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ORIGINAL ARTICLE

Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic

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ABSTRACT

Aim We examined relationships between climate–disturbance gradients and patterns of vegetation zonation and ecotones on a subtropical mountain range.

Location The study was conducted on the windward slopes of the Cordillera Central, Dominican Republic, where cloud forest appears to shift in a narrow ecotone to monodominant forest of *Pinus occidentalis*.

Methods Climate, disturbance and vegetation data were collected over the elevation range 1100–3100 m and in 50 paired plots along the ecotone. Aerial photographs were georeferenced to a high-resolution digital elevation model in order to enable the analysis of landscape-scale patterns of the ecotone.

Results A Shipley–Keddy test detected discrete compositional ecotones at 2200 and 2500 m; the distributions of tree species at lower elevations were continuous. The elevation of the ecotone determined with aerial photographs was fairly consistent, namely ± 164 m (SD) over its 124-km length, but it exhibited significant landscape variation, occurring at a lower elevation in a partially leeward, western zone. The ecotone also occurred significantly lower on ridges than it did in drainage gullies. Ecotone forest structure and composition differed markedly between paired plots. In pine paired plots, the canopy height was 1.7 times higher and the basal area of non-pine species was 6 times lower than in the cloud forest directly below. Fire evidence was ubiquitous in the pine forest but rare in the abutting cloud forest. Mesoclimate changed discontinuously around the elevation of the ecotone: humidity and cloud formation decreased markedly, and frost frequency increased exponentially.

Main conclusions The discreteness of the ecotone was produced primarily by fire. The elevational consistency of the ecotone, however, resulted from the overarching influence of mesoclimate on the elevational patterns of fire occurrence. Declining temperature and precipitation combine with the trade-wind inversion to create a narrow zone where high-elevation fires extinguish, enabling fire-sensitive and fire-tolerant taxa to abut. Once established, mesotopography and contrasting vegetation physiognomy probably reinforce this boundary through feedbacks on microenvironment and fire likelihood. The prominence of the pine in this study – and of temperate and fire-tolerant taxa in subtropical montane forests in general – highlights the importance of climate-disturbance–biogeography interactions in ecotone formation, particularly where fire mediates a dynamic between climate and vegetation.

Keywords

Cloud forest, Dominican Republic, disturbance, ecotone, fire regime, hurricanes, *Pinus occidentalis*, trade-wind inversion, tropical montane forest, zonation.

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INTRODUCTION

Discrete ecotones in vegetation composition and physiognomy have long fascinated ecologists (e.g. Whitney, 1898; Whittaker, 1956; Witty & Knox, 1964; Holdridge, 1967; Siccama, 1974; Young, 1993; Mast & Wolf, 2004; Hemp, 2006). Such discontinuities in composition may offer insights into the factors controlling the assembly of plant communities. Pioneering work by Whittaker (1956, 1967) and others advanced the now prevailing theory of individualistic species turnover along environmental gradients, such as those associated with elevational changes in temperature and moisture; in this theory, discrete vegetation boundaries should be associated with pronounced environmental discontinuities (e.g. soil parent materials) or with contrasting disturbance history.

An ecotone can also develop or sharpen from feedbacks of the dominant species on the microenvironment or disturbance likelihood (e.g. Siccama, 1974; Harmon *et al.*, 1983; Kalisz & Stone, 1984; Barton, 1993; Young, 1993; Biddulph & Kellman, 1998), the so-called vegetation switch (Wilson & Agnew, 1992).

