

Vegetation Zonation in a Neotropical Montane Forest: Environment, Disturbance and Ecotones

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Abstract

Gradual changes in vegetation structure and composition are expected to result from continuous environmental change with increasing elevation on mountains. Hence, the occurrence of abrupt or discrete ecotones in vegetation patterns is intriguing and may suggest key controls on community assembly in montane forests. We review tropical montane forest (TMF) zonation patterns focusing on a case study from the Cordillera Central, Hispaniola where a striking discontinuity in forest composition occurs consistently at ~2000 m elevation, with cloud forest below and monodominant pine forest above. We propose that a discontinuity in climatic factors (temperature, humidity) associated with the trade-wind inversion (TWI) is the primary cause of this and other ecotones in TMFs that occur at a generally consistent elevation. Low humidity, fires and occasional frost above the TWI favor pine over cloud forest species. Fires in the high-elevation pine forest have repeatedly burned down to the ecotone boundary and extinguished in the cloud forest owing to its low flammability, reinforced by high humidity, cloud immersion and epiphytic bryophyte cover. Small-scale fire patterns along the ecotone are influenced by topography and where forest structure is impacted by hurricanes and landslides. Analogous patterns are observed worldwide in other TMFs where the TWI is important, high-elevation fires are frequent, and the flora contains frost-tolerant species (often of temperate lineage). The response of this and other TMFs to anthropogenic climate change is highly uncertain owing to potentially countervailing effects of different climatic phenomena, including warming temperatures and decreased frost; changes in the TWI, high-elevation drought or cloudiness; and increased frequency or intensity of hurricanes and El Niño–Southern Oscillation events.

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Key words: cloud forest; Dominican Republic; fire; hurricane; *Pinus occidentalis*; trade-wind inversion; tropical montane forest.

FOREST PATTERNS ON TROPICAL MOUNTAINS HAVE LONG FASCINATED ECOLOGISTS going back to early biogeographers like Alexander von Humboldt (Lauer 1968). Recent concern about the future of tropical montane forests (TMFs) has prompted a rapid growth in the number of floristic surveys and ecological studies of TMFs (Gradstein *et al.* 2008), yet further quantitative study on the patterns and dynamics of these fragile ecosystems is needed (Bruijnzeel *et al.* 2010). We present an overview of TMFs that highlights the role of climate gradients and natural disturbance on vegetation zonation with particular reference to relatively discrete vegetation boundaries that have been reported on some tropical mountains (*e.g.*, Kitayama 1992, Kitayama & Mueller-Dombois 1994, Ashton 2003, Hemp 2005). We focus our review on a case study on the primary forests of the Cordillera Central, Dominican Republic where we hypothesize that a combination of discontinuities in environmental conditions, disturbance history and biogeographic affinities of the flora have resulted in a highly discrete ecotone (Martin *et al.* 2007). As TMFs worldwide continue to face severe threats by direct human exploitation (*e.g.*, logging, agricultural expansion) and the indirect influence of human-accelerated environmental change, an improved understanding of the controls on the species distributions in these ecological assemblages will contribute to the future management and protection of these forests.

The geographic extent of TMFs has typically been defined to encompass the region delimited by about 20° S and 20° N latitude and above ~1000 m elevation (Troll 1956, Stadtmüller 1987,

Churchill *et al.* 1995, Webster 1995). A mean annual temperature around 20°C is typically regarded as the minimum for lowland tropical rain forest and a floristic transition at an elevation of about 1000 m in tropical landscapes has been noted (Webster 1995). A variety of schemes for classifying elevational zones within the TMF landscape has been devised, including those based primarily on climate (Holdridge 1967), vegetation physiognomy (*e.g.*, Grubb 1977) or some combination (*e.g.*, Bruijnzeel 2001); in this review, we use Bruijnzeel's (2001) classification. Classifications work best on mountains high enough to encompass a wide range in climatic conditions and thresholds (*e.g.*, condensation conditions) along the elevation gradient. Most of these classifications recognize a change from lowland tropical forest to lower montane forest—on large, inland mountains in equatorial regions, this transition usually occurs at an elevation of 1200–1500 m, although it often occurs at much lower elevations on small island mountains and away from the equator. A more distinctive zonal boundary occurs between lower and upper montane forests, coinciding with the elevation where cloud formation becomes regular (Bruijnzeel 2001). On large, inland mountains in equatorial regions, this occurs at elevations of 2000–3000 m. Although the position of this boundary varies among TMF regions, reflecting local circumstances, nearly all such classifications recognize the upper montane area as a 'cloud' forest zone, reflecting the exceptionally frequent occurrence of cloud, mist or fog at higher elevations. The average elevation of the cloud base varies geographically and seasonally, but is comparatively uniform and consistent in elevation on mountains in the equatorial and oceanic tropics (Ashton 2003). Vegetation physiognomy within

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the cloud forest zone is particularly distinctive: canopy height is low; trees are often gnarled and twisted, with microphyllous leaves; tree ferns often are the dominant arborescent taxa especially in areas with disturbance (Stadtmüller 1987); and epiphytic bryophytes are abundant, often covering all surfaces from the canopy to the forest floor in a thick carpet (Frahm & Gradstein 1991). The causes of this distinctive physiognomy and presumed low primary productivity remain elusive having been ascribed to various processes including low soil fertility, saturated soils, wind, UV radiation and high humidity (see review in Bruijnzeel & Veneklaas 1998). At higher elevations, the cloud forest zone reaches its limits where sub-freezing temperatures restrict the distribution of tropical species that lack frost tolerance. Depending on the biogeographic setting, species from various temperate zone families often dominate this upper montane zone of the TMF, most commonly from the Pinaceae and Fagaceae (Martin *et al.* 2007). Where mountains are high enough, the upper forest limit (or 'treeline') of TMFs occurs at elevations from approximately 3600–4000 m (Ohsawa 1990, Korner & Paulsen 2004; in the Andes, scattered stands of the remarkable endemic tree genus *Polylophos* can occur much higher although these are usually above the 'continuous' forest line; Rada *et al.* 1996) and are strongly associated with a seasonal mean temperature isotherm of 5–7°C (Korner & Paulsen 2004). Vegetation above the treeline varies depending on the biogeographic and climatic setting of the region (Leuschner 1996). Increased drought and fires at high elevations, as well as the absence of cold-adapted tree species contribute to lower treelines on small, isolated tropical and subtropical islands (Leuschner 1996, Korner & Paulsen 2004). The elevations of tropical treelines and cloud forests are also greatly reduced on small isolated mountain ranges by the 'Massenerhebung' or mass elevation effect (Grubb 1971), a phenomenon where the size of a mountain range influences local climate and hence vegetation patterns—at a given elevation, bigger mountains have higher temperatures than smaller ones as larger high-elevation landmasses absorb more solar radiation.

