layer results in cooler temperatures, more rainfall, less light, and higher humidity but these conditions also lead to slower rates of decomposition and nutrient cycling (Grubb, 1977). In turn, soil properties vary predictably across elevation. Soil temperature and soil pH decrease, while soil moisture and soil C:N ratios increase (Marrs et al., 1988), which influence decomposition through changes in microbial communities and extracellular enzyme activity (de Boer et al., 2006). Extracellular enzyme activity is higher under warmer, drier conditions in tropical forests (Looby and Treseder, 2018). Although responses of plants to climate have been widely studied aboveground, parallel changes occur belowground where soils, strongly nutrient limited in mountains (Tanner et al., 1998), play a major role in plant growth (Fisher et al., 2013; Mohl et al., 2019). As a result, changes in soil nutrient availability and microbial community composition could also influence plant species and functional turnover across elevation (Dawes et al., 2017).

Further, we reasoned that major differences in life history strategies between woody and herbaceous species—rooting depth, demographic rates, and dispersal ability—may make herbaceous species even more dependent on cloud immersion. Herbaceous plants likely respond differently to resource gradients compared to woody plants (Murphy et al., 2016). First, the shallow roots of herbaceous species allow rapid physiological responses to soil water availability yet also increases their susceptibility to drought (Schenk and Jackson, 2002). Second, the faster demographic rates of herbaceous species (Grime et al., 1988) allow faster population-level responses (Smith and Beaulieu, 2009). Finally, the smaller seeds of herbaceous plants

relative to woody plants (e.g., Leishman et al., 2000) are thought to increase their dispersal limitation, leading to spatial aggregation along resource gradients (Leigh et al., 2004).

Here, we sought to: (1) disentangle how climate and soil properties structure plant communities in a tropical cloud forest; and (2) detect a signature of cloud base height using trait-based measurements of woody and herbaceous plants. To do this, we simultaneously quantified plant community composition and a key functional trait, specific leaf area, for woody and herbaceous species, and measured climatic and soil properties across elevation. Whereas other trait-environment studies are characterized by gradual trait changes along a resource gradient, we expected abrupt functional trait changes at cloud base height. We hypothesized that herbaceous plants would exhibit stronger trait changes related to cloud base height due to greater sensitivity to water availability; whereas woody species, with access to deeper water sources, would be more limited by soil nutrient availability.

MATERIALS AND METHODS

Study Site

Santa Elena Peninsula in northwestern Costa Rica (Guanacaste Province, 10°52'34.53"N, 85°49'10.97"W) is characterized by its ancient geological origins, topographical complexity, and edaphically dry and mineral-rich soils (Janzen, 1998; Reeves et al., 2007; Dauphin and Grayum, 2015). Santa Elena formed as an island in the Pacific Ocean 85 mya, the result of upward movement of deep seabed rocks rich in magnesium (Janzen, 1998). After its formation and by the time the Central American land bridge formed (3–4 mya), Santa Elena had been carried eastward by the Cocos Plate before colliding into Costa Rica (Janzen, 1998; Reeves et al., 2007). It is located within the driest region of the country (with an estimated 800 mm of annual precipitation). However, the peaks of Santa Elena Peninsula (720 m) are continually immersed in cloud cover, even during the six-month dry season lasting from December to May. Santa Elena Peninsula is roughly 30 km long and 15 km wide and became part of Area de Conservación Guanacaste (ACG, the first conservation area in the country) in 2000. The western portion of Santa Elena Peninsula harbors a rare type of old-growth dwarf forest that can be accessed by boat from Cuajiniquil, a small fishing town on its most northeastern coast. The eastern portion of Santa Elena Peninsula can be accessed during the dry season via dirt roads maintained by ACG. Sampling sites in this study were accessed by boat and a short (15 m) swim to shore, using Estación Biológica Isla San Jose (part of ACG's Islas Murcicalgo archipelago) as a base camp where samples were processed.