Early classifications of tropical montane forests (TMFs) maintained that distinctive elevational thresholds in climate, together with the sensitivity of TMF flora to cloud and frost occurrence, resulted in floristically distinct zones with discrete boundaries (Richards, 1952; Grubb & Whitmore, 1966; Holdridge, 1967; Grubb, 1974). Tropical mountains do have a largely aseasonal temperature regime, which results in discrete thermal zones with little temperature overlap, and temperature discontinuities along the elevational gradient (Janzen, 1967). Tropical montane mesoclimates are further stratified by a synoptic subsidence inversion – the trade-wind inversion (TWI). The TWI traps moist air and clouds on windward slopes below a roughly constant elevation (Riehl, 1979; Schubert *et al.*, 1995), above which pronounced decreases in humidity and precipitation can occur over short distances. Nevertheless, ensuing studies challenged the paradigm of vegetation zonation in TMFs, finding a continuum in species distributions with elevation (Hartshorn & Peralta, 1988; Burger, 1995; Lieberman *et al.*, 1996; Lovett, 1998; Vázquez & Givnish, 1998), while other studies continued to report discrete vegetation boundaries on tropical mountains (e.g. Woldu *et al.*, 1989; Kitayama, 1992; Kitayama & Mueller-Dombois, 1994b; Fernández-Palacios & de Nicolás, 1995; Kitayama, 1995; Ashton, 2003; Hemp, 2005). Robust quantitative studies of compositional distributions that could address this debate require highly replicated, fine-scale sampling (e.g. Vázquez & Givnish, 1998), but such studies are rare, primarily because of the large sampling area needed for species capture in species-rich tropical plant communities.

A promising line of inquiry is to integrate disturbance with gradient analysis. Discrete ecotones may not develop where environmental gradients are the primary control on TMF vegetation patterns (e.g. Lieberman *et al.*, 1996). Instead, environment, disturbance and vegetation may interact to form discrete ecotones. In particular, hurricanes (e.g. Boose *et al.*, 1994; Bellingham *et al.*, 1995) and wild fires (e.g. Ellenberg, 1979; Corlett, 1987; Lægaard, 1992; Young, 1993; Grau & Veblen, 2000) can have a pronounced influence on vegetation patterns in TMFs. However, the role of disturbance has received comparatively little attention in addressing these patterns (e.g. Lawton & Putz, 1988; Hamilton *et al.*, 1995; Waide *et al.*, 1998; Arriaga, 2000).

In the virgin forests on the windward slopes of the Cordillera Central, Dominican Republic, vegetation composition appears to shift abruptly from species-rich cloud forest to a monodominant forest of *Pinus occidentalis* Swartz (Fig. 1; Sherman *et al.*, 2005). Gradual decreases in temperature and moisture with elevation would not be expected to establish such a discrete ecotone; however, fires (Martin & Fahey, 2006) and catastrophic hurricane winds (Martin *et al.*, 2004; Sherman *et al.*, 2005) are common in this ecosystem. To contribute to the 'zonation vs. continuum' issue in TMFs, the goal of the present study was to determine if forest compositional change with elevation in the Cordillera Central is gradual or discrete, and to examine the interactions of environment, disturbance

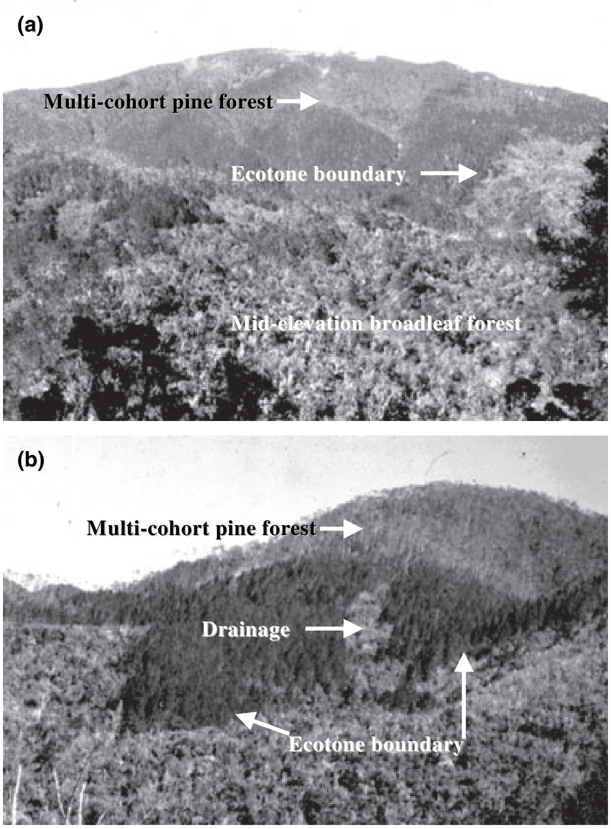

Figure 1 (a) The vegetation mosaic and pine–cloud forest ecotone on the windward slopes of the Cordillera Central, Dominican Republic. Darker areas at higher elevation are monodominant forest of *Pinus occidentalis*. At *c.* 2350 m elevation and higher, the pine forest changes from a single-cohort to a multi-cohort pine forest. (b) Close-up of the ecotone. The lowest extension of pine forest in this photograph occurs at *c.* 2100 m. (Photographs by P.H. Martin, January 2000).

