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Mesoclimatic patterns shape the striking vegetation mosaic in the Cordillera Central, Dominican Republic

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Abstract

A relationship between forest vegetation patterns and climate has been proposed for Caribbean mountains, but mesoscale temperature, precipitation (PPT), humidity, and cloud formation patterns are poorly documented. Half-hourly temperature and humidity observations were obtained from 2001 to 2011 from a network of 10 data-logging instruments ranging in elevation from 1500 to 2800 m on the windward slopes of the Cordillera Central, Dominican Republic. We report diurnal, seasonal, and annual patterns in temperature, PPT, humidity, and the trade wind inversion (TWI) along the elevation gradient. The elevational gradient in mean air temperature was non-linear during the dry season, with lapse rates decreasing to –0.5 °C km^{-1} between 1500 and 1900 m and –0.8 °C km^{-1} between 2100 and 2400 m. Relative humidity reached a maximum at 2100 m (mean of 91%), but remains above 85% over the entire gradient until 2600 m, above which it drops steeply. Relative humidity also showed marked seasonality but only at the highest elevations, dropping markedly above 2400 m and especially above 2600 m in the dry season, while remaining high at lower elevations throughout the year. PPT declined only slightly with elevation on windward slopes, but was markedly lower in leeward areas. Dry season PPT was lower on windward and leeward slopes at all elevations, except at ~2400 m on windward slopes where it remained nearly as high as the rest of the year. Sub-zero temperatures occurred at elevations ≥2325 m and increased markedly in frequency ≥2600 m. These observations support the hypothesis that the discrete vegetation ecotone between the cloud forest and subalpine pine forest at ~2200 m on windward slopes results from climatic discontinuities, especially during the dry season. In particular, the TWI effect on mesoclimatic patterns (especially moisture) regulates the elevational maximum of cloud forest flora and likely will represent a strong barrier to the future migration of cloud forest flora to higher elevations in response to warmer temperatures. Together with increased moisture stress due to higher temperatures, climate change in the high elevations of tropical mountains is therefore likely to disrupt the dynamics and distributions of tropical montane forests.

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Introduction

Climatic patterns on tropical mountains result in distinctive vegetation mosaics. On taller tropical mountain ranges, temperatures change from hot-tropical to temperate to frigid over comparatively short distances. Because climate is also largely aseasonal in these settings, discrete thermal zones with well-delineated vegetation boundaries can develop along the mountain side (Janzen, 1967). In particular, the frost line on tropical mountains is generally consistent in elevation, and in many regions orographic cloud formation also occurs in a discrete zone as rising humid air is cooled to the dew point at consistent elevations. Cloud formation and moisture patterns in many tropical and subtropical mountains are further delineated and stratified by a synoptic subsidence inversion—the trade wind inversion (TWI)—that traps moist air and clouds below a consistent elevation on windward slopes (Fig. 1; Riehl, 1979; Giambelluca and Nullet, 1991; Schubert et al., 1995), leading to a spatial discontinuity in humidity and precipitation patterns.

The wide range of climatic conditions encountered on tropical mountains makes climate the prevailing determinant of ecological patterns, especially in vegetation (Bruijnzeel, 2001). The transition from lowland tropical forest to lower montane forest typically coincides with the elevation at which the annual average minimum temperature drops below 18 °C (Kitayama, 1992). The lower montane forest transitions to upper montane forest at higher elevations where clouds form frequently. Here, forest structure becomes short-statured and epiphytic bryophytes grow abundantly (Frahm and Gradstein, 1991). The elevation of this "cloud forest" zone varies, as a result of geographic factors that influence cloud formation, such as the "Massenerhebung effect" where orographic clouds develop at lower elevations on smaller mountains than larger mountains. On the highest mountains, the upper montane forest gives way to frost-tolerant subalpine forests typically at elevations where the average maximum temperature falls below 10 °C (Bruijnzeel, 2001).

Many studies of tropical montane forests (TMFs) have concluded that forest composition and structure exhibit discrete elevational zonation, reflecting climatic influences (Richards, 1952, 1996; Holdridge, 1967; Grubb and Whitmore, 1966; Grubb, 1974; Woldu et al., 1989; Kitayama, 1992; Kitayama and Mueller-Dombois, 1994; Fernández-Palacios and de Nicolás, 1995; Kitayama, 1995; Ashton, 2003; Hemp, 2006). Other studies, however, maintain that species distributions on tropical mountains change continuously and individualistically along the elevation gradient (Hartshorn and Peralta, 1988; Burger, 1995; Lieberman et al., 1996; Lovett, 1998; Vázquez and Givnish, 1998). The reason for such divergent conclusions about the nature of vegetation distributions on tropical mountains remains

FIGURE 1. (a) Afternoon clouds capped by the trade wind inversion on the windward slopes of the Cordillera Central, Dominican Republic. The base of the inversion blocks cloud formation below a roughly constant elevation. The forest in the foreground is comprised entirely of a single species, the endemic *Pinus occidentalis* Swartz. The photo was taken above the inversion at ~2600 m elevation in January 2007. (b) A HOBO unit in the field at 2765 m elevation, showing the configuration and the radiation shield used throughout the study.

unclear—to some extent, it may reflect differences in methods and analysis (e.g., sampling intensity, community classification). However, geographic variation in climate on individual mountain ranges—due to differences in climate drivers like latitude, proximity to oceans, and topography—may cause divergent patterns in vegetation distribution, along with other site differences such as geology, disturbance history (Martin et al., 2007; Martin et al., 2011), and the biogeography of the available flora.

An exceptional example of tropical montane forest patterns exists on the windward slopes of the Cordillera Central on Hispaniola. Here, on the tallest mountain range in the Caribbean, the forest exhibits a discrete discontinuity along the elevation gradient (Sherman et al., 2005; Martin et al., 2007, 2011): the transition from upper montane cloud forest to subalpine pine forest is remarkably abrupt and occurs at a remarkably consistent elevation (~2200 m) across the windward slopes of the entire region. We reasoned that such a large-scale pattern must result from climatic influences and that these influences must be exceptionally strong and discontinuous, possibly connected with the average elevation of the TWI (Martin and Fahey, 2006; Martin et al., 2007; Sherman et al., 2008). The subalpine pine forest is frequently disturbed by natural fires that are typically ignited by lightning strikes in drier, high elevation areas during the late-winter dry season (Martin and Fahey, 2006). These fires burn down through the fire-tolerant pine forest, but are routinely extinguished at the cloud forest boundary, probably because of the low flammability of the vegetation and high humidity in the cloud zone (Martin and Fahey, 2006; Sherman et al., 2008). An additional climatic influence is the frequent occurrence of ground frost at higher elevations, possibly restricting many of the frost-sensitive tropical taxa from colonizing upper slopes. Thus, strong climatic drivers including a vegetation feedback (flammability) were hypothesized to shape this discrete ecotone. In contrast, the transition from the lower montane forest zone to upper montane cloud forest is continuous in this area, despite preliminary observations of a climatic discontinuity associated with the average elevation of the cloud base (Martin et al., 2007). Perhaps patterns in cloud base formation are insufficiently consistent or the vegetation feedback too weak to result in a vegetation discontinuity in this part of the landscape.