Plant Sampling

We quantified vegetation structure and composition in two 2 × 50 m vegetation transects every 50 m in elevation across a south-facing slope from 40 to 690 meters above sea level (m a.s.l.). An additional pair of transects was established at 720 m, representing the highest peak, for a total of 15 sampling sites. We determined whether the size and number of transects was sufficient to capture plant species richness across sites by calculating species accumulation curves (Appendix S1). Within each transect, we identified and quantified the abundance of woody and herbaceous species. Owing to the

small diameters of the stems (<2.5 cm) of many multi-stemmed woody trees and shrubs, and the extreme field conditions on exposed, steep, and windy slopes, we did not measure stem diameters. We then collected five mature, fully expanded, and minimally damaged leaves from three individuals for each species at each sampling site. Leaves were scanned with a flat-bed scanner (CanoScan LiDE 110, Canon, USA, Inc., Huntington, New York, USA) and leaf area was calculated using the image processing software ImageJ/FIJI (Abràmoff et al., 2004). We calculated specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) as the fresh leaf area (cm^2) divided by leaf dry mass (g; after drying at 60°C for 72 hours or until reaching a stable mass). Specific leaf area is a key functional trait associated with environmental tolerance (Poorter et al., 2009) and reflects a trade-off between rapid biomass production (high SLA) and efficient nutrient conservation (low SLA; Wright et al., 2004).

Climatic and Soil Properties

To quantify micro-climatic changes in air and soil temperature across elevation, we waterproofed ThermoChron iButtons (Maxim Integrated Products, San Jose, California, USA) in a layer of electrical tape and secured one iButton just below the canopy (1.5–2 m above the ground) and one iButton 5 cm below ground at each site. Each iButton was deployed on 21 May 2014 and retrieved on 11 July 2014. During this time, temperature was recorded hourly.

Because Santa Elena Peninsula is ancient in origin (~80 million years older than the rest of the landmass of Costa Rica) and serpentine soils are known to be nutrient poor, we suspected that soil properties may, in part, explain patterns of plant function across elevation. We collected three soil samples from 0–10 cm depth and homogenized by mixing samples within each sampling site. We stored soil samples in a cooler (in the field, packed with ice) and a refrigerator (at base camp) before transporting to a laboratory for processing within 24 hours of collection.

We measured labile or extractable nutrient concentrations on air-dried soils using the Mehlich III extraction (Mehlich, 1984) (Ca, Cu, Fe, K, Mg, Mn, Na, P, Zn; reported as mg kg^{-1}) at the Research Analytical Lab at the University of Minnesota (St. Paul, Minnesota, USA). Additionally, total carbon and nitrogen were measured on a COSTECH Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, California, USA) at the University of California Davis (Davis, California, USA). All data are reported as percentages of oven dry weight. To measure microbial nutrient demand, we quantified activities of three soil enzymes. Microbial enzyme allocation is sensitive to differences in nutrient and climate in predictable ways, making soil enzymes important functional indicators of biological diversity, ecosystem functioning, and soil fertility (Caldwell, 2005). We focused on commonly measured enzyme potentials that indicate microbial resource allocation to the acquisition of organic carbon (β -1,4-glucosidase; BG), nitrogen (β -1,4-N-acetylglucosaminidase; NAG), and phosphorous (acid or alkaline phosphatase; AP) using protocols outlined in Waring (2013).

Statistical Analyses

We first calculated abundance-weighted community mean ppSLA for each sampling site using the *FD* package in R (Laliberté et al., 2014), pooling data for both transects at each sampling site. We then used simple linear regression to determine the relationship between climate, soil nutrients and enzyme potentials, and functional

traits across elevation. When non-linearity was evident based on non-randomly distributed residuals, we included non-linear regression models and compared model fit using the bias-corrected Akaike's Information Criterion (AICc).