and vegetation in regulating the nature and position of this ecotone. We hypothesized that (1) vegetation composition and structure would differ across the ecotone as a result of contrasting disturbance history, (2) the elevation of the ecotone would generally coincide with the average elevation of the TWI across the mountain range, and (3) the elevation of the ecotone would vary in relation to mesotopography.

METHODS

Study area

The Cordillera Central mountain range is located in the centre of the Dominican Republic, Hispaniola (Fig. 2, inset). Our study area encompassed *c.* 65 km^2 of virgin forest within two national parks (Parques Bermúdez and Ramírez), ranging in elevation from 1100 m to over 3000 m, and spanning the windward (north-eastern) and leeward (south-western) slopes of the central massif. The climate in the study area is seasonal: December–March ('winter') is marked by drier and colder weather, and the higher elevations of the Cordillera Central (above 2000 m) are unique in the Caribbean in experiencing regular below-freezing temperatures (Pedersen, 1953). As reported by Sherman *et al.* (2005), annual precipitation on the windward slopes averages about 1800 mm, but only *c.* 80 mm month^{-1} in January–March. The Cordillera Central exhibits a marked rainshadow as influenced by the trade winds from the north-east, with markedly higher rainfall on windward slopes. The geology of the Cordillera Central is complex, dominated by volcanic, metamorphic and plutonic rocks of Cretaceous origin (Lewis, 1980). The topography is rugged, with steep and sharply dissected slopes. Forest vegetation across the study area has been classified into five major associations: (1) low-elevation riparian forests (see also Martin *et al.*, 2004); (2) low-to-mid-elevation evergreen broadleaf forests; (3) mixed broadleaf–pine forests; (4) high-elevation cloud forests; and (5) open and closed monodominant and monospecific pine forests at the highest elevations and on the leeward slopes (Sherman *et al.*, 2005). Hurricanes, landslides and fires frequently disturb the vegetation in the study area. The fire regime is mixed, with frequent surface fires and occasional crown fires; the site mean point fire return interval averages 31.5 years and exhibits significant elevational variation, with the longest fire interval at mid-elevations on the windward slope and the shortest on the leeward slopes (Martin & Fahey, 2006). Ignition sources are probably a combination of lightning and human actions (Horn *et al.*, 2000; Martin & Fahey, 2006): fires were frequent in the Dominican highlands thousands of years before the first human colonization of Hispaniola (Horn *et al.*, 2000).