In a previous vegetation study, we presented short-term evidence from a few climate stations in the Cordillera Central that suggested that climate is the principal determinant of the region's distinctive vegetation patterns (Martin et al., 2007); however, long-term and fine-scale climate observations are needed to improve understanding of climate-vegetation interactions in these ecosystems. In this study, we present 10 years of fine-scale climate data to address this gap. Using this long and robust climate record, we sought better evidence for spatial patterns and discontinuities in climate across the elevation gradient associated with vegetation patterns. In particular, we sought further evidence of climatic discontinuities at the cloud forest–pine ecotone, perhaps associated with the influence of the TWI (e.g., via a sharp drop in relative humidity). Moreover, we hypothesized that climatic discontinuities would be most pronounced during the winter dry season, which in turn determines the spatial patterns of fire frequency in this landscape. We also sought more extensive evidence of the frequency of ground frosts that might limit the upward extent of cloud forest species. Given the importance of climate influences on TMFs and the likely disruption of these dynamics with climate change, a better understanding of climate-vegetation patterns in TMFs is needed.

Methods

THE CORDILLERA CENTRAL, HISPANIOLA

The Cordillera Central is the largest mountain range in Hispaniola, with several peaks over 3000 m including the highest peak in the Caribbean Basin (Pico Duarte, 3087 m), and is home to one of the Caribbean's largest protected areas (Fig. 2). Although lower elevation portions of this range were logged and converted to agriculture, a core area of over 1500 km^2 was protected in two national parks (Parques Armando Bermúdez and José del Carmen Ramírez) in the late 1950s before any major logging or farming incursions (Hoppe, 1989). Our study area encompassed approximately 65 km^2 of virgin forest within the two parks, ranging in elevation from 1100 to over 3000 m, and spanning the windward (northeastern) and leeward (southwestern) slopes of the central massif. The NW-SE orientation of the Cordillera Central is generally perpendicular to the direction of the incoming northeasterly trade winds and creates a rain shadow on the lee of the mountains (Martin and Fahey, 2006).

Climatic patterns in the Caribbean are typical of the northern tropics and subtropics, with weak seasonality in temperature, strong seasonality in moisture, and the prevailing influence of trade winds. The trade winds occur for most of the year, but weaken with Intertropical Convergence Zone (ITCZ) proximity in summer (Horst, 1992). The TWI also occurs regularly in the region, and the

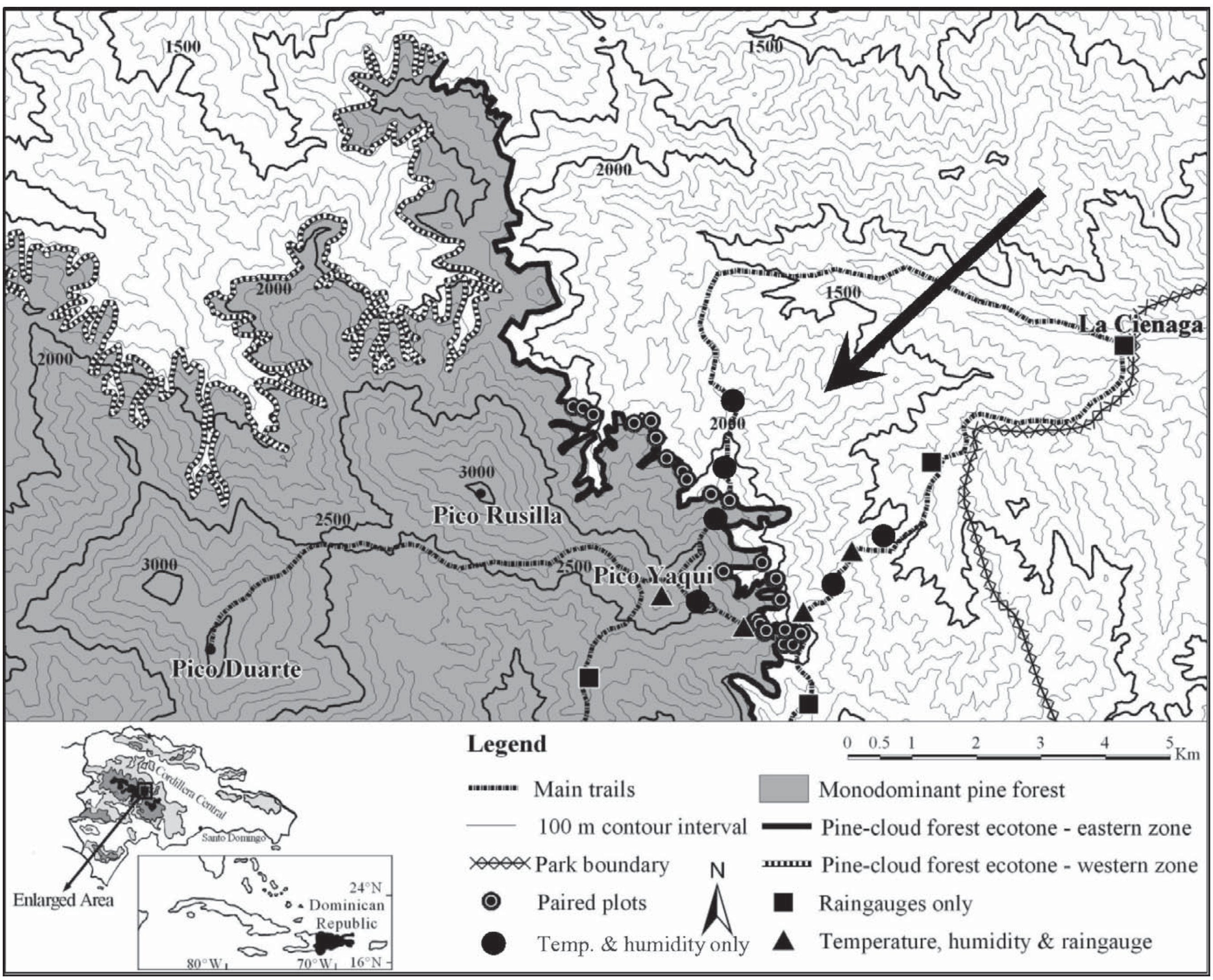

FIGURE 2. Map of the study area, weather station locations, the pine-cloud forest ecotone, and extent of monodominant pine forest in the Cordillera Central, Dominican Republic. The direction of the prevailing trade winds is shown with the black arrow. Monodominant pine forest extend was delineated with a photomosaic constructed from georeferenced aerial photographs taken in 1999 (Martin et al., 2007).