We hypothesized that cloud formation should cause abrupt turnover in plant community composition and trait values at the location of cloud base height. To test for a breakpoint between SLA (or air and soil temperature) and elevation, we fit piecewise regression models using an iterative search procedure. We calculated the residual mean squared error (MSE) for all plausible breakpoints, detected the estimated breakpoint as the model with the lowest residual MSE, and then calculated the slope, intercept, and significance of each segment. We used an iterative approach (as opposed to a continuous approach using maximum likelihood) to permit discontinuities between segments. In comparison, the calculation of breakpoints using a continuous approach based on maximum likelihood is based on the location (along the x-axis) that minimizes the distance between the end of the first segment and the beginning of the next, which inherently constrains the intercept of the second segment, forcing segments to be continuous (in other words, the second segment begins where the first segment ends). Instead, the iterative method used here allows segments to be discontinuous which is more biologically realistic, allowing for an abrupt functional shift at cloud base height. AICc scores for the discontinuous approach were always lower than for the continuous approach (Appendix S2).

Next, we were interested in whether abrupt turnover in plant community composition also occurred at cloud base height. To test for plant community composition turnover, we used a non-metric multidimensional scaling (NMDS) using the *metaMDS* function in the *vegan* package (Oksanen et al., 2019) with a maximum number of 100 runs and 1000 permutations for calculating the coefficient of determination (r^2) and significance (p -value). We used Bray-Curtis dissimilarities for the community-by-site matrix (Bray and Curtis, 1957), retained the best two-dimensional fits, and overlaid convex hulls connecting the vertices of the points made by communities above and below the identified breakpoints. We also fit environmental vectors onto the NMDS ordination using the *envfit* function, after eliminating highly correlated environmental variables, to detect which factors were associated with vegetation community composition. In NMDS, more similar vegetation communities (in terms of species composition) appear closer together, thus enabling comparisons of communities above and below the elevational breakpoints identified in the discontinuous regression models. Because only one individual of an herbaceous species was found at 90 m and not observed anywhere else, causing non-homogeneity and non-convergence, this site was removed from the NMDS analysis. Permutational multivariate analysis of variance (PERMANOVA) was used to test for significant differences between vegetation communities above and below the elevational breakpoints using the *adonis* function.

RESULTS

Air and soil temperature were positively correlated ($R^2 = 0.87$, $p < 0.001$); both variables were negatively correlated to elevation (Fig. 1A: $R^2 = 0.96$, $p < 0.001$; Fig. 1B: $R^2 = 0.82$, $p < 0.001$, respectively). The slope of air temperature with elevation was not different from the dry adiabatic lapse rate ($10^\circ\text{C} \cdot 1000 \text{ m}^{-1}$,