Although it is obvious that environmental changes associated with elevation (*i.e.*, the elevation gradient) control species distributions in tropical mountains, the exact nature of these controls is neither clear nor uniform across tropical regions. Some early classifications of TMF communities posited that discrete zones and thresholds in climate, and in particular temperature, result in floristically distinct vegetation zonation (Richards 1952, Holdridge 1967). Empirical studies demonstrate that plant species distribution patterns in many TMFs are individualistic and species turnover across the elevation gradient is continuous (Lieberman *et al.* 1996, Lovett 1998, Vázquez & Givnish 1998) while others continue to report relatively discrete vegetation boundaries on some tropical mountains (Kitayama & Mueller-Dombois 1994, Ashton 2003, Hemp 2005), presumably reflecting some combination of discontinuities in environmental conditions, disturbance history and biogeographic affinities of the flora.

THE CORDILLERA CENTRAL, HISPANIOLA AND THE TMF PANORAMA

The Cordillera Central is an extensive massif that occupies the central region of the island of Hispaniola, encompassing the highest

peak in the Caribbean Basin (Pico Duarte, 3087 m). Although many parts of this range were logged and converted to agricultural uses, a core area of over 1500 km² was placed under protection in two national parks (Parques Armando Bermúdez and José del Carmen Ramírez, Fig. S1) in the late 1950s before any major logging or farming incursions (Hoppe 1989). Our study focused on the steeply dissected slopes east of Pico Duarte where protected, unlogged forest extends from 1100 to over 3000 m elevation. In the direction of the prevailing trade winds, the Atlantic Ocean lies about 90 km to the northeast of the site. The Cordillera Central is notably higher in elevation and larger in area than other mountain ranges in the Caribbean. While still a fairly high moisture environment, these factors make the climate in the Cordillera Central comparatively dry for a TMF overall (Bruijnzeel 2001). Likewise, the Cordillera Central is comparatively dry, and also cooler and less windy, than more coastal TMFs in the Caribbean–Jamaica (Tanner 1977) and Puerto Rico (Weaver 1995). The geology of the Cordillera Central is complex, and the study area is underlain by a variety of igneous and metamorphic substrates (Draper & Lewis 1991), but distinct lithologic boundaries were not observed in the vicinity of the ecotone boundary, described below.

A complex vegetation mosaic of moderately high species richness and highly varying structure covers the montane landscape of the Cordillera Central (Table 1). In this island flora, a high proportion of the plant species are endemic (*e.g.*, 69 of 166 woody plant species), including the most abundant tree, the endemic Hispaniolan pine (*Pinus occidentalis* Swartz). The pine occurs naturally in monospecific stands and mixed stands with broadleaf tree species across elevations spanning 200–3100 m throughout the entire Cordillera Central (Darrow & Zanoni 1990). On the basis of 245 sample plots (0.05–0.1 ha) distributed across our study area (see Sherman *et al.* 2005 for full methods), the forest (stems ≥ 10 cm dbh) was statistically classified with TWINSpan (Centre for Ecology and Hydrology, Oxfordshire, UK) into distinct types that are arranged along the topo-elevation gradient along the windward slopes: (1) lower montane broadleaf forests of tall stature (up to 35 m), complex structure and high diversity; (2) mixed pine–broadleaf forests with varying degrees of dominance by Hispaniolan pine; (3) upper montane cloud forest usually dominated by tree ferns (Cyathaceae) and with a high abundance of epiphytic bryophytes and filmy ferns (though not as high as in many wetter TMFs; Frahm & Gradstein 1991); (4) a fire-maintained monodominant pine forest from ~2200 to 2500 m with varying degrees of cloud forest tree species colonization; and (5) above ~2500 m a mosaic of monospecific pine forest and pine–savanna with ground cover dominated by endemic grasses (*Danthonia domingensis* Hack & Pilger; *Agrostis hiemalis* (Walt.) B.S.P.). Monospecific pine forests also occur on all sampled elevations on leeward slopes south and west of the main ridgeline. The distribution patterns of many of the woody species show clear elevational affinities, presumably reflecting mesoclimatic controls, and for several of the dominant species we detected distribution patterns (nested within elevational patterns) related to local scale topographic and soil factors. For example, in the lower montane zone, the abundant palm species *Prestoea montana* (R. Graham) Nichols showed clear preference for concave

TABLE 1. Forest type classification, environment, structure and floristics along the windward elevation gradient in the Cordillera Central, Dominican Republic, determined from 245 permanent plots (0.05–0.1 ha). Forest type was derived with a third-division TWINSpan classification (Sherman et al. 2005)

Forest type	Elevation range (m)	PPT (mm) ^a	MAT (°C) ^b	Species density ^c (m ² /ha)	Basal area (m ² /ha)	Stem density ^d	Canopy height (m) ^e	Dominant tree family/genus/species	Frost	Fire
Lower montane broadleaf forests	1100–1900	1800–1950	12–16	20.6	27.7	688	11–35 (22.3)	Lauraceae– <i>Tabebuia</i> –Cycatheaceae– <i>Prestoea</i> – <i>Meliosma</i> – <i>Turpina</i>	No	No
Mixed pine–broadleaf forest	1200–2000	1700–1900	11.5–15.5	11.8	27.5	705	17–38 (22.3)	<i>Pinus occidentalis</i> – <i>Brunellia</i> – <i>Clusia</i> – <i>Lyonia</i>	No	Infrequent
Upper montane cloud forest	1900–2200	1750–1850	10.5–12	11.4	26.3	810	5–18 (11.3)	Cyatheaceae– <i>Brunellia</i> – <i>Podocarpus</i> – <i>Antirhea</i>	Rare	Rare
Monodominant pine forests	2200–2500	1400–1700	9–10.5	2.6	21.1	686	20–36 (27.5)	<i>Pinus occidentalis</i>	Regular	Frequent
Monospecific pine forests	2500–3087	1300–1700	6–9	1	17.1	352	13–30 (23.7)	<i>Pinus occidentalis</i>	Regular	Frequent

^aRange in mean annual precipitation.

^bRange in mean annual temperature.

^cMean tree species count per 1000 m².

^dStems (≥ 10 cm dbh)/ha.

^eRange (and mean) in canopy height.

hollows (*i.e.*, wet soils) as found with this species in Puerto Rico (Lugo *et al.* 1995), whereas the endemic tree *Didymopanax tremulus* Krug & Urb. usually occupied ridges and upper slopes (Sherman *et al.* 2005).