Cordillera Central rises well above its base, which is frequently observed at around 2200 m in the Caribbean (Schubert et al., 1995). In the Cordillera Central, climate patterns are poorly documented, but there is evidence of a dry season in December–March when precipitation drops to 80 mm month^{-1} on the windward slopes and 30 mm month^{-1} on leeward slopes (Martin and Fahey, 2006). The site also experiences a second, weaker dry season in July associated with a midsummer drought that occurs across much of the Caribbean and Central America (Small et al., 2007). Precipitation patterns also are influenced by the El Niño–Southern Oscillation (ENSO), as dry season precipitation throughout the Cordillera Central is 30%–50% lower during El Niño years (Martin and Fahey, 2006). Periods of colder weather also occur in this dry period, and the elevations above 2000 m are reported to experience freezing temperatures (Pedersen, 1953; Hudson, 1991), especially under clear skies in winter.

TEMPERATURE, HUMIDITY, AND PRECIPITATION

We measured air temperature and humidity at 1 m above the ground at 30-min intervals using HOBO H8 Pro RH/Temperature sensor data-logging instruments (Onset Computer Corp., Massachusetts, U.S.A.). Four HOBO units were placed in the field in June 2001 at 1515-m, 1880-m, 2400-m, and 2765-m elevation. Six additional units were added in January 2007: three were added at 1685 m, 2135 m, and 2590 m to the transect with the original four units, and three units were placed as replicates on a second transect at 1900 m, 2145 m, and 2325 m (Fig. 2). This network was maintained through May 2011. HOBO units were positioned in openings in the forest approximately ≥25 m in radius and mounted in a protective case designed to minimize heating from direct sunlight and to keep rain and debris from falling on the unit (Fig. 1, part b). These cases were small plastic boxes about 12.5-cm deep with a white plastic shield attached on top and with 1.25-cm holes regularly spaced in the sides to promote air flow. The unit was attached into the box just inside the lower edge of the case to minimize any heat loading. HOBO units have an accuracy of ±0.35 °C for temperature and ±3% for relative humidity (Onset Computer Corp., Massachusetts, U.S.A.). Precipitation was measured from February 1999 to October 2001 at six locations on windward slopes using recording rain gauges (Rainew Tipping Bucket Rain Gauge, RainWise Inc., Maine, U.S.A.) positioned in openings ≥30 m in radius. This climate transect spanned elevations from 1500 m to 2800 m over a projected distance of 4 m.

We checked our HOBO units at least twice a year for accuracy (by comparing a unit's real-time readings with readings from a thermometer, a sling psychrometer, and a new HOBO unit brought into the field) and function, and they were replaced as needed. Only one unit had to be replaced due to inaccurate function, while another three were replaced due to the complete failure of the unit. Even if functioning well, all units were replaced at least every 3 years to minimize the possibility of sensor drift and the risk of unit failure. Data were also checked for errors by visually examining the time series—values showing drift, systematic error, and/or instrument failure were removed. We found no problems with the temperature data, and the mean annual patterns of relative humidity data showed only a slight upward drift of +1% yr^{-1}. Despite these efforts, there were likely small sources of error in the data due to anomalies created by the heat shield and site-specific influences such as short-lived effects of differential heating between those stations exposed to direct sunshine versus those stations shaded by cloud cover.

FROST

To estimate the occurrence of ground frost, we used daily instrumental minimum air temperatures of <0, <1, and <2 °C (recorded 1 m above the ground) as indicators of ground frost. This temperature differential is based on field observations of air temperature and ground frost calibrated at a subtropical site (Hawaii) with a similar elevation gradient and the same latitude as our study area (Noguchi et al., 1987). Temperature studies on other tropical mountains indicate that this method provides a conservative estimate of ground frost occurrence (Sarmiento, 1986). Using min-max thermometers, we also recorded minimum and maximum temperatures for 48- to 72-hr periods on the surface of the ground below several climate stations to compare with data logger temperatures over the same periods (n = 15 comparisons).

FOREST ZONATION PATTERNS

Comparisons of climate and forest elevational patterns were made between the climate patterns in this study and previously published work on patterns in vegetation zonation along the elevation gradient. These prior studies detected discrete ecotones in forest composition on windward slopes at around 2200 m and 2500 m (Martin et al., 2007). In particular, Martin et al. (2007) used a Shipley and Keddy (1987) analysis to evaluate a suite of 245 vegetation plots distributed across the full elevational range of the study area, finding significantly higher rates of woody species turnover at these elevations. Martin et al. (2007) and Sherman et al. (2005) provide detailed descriptions of statistical analyses and the sampling design for the vegetation plots.

Results

ELEVATIONAL CLIMATE PATTERNS

The temperature profile on the windward slopes of the Cordillera Central follows a classic tropical montane pattern. Figure 3 shows mean annual and seasonal patterns in temperature, precipitation, relative humidity, and an index of cloud occurrence by elevation. We did not detect any temporal trends (e.g., warming) in mean monthly or mean annual temperatures for all temperatures or only nighttime temperatures over the period of measurement. For a given elevation, intra-annual variation in average monthly temperatures ranged from a low of 3.5 °C to a high of 6 °C over the entire transect (Fig. 4). Ranges in mean annual monthly nighttime temperatures were smaller, from 3.1 °C to 4.3 °C. Mean annual temperatures show an overall decline with elevation at an average rate of –5.4 °C km^{-1} from 1500 m to the top of the main windward ridge at ~2800 m. This lapse rate, however, showed marked seasonality (Fig. 3): the rate in July averaged –6.5 °C km^{-1} and was steady over the entire elevational transect; January temperatures declined more gradually overall at –4.1 °C km^{-1} and portions of the transect had much lower lapse rates. In particular, January lapse rates decreased to –0.5 °C km^{-1} between 1500 and 1900 m and –0.8 °C km^{-1} between 2100 and 2400 m. Above 2400 m, lapse rates increased to a range of –4.0 °C km^{-1} (in January) to –6.1 °C km^{-1} (in July). There was no seasonal variation in lapse rates at elevations from 100 to 1164 m based on data from the World Meteorological Organization (http://www.climate-charts.com).