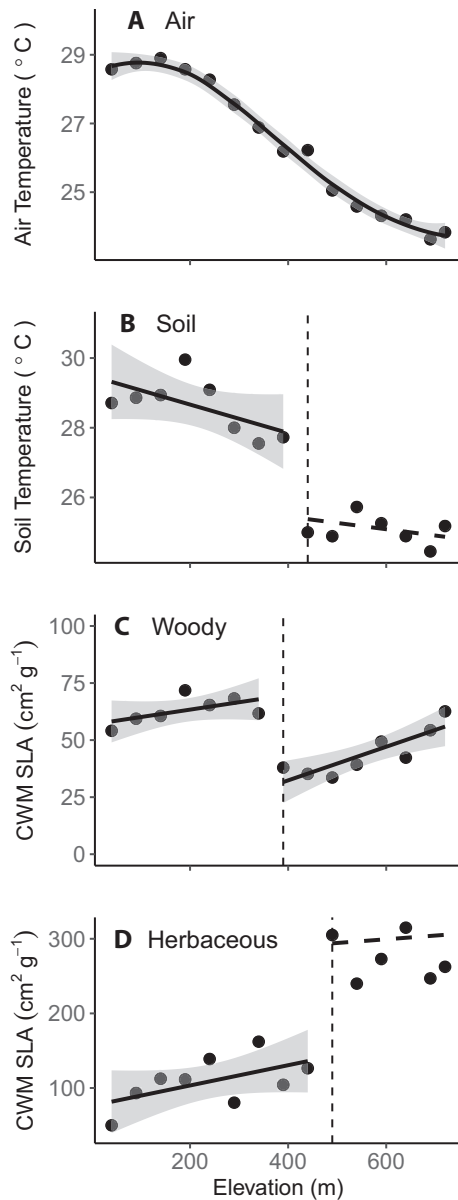


FIGURE 1. (A) Air and (B) soil temperature decreased with increasing elevation (non-linear ‘loess’ regression, $R^2 = 0.96$, $p < 0.001$; piecewise regression, $R^2 = 0.82$, $p < 0.001$, respectively). Soil temperature shifted abruptly at 440 m elevation (dashed vertical line). Community-weighted mean (CWM) specific leaf area (SLA) increased with increasing elevation for (C) woody (piecewise regression; $R^2 = 0.88$, $p < 0.001$) and (D) herbaceous (piecewise regression; $R^2 = 0.92$, $p < 0.001$) plant communities showing abrupt shifts at 390 m (dashed vertical line) for woody plant communities and 490 m (dashed vertical line) for herbaceous plant communities. Solid regression lines indicate statistical significance ($p < 0.05$); dashed regression lines indicate non-significance.

standardized major axis regression using the *smatr* package; Warton et al., 2012) while the slope of soil temperature with elevation was not different from the wet adiabatic lapse rate ($5^\circ\text{C} \cdot 1000 \text{ m}^{-1}$). A piecewise regression model improved overall fit between soil temperature and elevation ($R^2 = 0.93$, $p < 0.001$, $\text{AICc} = 32.95$) relative to a linear model ($R^2 = 0.82$, $p < 0.001$, $\text{AICc} = 41.95$). The

breakpoint that minimized the MSE between soil temperature and elevation occurred at 440 m.

Soil carbon (varying from 3.5–10.5%) and nitrogen (0.3–1%) concentrations were positively correlated to elevation ($R^2 = 0.34$, $p = 0.022$; $R^2 = 0.45$, $p = 0.007$ respectively). The C:N ratio reported here, which was not related to elevation, varied from 9 to 12 and was generally on the low end of values reported for other serpentine regions (e.g., Brooks, 1987; Roberts and Proctor, 1992). In general, soil variables were uncorrelated to elevation (or air or soil temperature) in neither linear or piecewise regressions except NAG:AP. The enzyme activity ratio NAG:AP is a measure of microbial resource allocation to the acquisition of nitrogen versus phosphorous, which increased linearly with increasing elevation (linear regression; $R^2 = 0.37$, $p = 0.02$). Piecewise regression between NAG:AP and elevation was not significant.

The range of community-weighted mean (CWM) SLA values for herbaceous plant communities was nearly seven times greater than that for the range of community-weighted mean SLA values for woody plant communities (Appendix S3). In addition, the mean CWM SLA was more than three times greater for herbaceous plant communities relative to woody plant communities (herbaceous: $175 \text{ cm}^2 \text{ g}^{-1}$, woody: $53.1 \text{ cm}^2 \text{ g}^{-1}$). Consistent with our hypothesis, there were also discontinuities in the relationship between CWM SLA and elevation for both woody (Fig. 1C: piecewise regression; $R^2 = 0.88$, $p < 0.001$) and herbaceous communities (Fig. 1D: piecewise regression; $R^2 = 0.92$, $p < 0.001$). In other words, the piecewise regression models performed better than linear regression models for both woody and herbaceous communities (Appendix S2). The breakpoint with the lowest MSE occurred at 390 m for woody plant communities and 490 m for herbaceous plant communities. For woody species, CWM SLA increased with increasing elevation above and below the 390 m breakpoint (slope below 390 m = 0.032 ± 0.002 , $p < 0.001$; slope above 390 m = 0.093 ± 0.002 , $p < 0.001$). For herbaceous species, CWM SLA increased with increasing elevation below the 490 m breakpoint (slope below 490 m = 0.14 ± 0.02 , $p = 0.058$). For herbaceous species above 490 m, CWM SLA did not change with elevation ($p = 0.345$).