Like many other tropical forests, the vegetation of the montane zone of the Cordillera Central is structurally complex, including varying mixtures of herbs and ferns, vascular epiphytes, vines, epiphytic bryophytes, shrubs, understory trees ('treelets'), palms, tree ferns, broadleaf canopy trees, and the needleleaf trees, pine and *Podocarpus aristulatus* (Martin *et al.* 2004, Sherman *et al.* 2005; Table 1). The relative abundance of these vegetation structural elements exhibited some clear trends across the elevation gradient. In particular, the abundance of vines decreased with increasing elevation, tree fern abundance increased markedly above 1700 m peaking at 2000 m, vascular epiphytes and treelets showed broad peaks in abundance between 1400 and 2200 m elevation, and the abundance of epiphytic bryophytes peaked between 1800 and 2200 m elevation (Fig. 1B). Bryophytes were most commonly restricted to the surfaces of subcanopy stems and branches, trunks and the forest floor, but in places covered all canopy surfaces especially in protected and cool/moist topographic positions. The canopy height of nonpine tree species declined steadily from about 30–35 m at 1200 m to 12 m at 1900 m, whereas the height of dominant pines remained relatively constant at about 30 m across the entire elevation gradient from 1200 to 2800 m, declining to 20 m at the highest elevations (Fig. 1D).

The vegetation transition from lower to upper montane in the Cordillera Central appears to be gradual in nature as reflected, for example, in the gradual increase in abundance of tree ferns between 1500 and 1800 m elevation (Fig. 1A). In contrast, at higher elevations, the most striking feature of the TMF mosaic throughout the Cordillera Central is the visibly discrete vegetation ecotone that occurs on all the windward slopes (Sherman *et al.* 2005, Martin *et al.* 2007; Fig. S2). Below the ecotone is a compositionally and structurally diverse cloud forest and above is a monodominant pine forest (Martin *et al.* 2007). The elevation of the ecotone is remarkably consistent at 2000–2100 m elevation across the entire northern and eastern slopes of the Cordillera Central (Martin *et al.* 2007). Elsewhere we have observed visually identical pine–cloud forest ecotones around the same elevation in two other protected areas in the Dominican Republic, Sierra de Bahoruco Park and Juan B. Pérez Rancier Park (formerly Valle Nuevo Scientific Reserve). What could account for such a discrete ecotone at such a consistent elevation across so broad a landscape? How does the answer to this question inform our understanding of montane forest dynamics in general and those of TMFs in particular?

THE NATURE AND POSITION OF THE PINE–CLOUD FOREST ECOTONE

Spatial discontinuities in the composition and physiognomy of vegetation provide opportunities to better understand the factors controlling the assembly of biotic communities (Whittaker 1956). Although discrete vegetation boundaries should be associated primarily with discontinuities in environment or disturbance history,

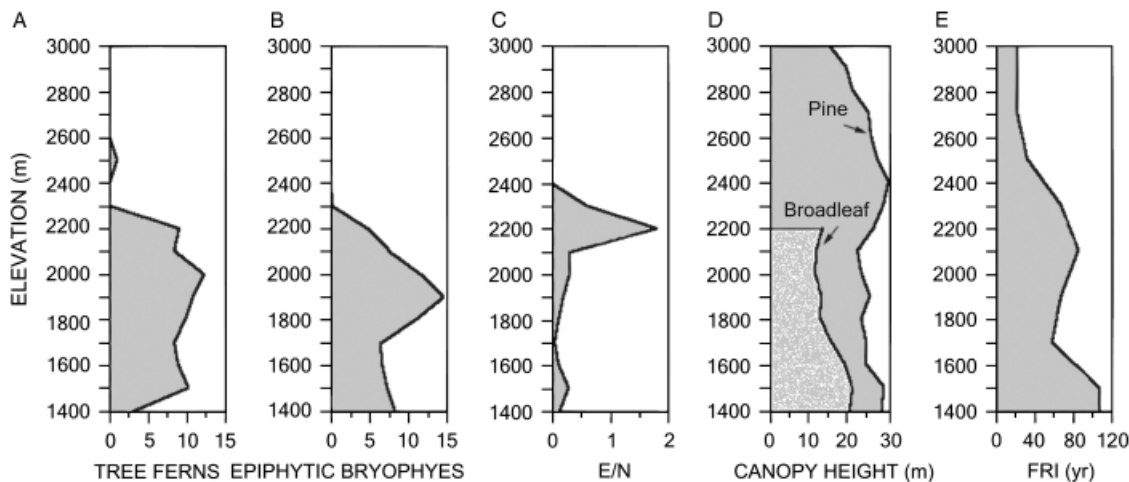


FIGURE 1. Elevation profile on the windward slopes of the Cordillera Central, Dominican Republic of: (A) relative density (%) of tree ferns; (B) relative frequency (%) of a very high abundance of epiphytic bryophytes on tree canopies and trunks; (C) number of species reaching elevational limits (E) vs. the number of species present not reaching elevational limits in each elevational band (N); (D) mean canopy height of pine and broadleaf tree species; and (E) mean fire return interval. For full methods, see Sherman *et al.* (2005) for panels a, b and d; see Martin *et al.* (2007) for panel c; and Martin and Fahey (2006) for panel e.

feedbacks by the dominant species on microenvironment or disturbance likelihood also can sharpen ecotones (Siccama 1974, Harmon *et al.* 1983, Barton 1993), the so-called vegetation switch (Wilson & Agnew 1992). To understand the discrete nature and position of the pine–cloud forest ecotone, we examined the interactions of climate, topography and disturbance in regulating vegetation patterns along the elevational gradient of these mountains. The striking contrast in forest composition and structure across this ecotone is readily distinguished in aerial photographs (1:24,000 scale), which allowed us to map the position of the ecotone across the remote and rugged landscape of the Cordillera Central (Martin *et al.* 2007).

The elevation and topographic position of the ecotone was estimated using a 20-m resolution digital elevation model along 124 km of the mapped ecotone boundary (see Martin *et al.* 2007 for full methods). The mean elevation of the ecotone was 2007 m, and the consistency of this elevation is indicated by a small standard deviation (across 2482 sample points) of 164 m. The mean elevation of the ecotone did not vary significantly with either slope angle or slope aspect—recall that the ecotone is only found on the moister, windward slopes, so here aspect refers to local aspect only. The boundary did significantly vary with topography, trending lower on ridges and higher in drainage gullies in the steeply dissected terrain. This pattern was consistent across the entire Cordillera Central, and not the product of local processes or events like landslides. Similar patterns are found across tropical mountains, where treelines usually attain their maximum elevation in gullies rather than ridges (Troll 1973, Ashton 2003).