INVERSIONS AND TEMPERATURE—HUMIDITY PROFILES

Figures 5 and 6 show a typical daily profile where two inversion layers develop during the day: at 1 p.m. a high-elevation

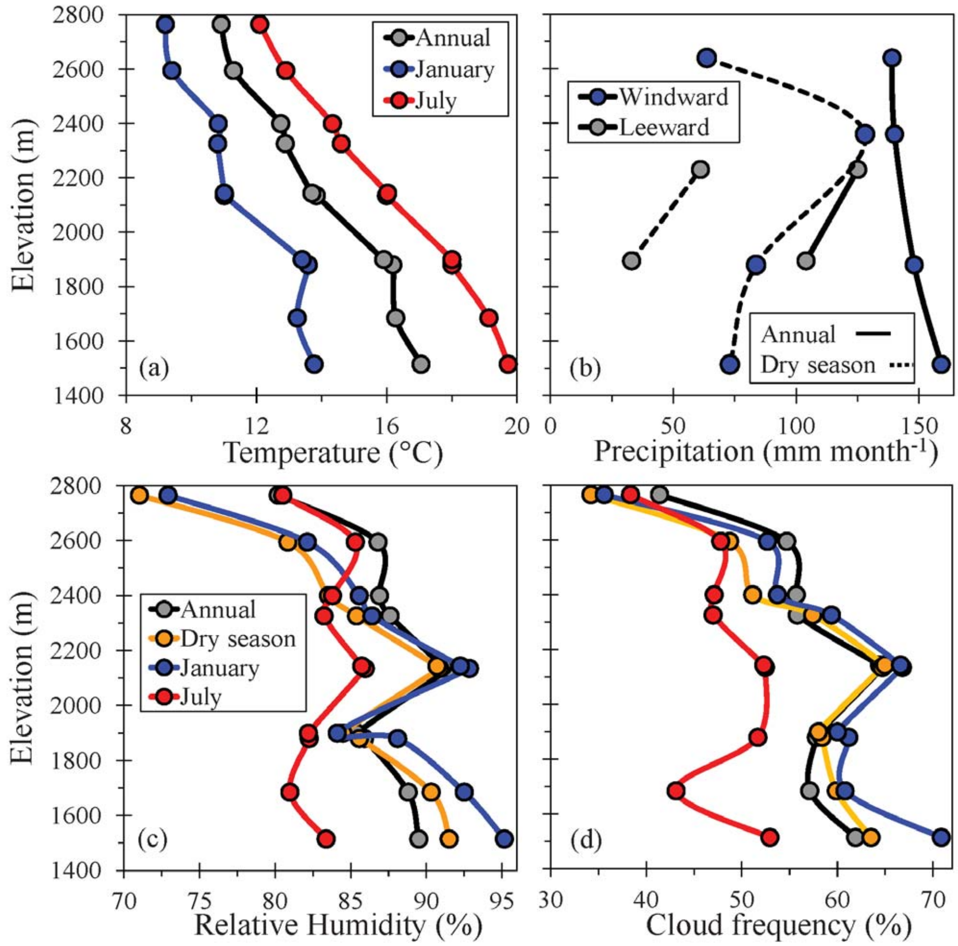

FIGURE 3. Climate patterns by elevation in the Cordillera Central, Dominican Republic. All data are windward locations except where noted. (a) Mean temperature: annual, January (coldest) and July (hottest) temperatures; (b) annual patterns in mean monthly precipitation and mean monthly precipitation in the dry season (January–March) at windward and leeward locations; (c) mean relative humidity: annual, January, July, and dry season (January–March); (d) Frequency of cloud occurrence (determined by the frequency of relative humidities ≥ 95%) annually, in January, July, and the dry season (January–March).

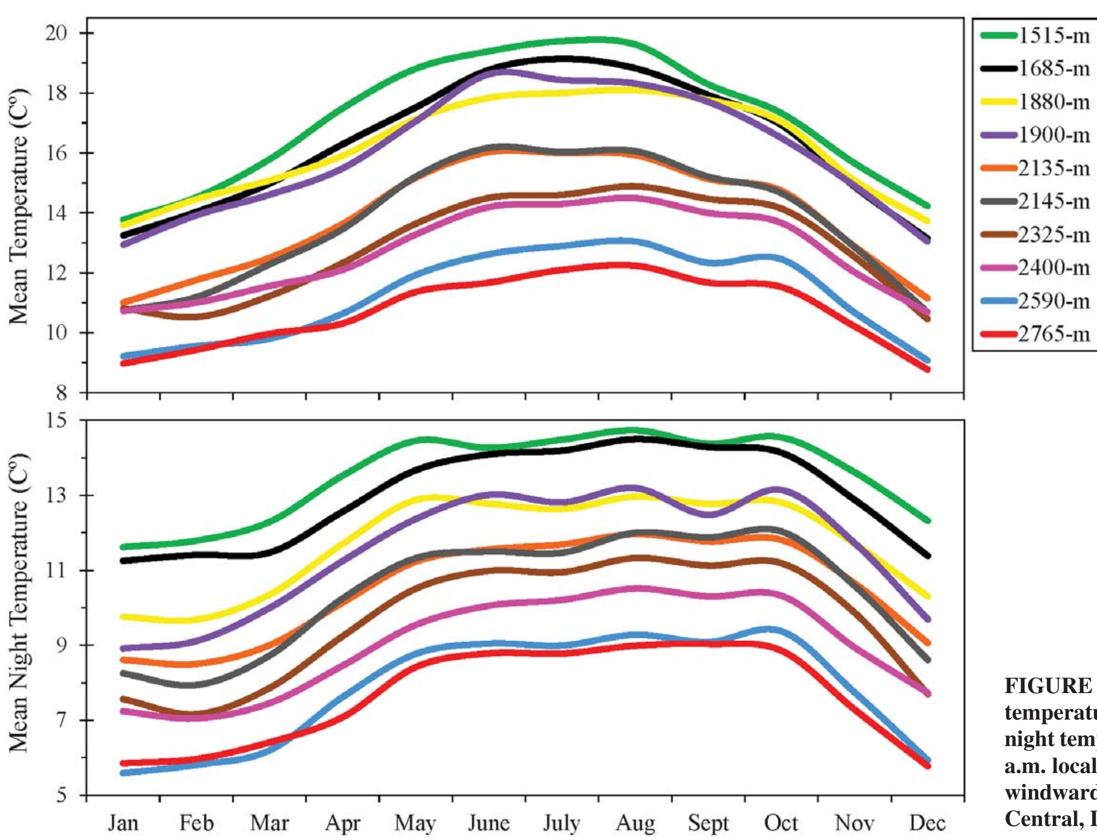

FIGURE 4. Mean monthly temperature and mean monthly night temperature (from 7 p.m. to 7 a.m. local time) by elevation on the windward slopes of the Cordillera Central, Dominican Republic.