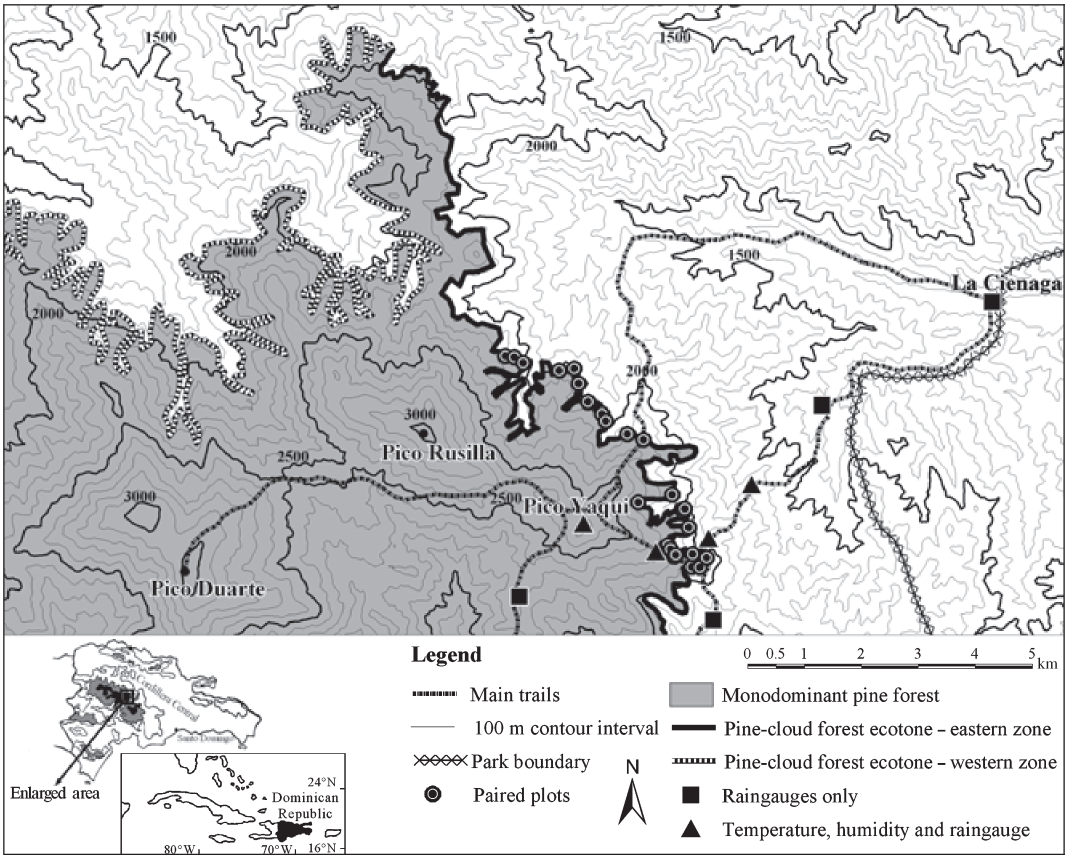

Figure 2 Map of the pine–cloud forest ecotone and the extent of monodominant pine forest in the Cordillera Central, Dominican Republic. Vegetation types were delineated with a photomosaic constructed from rectified, georeferenced aerial photographs taken in 1999.

Climate measurements

We measured selected climate parameters across the study area, as detailed climate records were lacking. Precipitation (PPT) was measured from February 1999 through September 2001 at nine locations (seven on the windward slope, two on the leeward slope) using recording rain gauges (Rainew Tipping Bucket Rain Gauge; RainWise Inc., Bar Harbor, ME) positioned in openings ≥ 30 m in radius. Estimates of cloud-base elevation on the windward slopes of the massif were made daily at 15:30 h from April 1999 through September 2000 by visual reconnaissance from a viewpoint at the park entrance in La Ciénaga de Manabáo. Air temperature and relative humidity were measured every half hour 1 m above the ground at four stations from June 2001 through May 2003 using HOBO H8 Pro RH/Temperature data loggers (Onset Computer Corp., Bourne, MA). We used daily minimum air temperatures of 2 and 3°C recorded 1 m above the ground as indicators of ground-frost frequency. 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).

Vegetation sampling

Fifty circular, 0.05-ha plots were paired along the ecotone (25 pairs) (Fig. 2). Given the rugged terrain, paired-plot sampling was focused on the portion of the ecotone where access was reasonably feasible with the existing system of trails. Paired plots were located at random every 0–250 m along the ecotone boundary: one plot in the pine forest, and the other in the cloud forest. Within each plot, all trees ≥ 10 cm DBH were measured, tagged, and identified in the field by their common name with the help of a local guide (Francisco Peralta, Dominican Park Service). Type specimens of all woody plants were identified to species or genus at the National Botanical Garden in Santo Domingo, Dominican Republic. Nomenclature follows Liogier (1982). Importance values (IV = relative basal area + relative density/2) were calculated for each species in both plot types of the paired plots. The heights of three canopy-dominant trees were measured using a digital hypsometer. Understorey woody plants < 10 cm DBH were identified and enumerated in a subplot 1-m wide and 25-m long oriented along the slope aspect of each plot. At the centre of each plot, we recorded location (with a Garmin GPS 12 receiver), elevation (with a calibrated altimeter), slope angle in the cardinal directions, and aspect. The average slope was calculated for each plot, and the convexity or concavity of each plot was quantified with a terrain shape index (TSI; McNab, 1989). We also inspected the topography between paired plots, noting any pronounced changes in slope angle and aspect.