In the NMDS ordination of species composition, communities above and below the elevational breakpoints for woody and herbaceous species generally occupied non-overlapping areas in ordination space (Fig. 2). For both woody and herbaceous plant communities, the stress (woody: 0.10; herbaceous: 0.14) indicated the communities were well-represented in two reduced dimensions (see Clarke and Warwick, 2001). Plant communities above and below elevational breakpoints were concentrated in positive and negative regions of axis 2, respectively. PERMANOVA indicated a significant difference between plant communities above and below the breakpoint for woody (at 390 m; $R^2 = 0.22$, $p = 0.001$) and herbaceous species (at 490 m; $R^2 = 0.24$, $p = 0.002$). The woody plant community at 340 m grouped more closely to the woody plant communities above the 390 m breakpoint. Air and soil temperature, Na, and percent nitrogen were associated with both woody and herbaceous species community composition. Soil C:N, Mg, and K were additionally associated with woody species composition (Fig. 2 and Appendix S4).

DISCUSSION

Many factors make it difficult to detect cloud formation, cloud base height and the effects of clouds on montane biota. Long-term biological and climatic data are sparse; topographical complexity leads

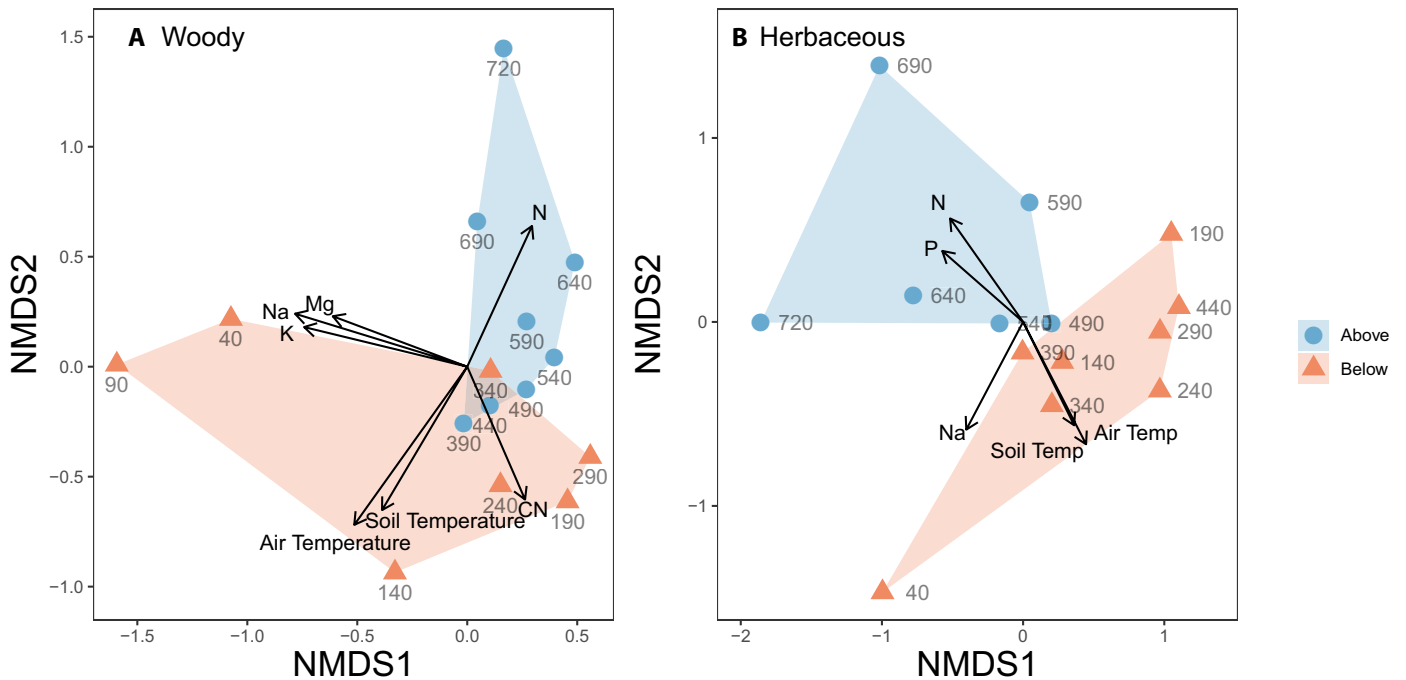


FIGURE 2. Non-metric multidimensional scaling (NMDS) ordination of (A) woody (lowest stress solution reached at two dimensions; stress = 0.10) and (B) herbaceous (lowest stress solution reached at two dimensions; stress = 0.14) plant communities above and below elevational breakpoints (390 m for woody plant communities and 490 m for herbaceous plant communities). *Envfit* vectors for environmental variables which were significantly correlated ($p < 0.5$) with the NMDS ordination are shown as arrows. The direction of arrows represents the increasing value of each variable while the length of arrows represents the strength of each correlation.

to high local variability; and ground-based or satellite data are limited. These conditions require alternative approaches for studying the effects of clouds in remote and biodiverse montane regions. In this study, we proposed a trait-based approach to detect signatures of cloud base height. We found evidence for a trait-based signature of cloud base height as detected by abrupt compositional and functional shifts in herbaceous and woody plant communities.

On large, inland mountains, persistent cloud formation typically occurs at elevations of 2000 to 3000 m, though intermittent clouds are observed as low as 1200 m (Bruijnzeel et al., 2011). On small, oceanic mountains, cloud formation may occur at even lower elevations (down to less than 500 m a.s.l.: Van Steenis, 1972). Based on the shift in soil temperature and herbaceous functional traits, we estimate cloud base height to occur between 440 and 490 m, making Santa Elena Peninsula cloud forests among the lowest lying in the world, likely due to abundant oceanic inputs to atmospheric moisture (Bruijnzeel et al., 2011).