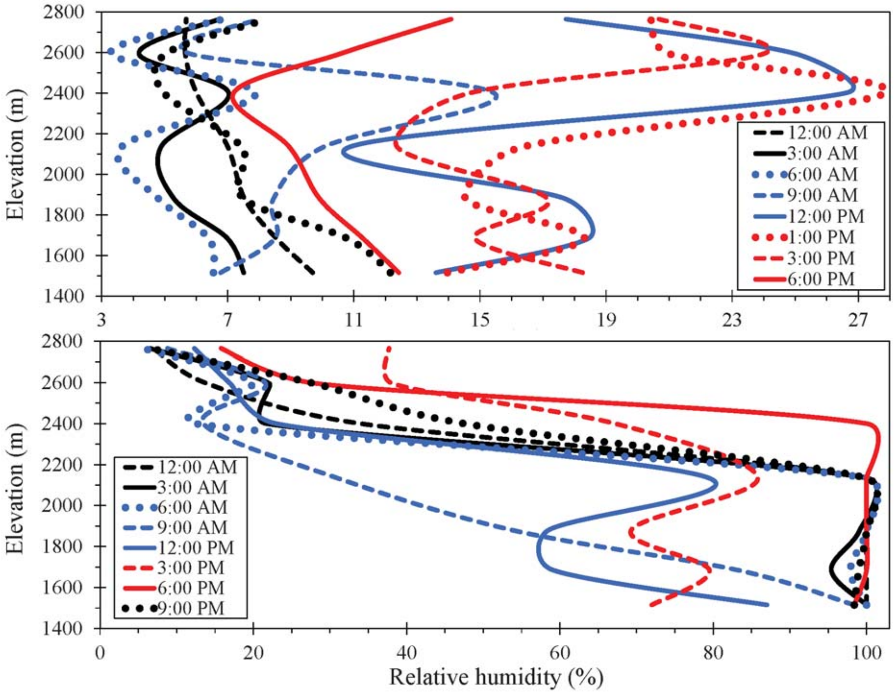

FIGURE 5. Daily development of temperature and humidity profiles by elevation on the windward slopes of the Cordillera Central, Dominican Republic. A single day is shown (15 January 2008) when the trade wind inversion (TWI) was present. Blue lines are the morning hours, red lines are afternoon hours, and black lines are nighttime hours. Two inversions develop during the day, one set by ambient TWI conditions and the other by diurnal surface heating and convection. Nighttime hours isolate the influence of the TWI most clearly at 2400–2500 m, as daytime influences are not present.

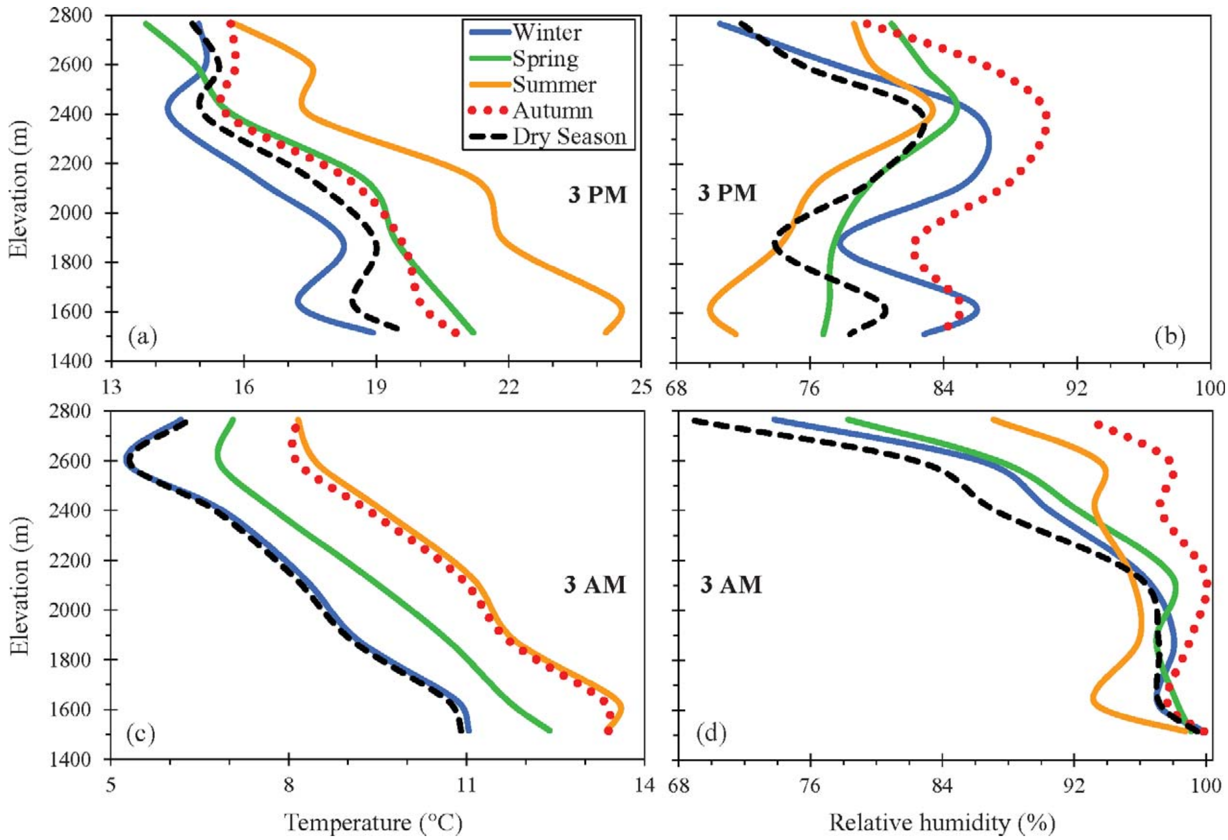

FIGURE 6. Seasonal patterns by elevation in (a) mean daily temperature at 3 p.m. local time, (b) mean daily relative humidity at 3 p.m., (c) mean daily temperature at 3 a.m., and (d) mean daily relative humidity at 3 a.m. Seasons were as follows: *Winter*: December–February; *Spring*: March–May; *Summer*: June–August; *Autumn*: September–November; *Dry Season*: January–March.

inversion peaked in strength at ~2400 m, and a second, weaker inversion developed at ~1700 m. This lower inversion dissipated after sunset, indicating it is probably the product of diurnal processes (e.g., surface heating and convection) rather than broader ambient conditions. Diurnal processes also pushed high levels of humidity to upper elevations during the day, with humidities of 100% reaching nearly 2500 m by 6 p.m. as surface heating and convection vent moisture upwards; these processes dissipated at night, causing the zone of high humidity to drop to 2200 m by 3 a.m. (Fig. 5). Figure 5 shows a single day, but there was marked diurnal and seasonal variation in inversion patterns (in strength and elevation), and the inversion failed to develop under certain weather conditions (e.g., during heavy precipitation events). Mean seasonal patterns incorporate this variability (Fig. 6), showing the strength of the inversion was weaker on average while demonstrating the diurnal influences on the temperature and humidity profiles. Mean patterns in temperature at 3 a.m. suggest that the inversion developed at 2600 m under ambient nighttime conditions throughout the year and that the main seasonal influence was on the average strength of inversion. Figure 5 has the inversion occurring around 2400 m at 3 a.m. The striking effects of the inversion on the vertical pattern in humidity is best seen in Figure 5, where relative humidity dropped from ~100% to ~20% at 3 a.m. over just a few hundred meters of elevation (between 2200 m and 2400 m). Nighttime patterns in mean relative humidity also strongly indicate that the base of the inversion was around 2600 m, as relative humidity dropped discontinuously above this elevation throughout the year (Fig. 6, part d). In the dry season, winter and spring, nighttime relative humidity also consistently declined above 2150 m, but not as sharply as above 2600 m, while in summer and fall relative humidity only showed a consistent decline above 2600 m.