Sherman *et al.* (2005) provided detailed descriptions of methods for a suite of 245 vegetation sampling plots (0.05 and 0.1 ha) distributed across the full elevational range of the study area. In the present study, we provide additional analysis from these plots to explore evidence of a discrete ecotone, including: (1) a test of elevational turnover of tree-species composition (Shipley & Keddy, 1987), (2) the elevational patterns of overstorey and understorey (saplings and seedlings) tree-species richness, and (3) the elevational ranges of tree species.

Vegetation mapping

To explore the landscape-scale spatial variation of the ecotone, we mapped forest vegetation from aerial photographs (1 : 24,000 scale) covering 150 km^2 of the region, including the core 65-km^2 study area. These photos were taken in 1999 by GPS Aerials, Inc., with standard practices of photo forward-lap and side-lap to enable stereoscopy and area correction. Remote sensing was useful because the ecotone extended west along the mountain range, where sampling and scouting were nearly impossible owing to the extreme terrain, tangled vegetation, and absence of trails. The ecotone was clearly visible in the photographs, and readily delineated as a linear feature based on the edge of canopy pine crowns. The ecotone was extensively ground-truthed and georeferenced with over 100 GPS control points. A photomosaic was constructed from the delineated aerial photographs using standard photogrammetric methods to minimize scale distortions (Paine, 1981). The mosaic was digitized and further corrected with a grid of georeferenced control points using ArcGIS software (ESRI 2002). This high-resolution map was overlaid on a 20-m digital elevation model (DEM; Dirección General de Minería) to compare the ecotone location with elevation and topography. These methods allow for a spatial resolution of ≤ 0.25 ha.

With this map and DEM, we estimated the elevation, slope angle and aspect of the pine–cloud forest boundary from points taken at 50-m intervals along the entire length of the ecotone boundary ($n = 2482$ sample points). In addition, we compared the eastern and western sections of the ecotone boundary, as bisected by a major north–south ridge (Fig. 2). Finally, to explore the influence of ridge-drainage topography on the elevation of the ecotone, we recorded the elevation of ridges and drainage gullies along the ecotone.

Disturbance characterization

We recorded disturbance evidence in each plot: fire evidence, canopy gaps, landslides, wind damage (uprooted, snapped-off trees, and old downed logs), standing dead stems, canopy damage, and vegetation indicators of recent disturbance. Fire evidence included: charcoal in the forest floor and soil (based upon five soil cores per plot), trunk charring, and number of fire scars on tree trunks. Windthrow was classified into ‘recent’ and ‘old’ categories according to the relative decay status of tip-ups and tree snaps: ‘recent’ windthrow was confined to trees with no evidence of advanced decay, fungi, and bark and foliage loss. Standing dead trees and snags were enumerated in each plot. When highly abundant, the presence of two ferns

– *Gleichenia revoluta* Kunth and *Pteridium aquilinum* var. *arachnoideum* (Kaulf.) Brade, both known as indicators of recent disturbance (Walker *et al.*, 1996) – was noted. Finally, a high abundance of epiphytic and forest-floor bryophytes was noted as an indicator of a lengthy fire-free interval, as most bryophytes are very fire-sensitive (Kessler, 2000).

Pinus occidentalis forms annual growth rings (Speer *et al.*, 2004) and frequently records surface fires as fire scars (Martin & Fahey, 2006), making it feasible to estimate stand age and fire patterns. Because the pine is a pioneer of disturbed areas (Darrow & Zanoni, 1990), increment cores were also extracted from the largest pines in each paired plot (3 cores plot^{-1}) to estimate the age of a stand. By standing downslope, it was possible to extract cores from the base of the truck because of the steep slopes. We surfaced cores in the laboratory, finishing with ANSI 400-grit. For cores that missed the pith, age was estimated with the method described by Arno & Sneck (1977).