The abrupt change in soil temperature above and below cloud line (compared to the more gradual decline in air temperature) is likely related to soil properties and increased humidity, strongly influencing the microclimate experienced by plant roots. The orographic cloud formation combined with the steep topography that

characterizes Santa Elena Peninsula, results in high light conditions below cloud line (Fig. 3). Under high light conditions below cloud line, the dark color of serpentine soil, caused by high iron content, leads to greater temperature extremes. Above cloud line, where solar radiation is reduced, the porous nature of serpentine soils and the increased humidity causes significant cooling. Soil temperature affects root and plant growth (Kaspar and Bland, 1992), influences optimal photosynthetic conditions, and determines high elevation tree-line in alpine and sub-alpine montane systems (Körner, 1998).



FIGURE 3. The most western tip of Santa Elena Peninsula, Costa Rica, looking north from Playa Respigue, demonstrating orographic cloud formation and the steep topography.

It is thus unsurprising that soil temperature seems to play an important role in the system studied here.

The elevational difference between the shift in soil temperature (at 440 m) and the shift in herbaceous community composition and functional traits (at 490 m) may reflect seasonal shifts in cloud base height between the rainy season (during which soil temperature was measured) and the dry season. During the rainy season, abundant moisture may lead to a lowering of cloud base height, followed by a rise in cloud base height during the dry season. Alternatively, the cloud base is a zone of rapid transitioning of temperature and humidity and the high turbulence and unpredictability may not support functional trait values found under more stable cloud conditions. The standard deviation of air temperature showed a peak at 440 m (not shown) partially supporting this idea. Cloud base height may also vary inter-annually as sea surface temperatures vary, such as during El Niño Southern Oscillation events. In a tropical dry forest in southern Mexico, sea surface temperatures of the North tropical Atlantic and Pacific Oceans strongly influenced climate in the region and, ultimately, tree growth (Brienen et al., 2010). The region where cloud base height is highly variable may be a strong selective filter against herbaceous species whose shallow roots and high values of specific leaf area (and relative growth rates) make them especially vulnerable to changes in soil moisture or temperature, and thus cloud line. Indeed, in a tropical understory in Panama, higher turnover in herbaceous plants (relative to woody ones) was attributed to stronger habitat filtering (Murphy et al., 2016).