PRECIPITATION

There were weak elevational patterns in mean annual precipitation (PPT), with a peak in mean rainfall of 1900 mm at 1520 m and small declines with increasing elevation on windward slopes (Fig. 3, part b). Rain shadow effects were pronounced, with nearby leeward slopes having up to one-third lower annual PPT than windward slopes. Mean monthly dry season PPT showed large declines on windward and leeward slopes at most elevations, dropping to a low of 64 mm in windward locations and as little as 33 mm in leeward ones. One exception occurred at 2360 m on windward slopes, where PPT remained nearly as high during the dry season as the rest of the year.

RELATIVE HUMIDITY

Mean annual relative humidity (RH) was fairly high over the transect, ranging from 89.5% at 1515 m to 80.2% at 2765 m with a peak of 91.5% at 2135 m. There were strong seasonal patterns in monthly mean relative humidities (Figs. 3, part c, and 7), with all elevations experiencing a peak in RH in November (except the highest station, which had an October maximum) when conditions are both cool and rainy. In general, the seasonal patterns in RH followed the region's bimodal pattern in PPT with peaks in May and October. In addition, there were strong elevation dissimilarities in RH seasonality—the higher elevations of the transect (2350–2800 m) had the lowest humidity during the January–March dry season, while all lower elevations had high RH during the dry season. Thus, the decline in RH at elevations above 2150 m was steeper during the dry season than the annual average reported previously by Martin et al. (2007); that is, from December to March the elevational difference in mean monthly RH was far more pronounced than during the rest of the year, averaging 19.7% lower at the highest elevations. In contrast, during the wetter months of May through October, this difference was only 6.9% (Fig. 7). The marked discontinuity in mean monthly dry season RH occurred between 2145 m, where RH remained high in the dry season, and 2325 m where RH dropped markedly during the dry season. Some of this seasonal effect in RH at high elevations may be attributable to greater solar loading during the dry season on the instruments located above the TWI.

An index of cloud occurrence (RH ≥ 95%) suggests that cloudy conditions developed regularly between 1500 and 2300 m during the dry season, ranging in daily frequency from a low of 58% to a high of 65% at 2150 m (Fig. 3, part d; Appendix Fig. A1). However, dry season cloud frequency dropped sharply above 2300 m, falling to 50% by 2400 m and to a low of 34% between 2600 and 2800 m. Elevational patterns of cloud occurrence were much weaker, being fairly uniform from 1500–2600 m.

FREEZING TEMPERATURES AND GROUND FROSTS

Marked elevational patterns in the frequency of freezing temperatures and the likely incidence of frost were observed (Fig. 8). At our high-elevation campsite (2650 m), we witnessed ground

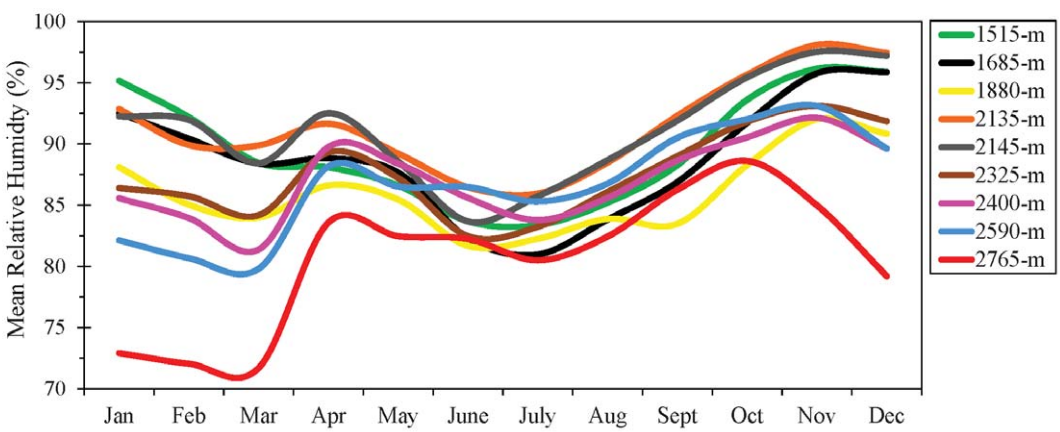

FIGURE 7. Seasonal patterns in mean monthly relative humidity by elevation on the windward slopes of the Cordillera Central, Dominican Republic.

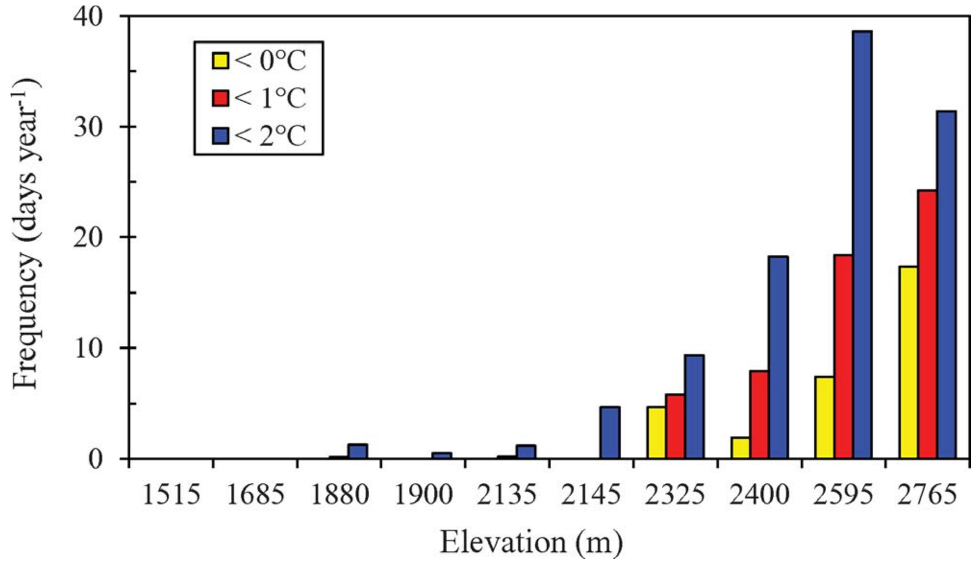

FIGURE 8. Annual frequency of freezing and near-freezing air temperatures by elevation on the windward slopes of the Cordillera Central, Dominican Republic. Temperatures were measured every 30 min at 1 m above the ground. Frequencies of measurements below a threshold (e.g., <2 °C) include all temperatures recorded below that threshold, and so are inclusive of the lower thresholds. A day was only counted once even if it experienced temperatures below a given threshold repeatedly throughout that day.

frost on many mornings during January and February, usually after cloudless nights. Air temperatures of <0 °C (measured at 1 m above the ground) were recorded as low as 2325 m, and the frequency of freezing temperatures increased with elevation, occurring on average 17 days $year^{-1}$ at 2800 m. Data recorded on the ground with min-max thermometers suggested that minimum temperatures were consistently 4.5 °C lower on the ground compared to temperatures taken at 1 m above the ground. Hence, using <2 °C as an index, freezing temperatures occurred up to 5 days a year at ≥2145 m.