CLIMATIC PROFILE OF CORDILLERA CENTRAL

The principal environmental factors that vary along an elevation gradient are connected to climate (temperature, precipitation, humidity, wind). Climatic patterns in the Caribbean reflect the over-

arching influence of the prevailing northeast trade winds: northeastern mountain slopes on islands intercept moisture-laden air, resulting in relatively high cloudiness and precipitation; leeward southwest slopes are much drier. Annual precipitation on the windward slopes of the Cordillera Central averages about 1900 mm whereas 1300 mm of annual rainfall is observed on leeward slopes (Sherman *et al.* 2005). At the latitude of Hispaniola (19° N), a marked seasonality in precipitation and a weak seasonality in temperature are observed. Drier and cooler weather prevails from January to March when average monthly precipitation drops to 80 mm on the windward slopes and 31 mm on leeward slopes (Martin & Fahey 2006). Precipitation patterns in the Caribbean basin also are influenced by the El Niño–Southern Oscillation (ENSO) when dry season precipitation throughout the Cordillera Central is 30–50 percent lower during ‘strong’ and ‘very strong’ El Niño years, as defined by Quinn *et al.* (1987) (Martin & Fahey 2006). Independent of ENSO activity, the positive phase of the North Atlantic Oscillation is also known to reduce spring precipitation throughout the Caribbean basin (Giannini *et al.* 2001).

Regular ground frosts (more than three times per year) in the Cordillera Central usually occur at elevations above 2350 m (Martin *et al.* 2007). Most tropical forest species lack the ability to withstand hard frosts (Sakai & Larcher 1987), and the upper-elevation limits of the cloud forest in the Cordillera Central probably depend in part on low temperatures and the recurrence of ground frost (Fig. 2). The coincidence between the elevation where 12 of 14 cloud forest species reach their upper limit (2200–2350 m) (Fig. 1C), the maximum elevation of the pine–cloud forest ecotone (2388 m), and the zone where minimum annual temperatures indicate regular ground frost (> 2350 m) is suggestive of a causal relationship. Indeed, although cloud forest patches occur up to about 2350 m in concave terrain that is likely protected from fire, above that elevation pines occupy even the most protected gullies and ravines. The monospecific pine forest that dominates the upper slopes

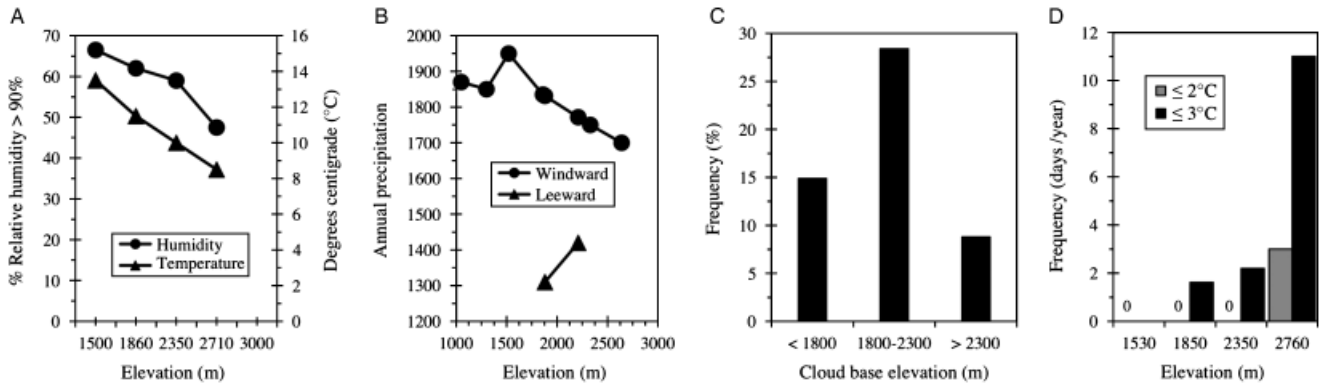


FIGURE 2. Climate data collected along an elevational gradient in the Cordillera Central, Dominican Republic: (A) mean annual night temperature and relative humidity (percentage of measurements $\geq 90\%$ relative humidity) 1-m above the ground; (B) mean annual precipitation on windward and leeward slopes; (C) mean annual frequency of afternoon cloud-base formation by elevation; and (D) annual frequency of air temperature $\leq 2^\circ\text{C}$ and $\leq 3^\circ\text{C}$ 1-m above the ground by elevation. Estimates of frost were based on a calibration showing temperatures $\leq 3^\circ\text{C}$ at 1-m above the ground indicated the occurrence of ground frost. The data were collected from 1999 to 2004. See Martin *et al.* (2007) for full methods.

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).

Montane mesoclimates in many tropical and subtropical regions are strongly shaped by a temperature inversion associated with large-scale atmospheric circulation patterns, known as the trade-wind inversion (TWI). The TWI frequently forms on mountain slopes in the tropics where descending cool-dry air (which moves poleward from the high atmosphere of equatorial regions) meets rising warm-moist air driven toward the equator by the trade winds. Despite seasonal fluctuations in its magnitude and position (*e.g.*, Guangxia *et al.* 2007), the TWI traps moist air and clouds below a roughly constant elevation (Riehl 1979). In the Caribbean basin, the base of the TWI is frequently observed between 1900 and 2300 m elevations (Schubert *et al.* 1995). On the windward slope of the Cordillera Central, the position of the TWI is clearly reflected by three climatic discontinuities (Fig. 2): (1) changes in the temperature lapse rate, dropping from $6.2^\circ\text{C}/\text{km}$ between 500 and 1850 m to $3.1^\circ\text{C}/\text{km}$ between 1850 and 2350 m, and rising to $4.2^\circ\text{C}/\text{km}$ between 2350 and 2800 m, similar to observations in Hawai'i (Giambelluca & Nullet 1991); (2) a high frequency of occurrence of the cloud base between 1800 and 2300 m; and (3) a marked decline in atmospheric humidity above 2300 m. Taken together with the observations of the minimum elevation of regular ground frost, the effects of the TWI on climatic factors result in a marked discontinuity in key environmental drivers along the elevation gradient.

DISTURBANCE REGIMES: FIRES ABOVE THE CLOUDS

Ecologists have long recognized the key role played by natural disturbances in shaping patterns of species distribution, yet comparatively little quantitative research has been conducted on disturbance regimes in TMFs (*e.g.*, Arriaga 2000, Martin *et al.* 2007). In equa-

torial TMFs, small gaps and landslides are typically the principal mechanism of canopy turnover (*e.g.*, Lawton & Putz 1988). Fire has been acknowledged as an important driver of vegetation dynamics at high elevations in some TMFs (Smith & Young 1987, Ashton 2003, Román-Cuesta *et al.* 2004), but the role of fire has received limited quantitative study in the tropics (Cochrane 2003) in part because of a lack of tropical tree species known to be suitable for dendrochronological reconstruction of fire history (Worbes 2002, Brienen *et al.* 2009). The Hispaniolan pine, however, forms reliable annual growth rings (Speer *et al.* 2004) throughout much of the Cordillera Central and provides a record of fire history over the past 250 yr (Martin & Fahey 2006).