Like previous studies, herbaceous species showed higher values of SLA relative to woody ones (community-weighted mean for herbaceous plants: 175 cm² g⁻¹, for woody plants: 53.1 cm² g⁻¹) (e.g., Reich et al., 1999; Wright et al., 2004; Pierce et al., 2013), at or above the global mean, reflecting an acquisitive life history strategy to capitalize on rainy season precipitation below cloud line and cloud-derived humidity above cloud line. The greater values of SLA above cloud line in herbaceous plants (which did not increase with increasing elevation) points to an interaction between solar radiation and nutrient limitation. The greater values above cloud line reflect the increased surface area necessary for photosynthesis to sustain plant growth under reduced solar input but further increases in SLA may be limited by soil nutrient availability. Indeed, patterns of soil nutrients and microbial enzyme ratios indicate that the soils of Santa Elena Peninsula are more C- and N-limited compared to other tropical soils. The positive relationship between the NAG:AP ratio and elevation suggests that soil microbial demand for N relative to P increased at higher elevation. This is consistent with temperature-induced N-limitation of plant and microbial growth with increasing elevation in tropical forests (Marrs et al., 1988; Vitousek and Matson, 1988; Tanner et al., 1998; Houlton et al., 2007).

The extremely low values of SLA of woody plants below cloud line (among the lowest values reported globally in Kattge et al., 2011) characterize drought-induced sclerophylly (Reich et al., 1999; Wright et al., 2002) typical of serpentine flora (Brady et al., 2005). Low SLA values have been interpreted as a means of nutrient retention or a response to pulsing of resources and protection from desiccation (Mooney et al., 1970). In contrast to the well-known elevational reduction of SLA (e.g., Hulshof et al., 2013), we showed an increase in SLA with elevation. The atypical increase in SLA with elevation shown here likely reflects the role of increasing water availability at higher elevations, suggesting that the slope of the relationship between SLA and elevation may be dependent on water

availability (Reich et al., 1999). Yet, SLA values of woody species at higher elevations remain on the low end of global values, possibly reflecting nutrient-induced sclerophylly, in line with nutrient deficiencies found at higher elevations (Vitousek and Matson, 1988). In short, woody plant communities below cloud line were characterized by drought-induced sclerophylly, whereas plant communities above cloud base height reflected decreasing nutrient availability with increasing elevation and nutrient-induced sclerophylly.

Few studies have documented cloud base height. Cloud base height was related to El Niño events in the tropical Andes (Diaz and Graham, 1996), to sea surface temperature and trade winds in Puerto Rico (Scatena, 1998; Miller et al., 2018), and to lowland land-use in Costa Rica (Lawton et al., 2001). These studies emphasized changes in cloud base height directly through ground-based observations or satellite data. Other studies have indirectly inferred changes in cloud base height by documenting the upslope migration of species (e.g., Grabherr, 1994; Pounds et al., 1999; McCain and Colwell, 2011; Feeley et al., 2011) or drought-induced mortality (Karpa and Vitousek, 1994; Lohse et al., 1995). These studies emphasize that cloud base height is dynamic in both space and time. In our study, the differing elevation where abrupt functional turnover occurred in herbaceous relative to woody plants (a difference of 100 m in elevation) may rather reflect a recent rise in cloud base height coupled with a lag time in the response of woody plant species, undoubtedly a result of their extremely slow growth rates (as reflected by their extremely low values of SLA).