Discussion

This paper details patterns in temperature, precipitation, and humidity on the windward slopes of the Cordillera Central, Dominican Republic. Previously, the climate in this region was poorly described, with only one short-term study (Martin et al., 2007). Our longer-term data set shows that linear models of climate patterns based on elevation alone would be unsuitable for characterizing this system, mainly because the rates of change in temperature and moisture are punctuated with marked discontinuities in the vicinity of the TWI at high elevations.

HUMIDITY, CLOUDS, AND THE TRADE WIND INVERSION

During the dry season, zones of high humidity with condensing conditions and cloud formation occur on the mountainside, evident in the vertical profile. Depending on the time of day, these zones are most likely due to the effects of the TWI, condensing conditions, and diurnal influences. Based on temperature, humidity, and cloud data together (Fig. 3; Appendix Fig. A1), it appears that the lower zone (1500 to 1900 m) is a high humidity area but not as frequently cloudy, while the higher zone (2100 to 2400 m) is the main cloud zone particularly during the dry season.

The principal seasonal pattern in relative humidity is pronounced dryness at high elevations during the winter dry season. The data indicate that clouds (i.e., RH ≥ 95%) are consistently capped between 2400 and 2600 m elevation, dropping sharply in frequency during the dry season from a mean occurrence of 68% at 2100 m to 51% at 2400 m and to 35% at 2765 m. These sharp drops over short distances from high to low humidity create a well-defined discontinuity in cloud occurrence especially evident during the dry season. In the warmer summer months, the pronounced differences in humidity on the elevation gradient weaken as humidity increases at high elevations while declining at lower elevations from the high levels experienced during the dry season. Taken together, these seasonal shifts in elevation patterns of relative humidity indicate likely changes in the influence of the TWI, which keeps humidity high below the inversion during the dry season but allows moist air to reach higher elevations when it weakens in the summer (Blume, 1974; Riehl, 1979). On Mauna Loa, Hawaii, at the same latitude as the Cordillera Central, there is also a well-defined cloud belt on the windward slope between 1500 and 2500 m, related to orographic clouds capped below the TWI (Juvik and Ekern, 1978).

Precipitation patterns on windward slopes only weakly reflect the patterns of humidity because significant rainfall events in the Cordillera Central are frequently caused by synoptic-scale frontal zones dissipating over the region (Garcia et al., 1978), during which the TWI weakens or dissipates entirely, and the rainiest periods of the year (with peaks in May and October–November) occur when the TWI is not as strong. A primary influence of the TWI on PPT patterns can be seen during the dry season on windward slopes when PPT levels remain high only at the elevation just below the TWI (2360 m; Fig. 3, part b). Overall, precipitation patterns are driven more by seasonal shifts in the ITCZ (Small et al., 2007), synoptic-scale frontal activity (Garcia et al., 1978), and the orographic influences of the central massif at landscape scales.

Based on the seasonal movements of the ITCZ, the TWI may occur at lower elevations in the winter and higher elevations in the summer, as the TWI goes through seasonal fluctuations in magnitude and position (e.g., Schubert et al., 1995; Cao et al., 2007). For the broader Caribbean region, it has been reported that the TWI occurs at lower elevations in the winter than in the summer (Blume, 1974). Our nighttime data suggest it is more the strength and consistency of the TWI, rather than its elevation, that varies seasonally in the Cordillera Central (Figs. 6, parts c and d).

Important caveats apply to these data. Usually, vertical temperature profiles are constructed with radiosonde data (e.g., Cao et al., 2007), which provide measurements of "free atmosphere" conditions. Our data are ground-based and so reflect the local influences of topography, vegetation, and land-mass (Duane et al., 2008). Also, some errors in the data likely result from the instrumentation. Given these realities, the temptation to directly attribute the patterns in this data set directly to the TWI should be tempered with considerations of secondary influences like diurnal forcing and convectional venting. Although our instruments were all placed in consistent topography (broad, northeast-facing slopes) in open areas, temperature and humidity are nonetheless influenced by local conditions and by the prevailing vegetation types in a given elevation zone. However, from an ecological standpoint, these data reflect the conditions experienced by the biota and can be used to resolve diurnal cycles (unlike radiosonde data) by comparing the degree of daytime influences on the profile versus nighttime ambient conditions (Fig. 6). It is encouraging, despite the potential for spurious results, that the overall patterns remain robust; in particular, the coherence of the patterns in Figure 4 argues for the validity of our temperature interpretations.

CLIMATE AND FOREST ZONATION PATTERNS

The climate profile across the study site showed several distinct patterns related to vegetation zonation. Prior study detected discrete ecotones in forest composition on windward slopes in the Cordillera Central around 2200 m and 2500 m (Martin et al., 2007). By 2500 m, 12 of the 14 cloud forest tree species reach their elevational limit, above which *Pinus occidentalis* is the only arborescent plant (two cloud forest tree species occur as small-statured shrubs up to ~2700 m), forming a mono-dominant pine forest. The limit on cloud forest distribution at this elevation most likely results from a coincident drop in humidity (especially during the dry season) and the marked increase in the frequency of freezing temperatures. Mean annual RH drops steeply above its maximum at 2100 m and even more steeply above 2600 m where the TWI occurs (Figs. 3, part c, and 6, part c). Seasonally, this aridity at high elevations is far more pronounced as mean monthly RH dropped at all elevations above 2300 m in December through March, while RH at all lower elevations remained high during this period (Fig. 7). Freezing temperatures and ground frosts also are common above 2325 m, increasing markedly between 2600–2800 m (Fig. 8). Most tropical forest species lack the ability to withstand hard frosts (Sakai and Larcher, 1987), and the upper-elevation limits of the cloud forest in the Cordillera Central is probably dependent in part on the recurrence of subzero temperatures. The pine forest that covers the highest elevations of the Cordillera Central is reminiscent of many other TMFs where frost-tolerant species from temperate zone families, especially Pinaceae and Fagaceae, dominate the highest and coldest elevations (Troll, 1968; Ohsawa, 1995; Ashton, 2003). We argue that when such climatic discontinuities in moisture and temperature occur together, striking discontinuities in vegetation patterns are more likely to develop. Moreover, these results indicate that seasonal extremes in dryness and low temperatures—as much as mean annual conditions—drive the discreteness in vegetation patterns of the Cordillera Central. At lower elevations where forest floristics change continuously with elevation (Martin et al., 2007), the typical location of cloud base does not create any discontinuities in vegetation, either because the elevation of the cloud base is insufficiently consistent to create a discontinuity or because humid conditions (which can occur without cloud formation) are not effectively different from cloudy conditions.