Pinus occidentalis displays many classic fire-adapted traits (*sensu* Agee 1998); while its cones are not serotinous, its very thick bark, rapid juvenile growth rates and self-pruning habit provide protection from surface fires (Darrow & Zandoni 1990, Martin & Fahey 2006). Moreover, the widespread presence of multiple fire scars on living pines and its rapid colonization of recently burned areas (Sherman *et al.* 2008) indicate a species well adapted to repeated fires. Hence, the extensive dominance of the pine, together with the distinct dry season, suggested a key role of fire in this TMF, and we reconstructed the fire history of these forests on the basis of 72 fire-scarred individuals distributed across the study area. We dated 339 individual fire scars representing 41 separate fire years since 1725 (Martin & Fahey 2006). On this basis, the fire regime of the high-elevation pine forests in the Cordillera Central can be classified as mixed, with relatively frequent surface fires and occasional crown fires. The mean fire return interval (FRI) of the entire study area was 31.5 yr (Fig. 1E); FRI provides a point estimate of fire frequency (Romme 1980, Baker & Ehler 2001) and will underestimate large-scale fire frequency if many fires are unrecorded by the sample trees. The mean fire interval, the average number of years between fire dates recorded in sample trees for the entire study area, provides an upper-bound estimate of fire frequency of 5.6 yr. Not surprisingly, major fire years are clearly linked to the intensity of dry-season droughts as the average dry-season precipitation was 50

percent lower in fire years than nonfire years (Martin & Fahey 2006). Moreover, given the link between El Niño events and droughts, it is not surprising that many large fires (six of nine recorded in our fire-scar records between 1856 and 1965) were synchronized with strong El Niño years (Quinn *et al.* 1987); most recently, severe and widespread fires in 1983 and 1997 coincided with very strong El Niño events and in 2005 with moderate El Niño conditions (Martin & Fahey 2006).

Fire frequency is highly nonuniform across the Cordillera Central, primarily reflecting the influence of the orographic rain shadow and the TWI. The mean interval without fires was much longer on moist windward slopes (FRI 42.1 yr) than drier leeward ones (FRI 16.7 yr) (Martin & Fahey 2006). On the windward slopes, the length of fire-free intervals increased with elevation to a peak at about 2100 m and declined markedly above (Fig. 1E). This pattern presumably reflects the position of the base of the TWI above which drier atmospheric conditions prevail, as well as the fire-resistant nature of the cloud forest (Sherman *et al.* 2008; see below) and the comparatively high flammability of the pine forests that dominate higher elevations.

Clearly, fire has played a key role in shaping current vegetation patterns, promoting the abundance of pine forests in the landscape; but are these fire frequency and fire regime observations representative of the natural (pre-anthropogenic) situation? Paleocological evidence indicates that fires were common in the Cordillera Central thousands of years before human colonization of Hispaniola (Horn *et al.* 2000), showing that nonanthropogenic ignitions occur in this ecosystem. Furthermore, archaeological evidence indicates that Amerindians rarely visited the Cordillera Central in the pre-Columbian era (Bolya 1997), and Dominicans did not begin to use the highlands for timber or grazing until the early twentieth century (Kustudia 1998). A notable change in fire frequency occurred with the increase in human activity in the region, as FRI was significantly shorter from 1900 to 1965 (24.1 yr) than pre-1900 (37.3 yr). Since the 1960s, the FRI again declined (31.9 yr), presumably owing to the creation of the national parks, elimination of some small human settlements within the park boundaries, and especially the aggressive enforcement of fire prohibition and consequent changing attitudes of rural communities about the desirability of igniting fires near or within the parks (Schelhas *et al.* 2002). Fire suppression efforts have probably exerted minimal influence on fire spread because of limited access to remote areas and modest fire-fighting resources of government agencies (Martin & Fahey 2006). In sum, human activity undoubtedly influenced fire frequency during the twentieth century, but the degree of this influence was limited, and landscape-scale fire regime and vegetation patterns probably do not depart substantially from the natural situation (Martin & Fahey 2006). We conclude that pine forests on the upper and drier slopes of the Cordillera Central have been maintained by recurring fires over millennial time scales (Horn *et al.* 2000, Kennedy *et al.* 2006, Martin & Fahey 2006).

HURRICANE DISTURBANCE

While a nonissue in equatorial TMFs, catastrophic disturbance associated with hurricanes can be important in many tropical regions

including East Asia and the western Pacific (Whitmore 1989), and the Caribbean basin, eastern Central America and southern North American (Brokaw & Walker 1991, Arriaga 2000). Puerto Rico has been hit by 70 hurricanes since 1700, including several severe ones (Boose *et al.* 1994, Boose *et al.* 2004). The Cordillera Central recently experienced two hurricanes in 1979—a Class 5 hurricane (David) and followed 6 d later by a Class 4 hurricane (Frederic)—and in 1998 by a Class 2 hurricane (Georges). Three distinct categories of disturbance are associated with these severe storms: extensive blowdowns, large landslides and major floods (Boose *et al.* 2004). All three have influenced vegetation patterns in the Cordillera Central: extensive areas suffered blowdown in both storms, and the extremely heavy rainfall (as much as 100 cm in a 24-h period in Hurricane Georges: <http://www.nhc.noaa.gov/1998georges.html>) caused widespread flood damage to riparian forest along higher order streams (Martin *et al.* 2004) as well as hundreds of landslides (P. H. Martin, unpubl. data). The spatial patterns of these disturbances are intimately connected with topographic features. For example, in nearby Puerto Rico typical storm tracks result in wind fields that favor wind damage on ridges and north-facing slopes (Boose *et al.* 1994, Boose *et al.* 2004). Wind speeds in hurricanes are, however, undoubtedly lower at our inland study site (~90 km from the coast) than for coastal mountains like Puerto Rico. Forest composition also influences the severity of wind damage as the pine trees are more susceptible to trunk snapping and blowdown than cloud forest trees (Martin *et al.* 2007, Lenart *et al.* 2010). Such hurricane damage can also influence subsequent fires by leaving high fuel loads and facilitating more rapid drying of fuels in the high light conditions (Myers & van Lear 1998, Sherman *et al.* 2008).