Under this alternative explanation, herbaceous species may arguably better track rapidly changing environmental conditions relative to woody species whose slower demographic rates create lag times and a potential mismatch between trait values and the environment. Other lifeforms, such as epiphytes, are exceptionally climate-sensitive and likely even more dependent on cloud immersion than herbaceous species (Benzing, 1998). Based on initial observations, we hypothesize that epiphytes in this system are absent from the region where cloud base height is dynamic and restricted to regions with more stable and constant cloud immersion. As a result, a shift in epiphyte abundance is likely to occur at higher elevations compared to herbaceous species. The ability of herbaceous species to more closely track cloud base height than woody species may be facilitated by smaller, wind-dispersed seeds (Grime, 1977) that disperse farther (Thomson et al., 2011). Indeed, life history traits have been shown to affect species' abilities to track climate change (Dullinger et al., 2004; Lenoir et al., 2008; Nathan et al., 2011). Species with high fecundity, short generation times, and good dispersal abilities track rapid climate change better than species lacking these traits (Phillips et al., 2010). Thus, significant lags between biotic responses and contemporary climate change (i.e., Bertrand et al., 2011) create a signature of past climate. Based on this interpretation, the elevation where abrupt compositional and functional change occurred in woody plants may reflect past cloud base height whereas the elevation where abrupt compositional and functional change occurred in herbaceous plants may reflect present-day cloud base height, a difference of 100 m in elevation. That the woody plant community at 340 m grouped more closely to the woody plant communities above the 390 m breakpoint in NMDS space lends some evidence to the idea that cloud base height was once lower. The use of dendrochronology could help distinguish between these two possible drivers of abrupt compositional and functional turnover. Although most tropical trees lack annual rings (Anchukaitis et al., 2008), the high precipitation seasonality of the region makes annual tree growth likely, as found in other seasonal dry forests (Brienen et al., 2010).

Central America is a major emerging hot spot of climate change (Giorgi, 2006). Within Costa Rica, increases in temperature and decreases in precipitation are already occurring (Karmalkar et al., 2008). Drying trends appear in the meteorological record and have been attributed to the increase in the intensity of El Niño Southern Oscillation events, a warm Pacific Decadal Oscillation regime, and increases in atmospheric temperature throughout the tropics (Enquist and Enquist, 2011). Climate change effects will be more pronounced at high elevations on the Pacific side (Karmalkar et al., 2008). A primary consequence of climate change in tropical cloud forests is the potential for a decrease in cloud cover due to either an increase in the number of cloud-free days (Pounds et al., 1999) or from an increase in the height of cloud formation (Still et al., 1999). Lowland land-use change and deforestation negatively affect cloud formation (Lawton et al., 2001). However, this is unlikely to cause rising cloud base height in Santa Elena Peninsula. Up-wind regions are protected within the boundaries of Area de Conservación Guanacaste and water vapor is primarily derived from the Pacific Ocean. It is more likely that sea surface temperatures drive cloud base height in this system.

CONCLUSIONS

Together our results point to the dominant effect of cloud formation and climate-soil interactions for the flora of Santa Elena Peninsula. Santa Elena Peninsula harbors a rare type of vegetation that requires specialized conditions. It may be impossible for seeds of these species to disperse to other suitable habitats given that the nearest serpentine outcrops are located in Nicaragua (consisting of small and patchy outcrops at low elevations) and Colombia (separated by major mountain chains). It is conceivable that if cloud formation disappears, the cloud forests of Santa Elena Peninsula may also disappear. Given enough time, low elevation woody species may disperse upward, eventually replacing cloud forest trees. Here we show taxonomic and trait-based signatures of cloud base height can be useful approximations when it is not possible to measure cloud base height directly. In remote areas lacking baseline information, such data are critical for establishing current conditions and monitoring future changes.

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AUTHOR CONTRIBUTIONS

C.M.H. conceived the idea and designed the methodology. All authors collected the data. C.M.H. analyzed the data and led the

writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Species accumulation curves for exact, random, and rarefaction methods.

APPENDIX S2. Performance of linear, continuous (maximum likelihood approach) and discontinuous (iterative approach) piecewise regression models for woody and herbaceous community-weighted mean specific leaf area (SLA) and soil temperature against elevation.

APPENDIX S3. A boxplot depicting community-weighted mean specific leaf area (CWM SLA $\text{cm}^2 \text{g}^{-1}$) of herbaceous and woody plant communities across all sampling sites.

APPENDIX S4. Permutational multivariate analysis of variance (PERMANOVA) using distance matrices from non-metric multidimensional scaling analysis for woody and herbaceous plant communities.

APPENDIX S5. Climatic, edaphic, and functional trait data.

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