These results indicate the maximum elevation of the cloud forest at 2500 m is set directly by climatic conditions. The causes of the ecotone at 2200 m, however, are not as clear—it appears to form due to a complex set of interactions where climate plays a more indirect role on vegetation through its influence on the fire regime, controlling how low fires are likely to extend. Frequent clouds at 2100 m prevent most fires (which usually occur in the dry season; Martin and Fahey, 2006) from burning lower than 2200 m. Indeed, the scarcity of fire in this zone is evident in the near complete absence of *Pinus occidentalis* in the cloud forest (Gannon and Martin, 2014). Direct observations of the behavior of a severe fire also indicated that it soon extinguished as it entered the cloud forest vegetation from the pine forest above (Sherman et al. 2008). Cloud occurrence is important in vegetation flammability, both directly because of fuel wetness and indirectly by influencing the composition and abundance of the vegetation, especially bryophytes. Epiphytic and forest floor bryophytes increase in abundance above 1700 m in the Cordillera Central, peak at ~2000–2200 m, and decline sharply above until they are almost completely absent by 2300 m (Martin et al., 2011). Epiphytes, with exceptionally high surface area and high water storage capacity, are well known to enhance interception and retention of cloud and rain water (e.g., Veneklaas et al., 1990; Clark et al., 1998; Hölscher et al., 2004), especially where abundant. At the same time, epiphytes do not have access to soil water, and hence are dependent on cloud interception for moisture (Benzing, 1998), creating a vegetation feedback. In prior studies of fire in the Cordillera Central, a strong correlative relationship was observed between decreased fire frequency and increased bryophytic epiphyte abundance (Martin and Fahey, 2006; Martin et al., 2007; Sherman et al., 2008). In effect, these studies argued that the coincidence of frequent cloud formation during the fire season and high bryophytic epiphyte abundance result in a cloud forest zone that is rarely burned despite the frequent occurrence of fires on adjacent slopes.

These findings have important implications for the future of TMCFs as the climate undergoes human-accelerated change. High elevation areas of tropical mountains are important for the conservation of biodiversity, for their flora rich in endemic and rare species (e.g., Kessler et al., 2001; Steinbauer et al., 2012), and also as an upslope "escape route" for lower elevation biota as temperatures warm (Laurance et al., 2011). This climate record shows that the position of the TWI regulates the elevational maximum of TMCF flora in this system and likely represents a strong barrier to future upward migration of cloud forest flora. The effects of warming temperatures on the TWI remain uncertain, but an observed increase in the frequency of the TWI in Hawaii over the last 24 years (Cao et al., 2007) may indicate a warming-related decline in the frequency of disruptions of Hadley cell subsidence over TWI-affected regions (Cao et al., 2007). If such observations are indicative of long-term trends in the frequency of the TWI, then a shift toward drier conditions for TWI areas would be expected as temperatures increase. Together with increased moisture stress due to higher temperatures and the elevational cap of the TWI, climate change in the high elevations of tropical mountains seems destined to strongly disrupt vegetation dynamics and directly threaten the future of TMCFs.

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APPENDIX

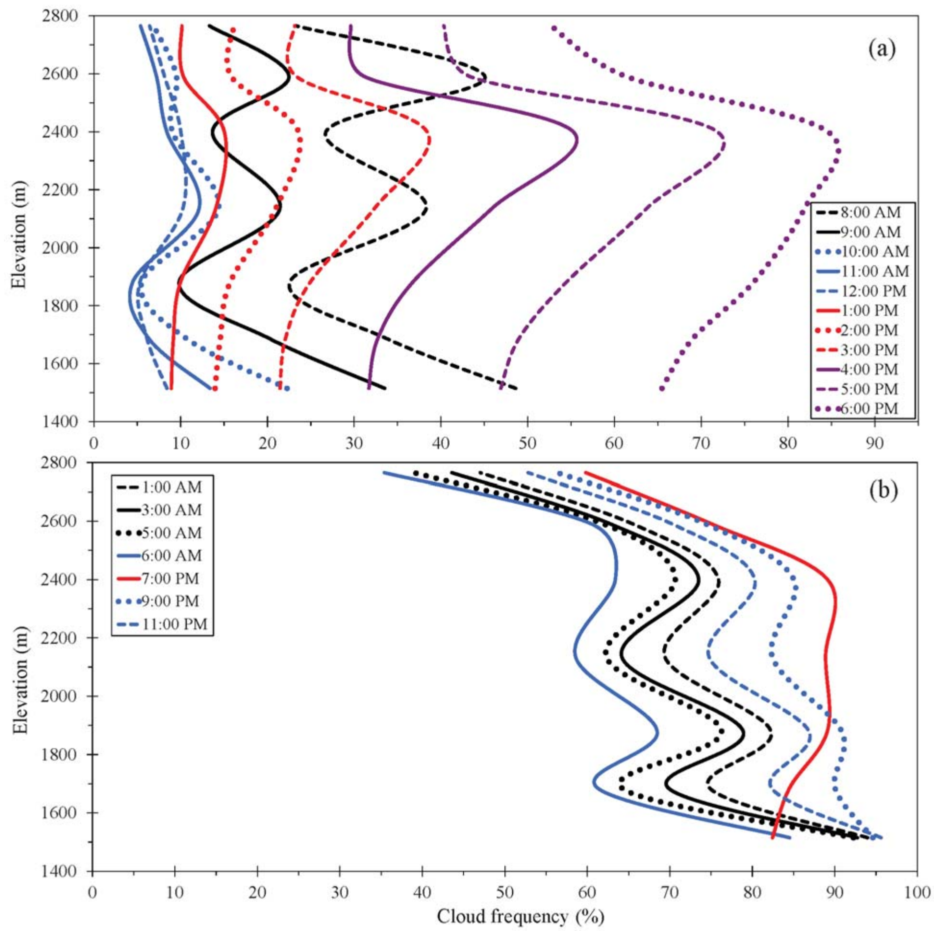

FIGURE A1. Mean frequency of cloud occurrence (indexed by the frequency of relative humidities ≥ 95%) by elevation and hour of the day. Panel (a) shows daytime hours and panel (b) nighttime hours. Values of ≥ 95% relative humidity do not indicate clouds categorically occurred, especially after sunset when dropping temperatures can result in high relative humidities and dew formation. However, during the daytime this threshold is a much more reliable index of cloud formation as temperatures are generally high enough to keep relative humidity below 95% in areas free of clouds. These patterns include all climatic conditions that occurred at an elevation over the entire period of measurement, including conditions that reduce or eliminate the elevational signal in cloud formation patterns (e.g. frontal storms, periods without the TWI, seasonal influences). Despite these influences, strong elevational patterns are evident in the daytime frequency of cloud formation. In particular, cloud development during the day is notably high at 2400 m; by 4:00 p.m.; clouds develop daily more than 55% of the year at this elevation while occurring less than 31% of the year just 200 m higher. This translates into ~3 months of additional cloud formation at 2400 m than 2590 m. We expect these elevational patterns would be even stronger if we only compared clear, sunny days when the TWI was present, but this data is not available.