DISTURBANCE HISTORY AT THE ECOTONE

Clearly the sharp ecotone between the pine and cloud forest in the Cordillera Central reflects in part a contrast in history of disturbance by fire. We established 25 pairs of sample plots on either immediate side of the ecotone to measure forest composition and disturbance indicators (Martin *et al.* 2007). The incidence of indicators of past fires (soil charcoal, charred trunks, fire scars) was much higher in the pine than the cloud forest paired plots; for example, soil charcoal was found in all the pine plots but only 22 percent of the cloud-forest plots. Fire scars indicated that 60 percent of the pine-paired plots had experienced repeated fires (≥ 2 fire scars), and ring counts of the largest pine trees at the ecotone demonstrated a wide range in stand ages (35–150 yr). Together, these observations illustrate that the pine–cloud forest ecotone reflects repeated disturbance by fires rather than the legacy of one or a few major fires.

Evidence of damage by windstorms in the form of groups of uprooted, or more frequently, snapped-off trees also was common along the ecotone (Martin *et al.* 2007). Across the landscape, wind damage associated with recent hurricanes was documented more frequently in cloud forest than pine forest (Sherman *et al.* 2005), but much of the damage along the ecotone consisted of scattered windthrown and snapped pine trees (rather than large openings that

favor pine regeneration), which in places converted areas to cloud forest by removing the pine overstory and leaving the smaller-statured, shade-tolerant cloud forest species intact in the subcanopy and understory.

ENVIRONMENT, DISTURBANCE AND THE ECOTONE

Any explanation of the pine–cloud forest ecotone in the Cordillera Central needs to account for both the sharpness of the boundary as well as its striking elevational consistency. The current position and sharpness of the boundary are coincident with past fires that have burned down through the pine forest and been extinguished in the cloud forest. We hypothesize that climatic factors influenced by the TWI provide the ultimate cause of the average elevation of the ecotone; the exceptional consistency of the ecotone elevation may result from an environmental discontinuity associated with the average position of the lower boundary of the TWI where cloud frequency is very high and above which atmospheric moisture declines (Fig. 2). The TWI is thought to cause a similarly sharp ecotone at 1900–2000 m elevation in Hawai'i, where montane cloud forest gives way to dry subalpine scrub (Kitayama & Mueller-Dombois 1994). In addition to the direct influence of moisture on fire likelihood, the high frequency of cloud immersion may facilitate the growth and development of epiphytic bryophytes (Proctor 1982, Frahm & Gradstein 1991), which strip moisture from the air and retain high water content and thereby lower vegetation flammability (Brujinzeel & Proctor 1995). Repeated surface fires in the highly flammable pine understory are favored by the distinct

January–March dry season that is reinforced by El Niño conditions. These fires appear to restrict the invasion by cloud forest species, many of which are capable of establishing at elevations of up to 2300 m (Martin *et al.* 2007). Hence, we posit that the combination of macroenvironmental discontinuity and strong vegetation–micro-environment feedback facilitates the establishment of the highly ordered pattern of vegetation zonation in this TMF. These principal features set the general elevation of the ecotone and interact with the secondary forces of topography and vegetation composition to set the local elevation of the ecotone, resulting in a dynamic equilibrium in the ecotonal area (Fig. 3).

A PARTIAL TEST: THE FIRE OF 2005

On 7 March 2005, a fire escaped from an agricultural field at low elevation on the leeward side of Pico Duarte adjacent to our study area. The fire burned for 28 d, eventually spreading through most of the pine forests on both the leeward and windward slopes in our study area. Once finished, this fire burned through over 96 percent of the monodominant pine forest area in the parks and it was easily the largest fire in the windward areas of the Cordillera Central since the 1960s (Martin & Fahey 2006). The behavior of this fire at the pine–cloud forest ecotone provided direct evidence and new insights on the nature and causes of the ecotone (Sherman *et al.* 2008). The intensity of the March 2005 fire ranged from severe, stand-replacing crown fire (Class 4–6 burn severity per Jain *et al.* 2008); to moderate burns that scorched tree trunks and killed understory vegetation (Class 2–3); to light surface fires where understory shrubs and pine saplings survived (Class 1). Much of the

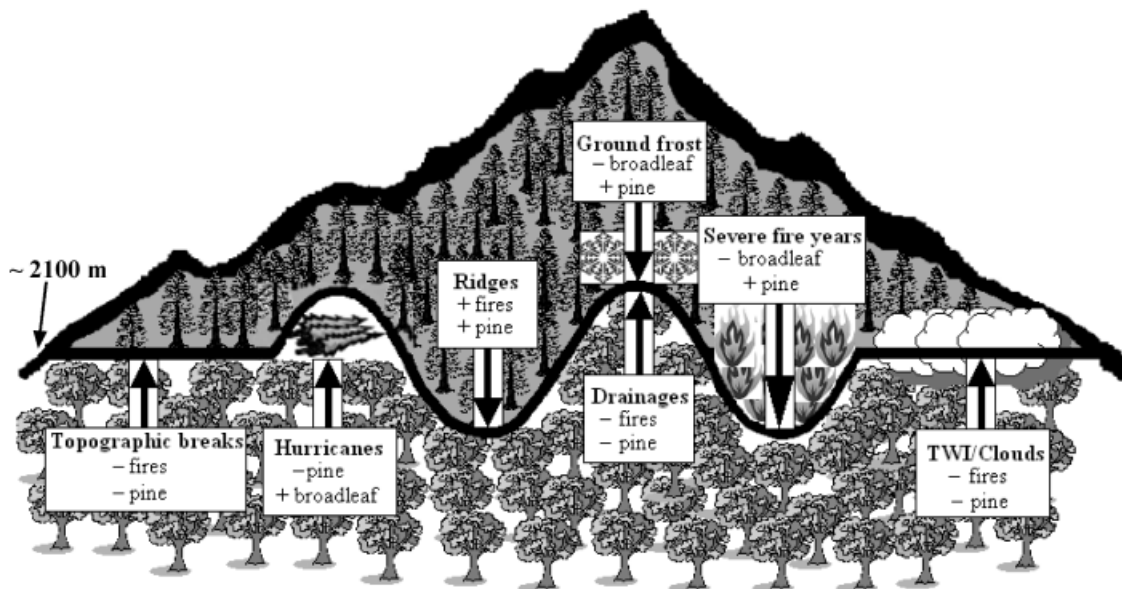


FIGURE 3. Diagrammatic model of the influences on the elevation of the pine–cloud forest ecotone in the Cordillera Central, Dominican Republic. Arrows indicate forces raising (↑) or lowering (↓) the ecotone, and positive (+) and negative (–) signs indicate effects on pine forest, cloud forest or fire likelihood. Discontinuities and thresholds in climate (especially humidity and temperature) determine the general elevation of the ecotone (~2000–2100 m) by affecting fire likelihood and setting the upper elevation limit of cloud forest species. Small-scale variation in the ecotone elevation results from topographic influences on fire likelihood and microclimate. Severe fires during droughts lower the ecotone and hurricanes raise it by felling windthrow-prone pines.

severe burning occurred on an exceptionally windy day (March 22) when strong upslope advection resulted in widespread mortality in pine forest on the leeward slopes of Cordillera (F. Peralta, Dominican Park Service, pers. comm.).

As expected the fire usually burned out at the pine–cloud forest ecotone (Sherman *et al.* 2008). We quantified the mean elevation of the fire perimeter on the windward slopes using Quickbird satellite images georeferenced to the 20-m DEM (see Sherman *et al.* 2008 for full details). The mean elevation of the fire perimeter (2073 ± 156 m) was similar to that of the pine–cloud forest ecotone (2007 m). Field surveys indicated where the fire reached the ecotone, it burned on average ~ 15 m into the cloud forest before being extinguished. Usually, the limit of burning into the cloud forest coincided with the occurrence of dense cover of bryophytes on the ground and in the canopy of the cloud forest. A similar pattern was observed on the dry, leeward slope: the fire went out near the edge of small broadleaf forest patches located in drainage gullies within the burned-over pine forest matrix.

Our field surveys encountered a few areas where the fire burned extensively and intensely into the cloud forest (> 100 m distance from the ecotone); the forest canopy and deep accumulations of mossy peat were consumed exposing mineral soil below, and most trees were killed (Sherman *et al.* 2008). These intense burns coincided with the same windy conditions that resulted in the severe crown fires in the pine forest (F. Peralta, Dominican Park Service, pers. comm.). Hence, the susceptibility of the cloud forest to burning during this fire event depended in part on the particular location of the fire perimeter relative to the pine–cloud forest ecotone at the time of high winds. Four of the six extensively burned cloud forest stands that we surveyed had large accumulations of woody fuels from earlier hurricane disturbance which may have favored fire spread. Although cloud forests rarely burn, when they do, fires can be highly destructive (Asbjornsen *et al.* 2005).

Our surveys of vegetation recovery in 2006–2010 did not encounter pine regeneration colonizing the post-fire cloud forest areas along the ecotone (see Sherman *et al.* 2008). To date, abundant pine regeneration has been restricted to post-fire monodominant and monospecific pine forests at higher elevations, whereas cloud forest regeneration has consisted predominantly of basal sprouting by a few tree species (especially *Garrya fadyenii*), seedling recruitment by *Brunellia comocladifolia*, and widespread colonization by large ground ferns (*Dicranopteris pectinata* [Willd.] Underw. and *Pteridium aquilinum* var. *arachnoideum* [Kaulf.] Brade). More recent surveys in 2008–2010 found ~ 3 m tall fern thickets in the larger burns into the cloud forest, blocking any significant post-fire tree seedling establishment (P. H. Martin, unpubl. data). These native ferns are known to aggressively colonize post-logging, post-agriculture, and post-fire areas throughout the Cordillera Central (Slocum *et al.* 2006). A somewhat analogous pattern has been reported in Hawai'i, where fires burn into submontane forests (elevations 300–1200 m) and post-fire succession is dominated by exotic, fire-tolerant grasses (Hughes *et al.* 1991). It will be fascinating to follow the long-term, post-fire vegetation dynamics along the ecotone in the Dominican Republic.

BROADER IMPLICATIONS

DISTURBANCE AND VEGETATION PATTERNS IN TMFs.—In theory, wherever environmental conditions and biotic components are comparable across the world, similar patterns of vegetation dynamics can be expected to occur. Among the most striking of such examples are the widely separated yet nearly identical wave-regenerated stands on windward slopes in the subalpine Abies-dominated forest of Japan and New England (Sprugel & Bormann 1981). Tantalizing examples of forest patterns comparable with the pine–cloud forest ecotone of the Cordillera Central can be gleaned from the literature. We would expect in situations where high mountains exist in the tropics under the influence of the TWI that a similar ecotone should occur. Perhaps the most similar setting is on Mindanao in the Philippines where a pine–cloud forest ecotone occurs, of which Kowal (1966) notes: ‘...at the border where pine forest and montane forest meet. . . one can clearly observe the role of fire in determining the balance. The boundaries. . . are rather distinct, the ecotone being very narrow. The fires burn up to the nonflammable montane forest and are extinguished’. In the Philippines, however, fire history has been much more radically influenced by long human presence, and probably because of a more severe dry season, pine forests commonly dominate fire successions below the montane cloud forest zone. This arrangement of fire-influenced pine forest both below and above the cloud forest zone seems to prevail in other TMFs where the windward climate at elevations below the cloud zone is somewhat drier than in Hispaniola, such in parts of Mexico (Rzedowski 1978) and the Canary Islands (Fernández-Palacios & de Nicolás 1995). In many other regions, such as Chiapas in southern Mexico, tropical-temperate TMF interactions have been strongly influenced by human disturbances (Ramírez-Marcial *et al.* 2001, Cayuela *et al.* 2006). Even outside the strong influence of the TWI (per Stadtmüller 1987), other tropical-temperate TMF transitions comparable with Hispaniola occur in Central America (Kappelle & Zamora 1995), Southeast Asia (Ohsawa 1990) and South America (Grau & Veblen 2000).

The TMF patterns and dynamics in the Cordillera Central might be expected to be most similar to other mountains in the Greater Antilles; however, in comparison with well-studied sites in Puerto Rico and Jamaica, the TMF in our site is considerably drier (1950 mm vs. 3500–4500 mm maximum mean annual precipitation), and the key role of fire on Hispaniola is not found in these wetter settings. Moreover, although intensive hurricane winds are common throughout the Antilles, wind damage is probably less frequent and extensive at our site because of the greater distance from the coast. Hence, disturbance regimes are quite different across TMFs in the Greater Antilles, and so not surprisingly, TMF structure, composition and dynamics are very different among these sites. For example, although TMF stature generally declines with elevation (Fig. 1D), the TMF in our site does not include true ‘elfin stands’ (Lawton 1982), presumably because of lower moisture (rainfall, cloud immersion) and less wind at this inland location. To our knowledge, the only TMFs in the Caribbean with discrete forest ecotones are found in Hispaniola, with the caveat that

quantitative vegetation patterns in Cuban TMFs remain largely unexplored. In terms of forest composition, perhaps the most striking difference between the Cordillera Central and other Caribbean TMFs is the prominence of *Pinus*: with the exception of Cuba, pine forests at elevations greater than 1000 m are confined to the mountains of Hispaniola (Wadsworth 1999). Also notable is the high abundance of tree ferns (Cyatheaceae) in the Cordillera Central where they comprise ~30 percent of basal area of the cloud forest (Martin *et al.* 2007) vs. < 10 percent in Jamaica (Tanner 1977) and Puerto Rico (Weaver 1995), and species of *Cyrtilla* that dominate parts of high-elevation Cuban, Puerto Rican and Jamaican TMFs yet appear to be wholly absent from the Cordillera Central. Overall, taxonomic overlap between the TMF tree floras of these three sites also is very low, both at the species (< 10%) and even the genus (15–20%) level.

The role of catastrophic disturbances in shaping the dynamics of TMFs has gained greater appreciation in recent years compared with the previously prevailing emphasis placed on environmental controls (Hamilton *et al.* 1995). Our observations highlight the apparent interactions among environment, disturbance regime and vegetation zonation. Although the frequency of catastrophic disturbances by fire and hurricanes in the Cordillera Central is higher than for most other TMFs, it seems clear that more quantitative study of the long-term role of disturbances in shaping TMF vegetation is needed.

CLIMATE CHANGE AND THE FUTURE OF TMFs.—The outlook for TMFs under rapidly changing global climatic conditions has been the subject of much speculation (Hamilton *et al.* 1995, Loope & Giambelluca 1998, Hotchkiss & Juvik 1999, Foster 2001) and remains highly uncertain. The nature of these uncertainties is particularly apparent in the case of the cloud forest of the Cordillera Central, where changes in at least five climatic phenomena can be expected to exert an overarching influence on patterns of vegetation distribution: (1) warming temperatures and decreased frequency of winter frost; (2) increased frequency or intensity of hurricanes (Webster *et al.* 2005); (3) high-elevation drought and decreased cloudiness (Loope & Giambelluca 1998); (4) changes in frequency of ENSO (Timmermann *et al.* 1999); and (5) changes in the elevation of the TWI (Loope & Giambelluca 1998). On one hand, the elevation optima and upper elevation limits of many tropical species could be shifted upward by warming climate. Moreover, increased hurricane damage to pine forest could favor invasion by cloud forest species as noted following Hurricane Georges (Martin *et al.* 2007). These responses, however, could be counteracted by reductions in cloudiness and increases in the frequency or intensity of high-elevation drought.

The role of climate change on the fire regime will be critical and the direct effects of these climatic drivers on fire probability (*e.g.*, increased droughts) will likely interact with the feedback effects of vegetation structure and composition (*i.e.*, differences in flammability between pine and cloud forest), with the fire-resistant cloud forest perhaps buffering lower elevation forests from an increase in high-elevation fire frequency. Cloud forest is highly dependent on cloud immersion, however, so its distribution and

continuity also will be subject to changes in the TWI and the elevation and frequency of cloud formation. Given the role that prior climate fluctuations—particularly the warm and dry period during the Holocene optimum documented in some TMFs—have played historically in increasing fire in TMFs (*e.g.*, Bush *et al.* 2005) and the evidence that fires are increasing in frequency and severity throughout TMFs in recent decades (Asbjornsen & Wickel 2009), we expect that fire will continue to exert a major and increasing influence on the forests of Cordillera Central and other similar TMFs.

In sum, a suite of highly uncertain and potentially countervailing forces can be expected to influence cloud forest distribution in the era of rapid global climatic change. One potential outcome might be the elimination of the particular combinations of vegetation components we see today as new combinations of climatic factors prevail across the montane landscape, in a manner comparable with paleoecological observations from changing Holocene climatic environments in the temperate zone (Webb 1987) and in other tropical montane regions (Bush *et al.* 2005).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of study area and permanent vegetation plots established in 1999–2000, Bermúdez and Ramírez National Parks, Cordillera Central, Dominican Republic.

FIGURE S2. View of the pine-cloud forest ecotone on a windward slope in the Cordillera Central, Dominican Republic.

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Supporting Information

FIGURE S1. Map of the study area in the Bermúdez and Ramírez National Parks, Cordillera Central, Dominican Republic showing the location of the 0.1 ha vegetation plots established in 1999–2000.

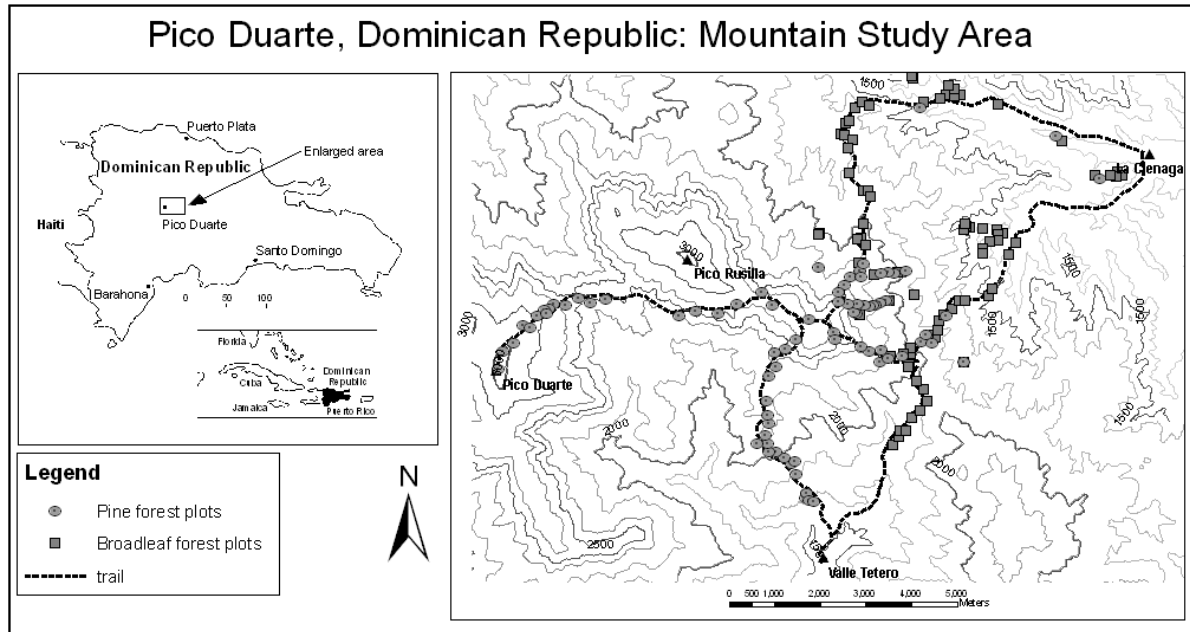


FIGURE S2. View of the distinct pine-broadleaf forest ecotone on a windward slope in the Cordillera Central, Dominican Republic. The higher elevation pine forest experienced moderate to severe burn in the March, 2005 fire, but the fire quickly extinguished in the cloud forest. Note the small-scale variation in the elevation of the ecotone associated with topography and slope aspect.