Data analysis

To determine if the distributions of tree species were individualistically or discretely zoned with elevation, we conducted a statistical analysis of the spatial aggregation of species' elevational limits (Shipley & Keddy, 1987; see Vázquez & Givnish, 1998). We also analysed spatial variation in the elevation of the ecotone boundary as a function of landscape position (eastern vs. western) and topography (slope, aspect and ridge drainage) with *t*-tests with a Bonferroni correction for multiple comparisons. However, as estimates of the ecotone elevation were made from mapped data, some degree of spatial autocorrelation is probable, as nearby observations are more likely to have similar elevations than distant locations (Fortin, 1999). This lack of independence requires a reduction in the degrees of freedom as a function of the degree of spatial autocorrelation (Fortin & Payette, 2002). We performed an autocorrelation function (analogous to a time-series analysis; Box *et al.*, 1994) on the elevation of the ecotone to determine the degree of spatial autocorrelation, and reduced the degrees of freedom in the statistical analysis accordingly.

Structure and species counts between paired plots were analysed with a one-way analysis of variance (ANOVA). All post-hoc comparisons were made with the Tukey–Kramer honestly significant difference (HSD) (familywise error rate < 0.05). Differences in the frequencies of disturbance and vegetation categories along the ecotone were assessed in a contingency table with Fisher's exact test with a Bonferroni correction for multiple comparisons. A stepwise multiple linear regression ('forward' type) was used to explore the variables most predictive of cloud-forest invasion (expressed as a percentage of basal area) of pine plots along the ecotone: (1) environment (elevation, slope, TSI, and aspect), (2) disturbance, (3) vegetation indicators, and (4) pine structure (pine basal area, pine density, pine maximum DBH). We could not use charcoal as a predictor, because 100% of pine plots had charcoal evidence. All independent variables were checked for pairwise collinearity < 0.8 with a correlation matrix. All residuals were normal as verified with a Shapiro–Wilk test. Statistical analyses were performed with JMP IN version 5.1 software (SAS Institute, Cary, NC).

RESULTS

Climate

Temperature and precipitation declined gradually with increasing elevation on the windward slope of the Cordillera Central (Fig. 3a,b). Atmospheric humidity declined gradually from 1500 to 2300 m, but more abruptly from 2300 to 2710 m (Fig. 3a). We noted that a cloud belt developed on most days, although occasionally after our observation time. The elevation of the cloud base, which had developed in 52% of the observations by 15:30 h, occurred most frequently between 1800 and 2300 m (Fig. 3c), dropping off sharply at higher elevations. Above 2300 m, we witnessed repeated winter

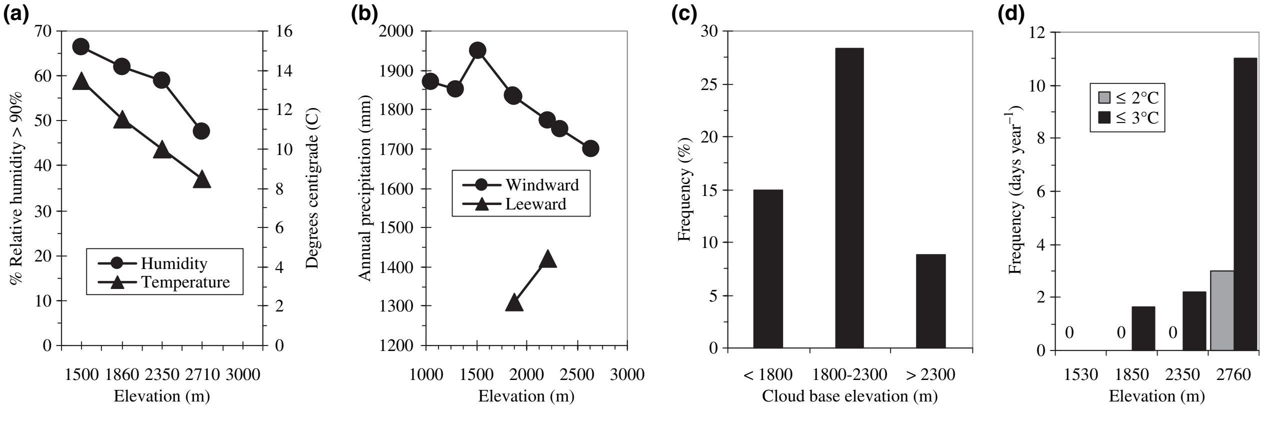

Figure 3 Climate measurements along the elevational gradient in the Cordillera Central, Dominican Republic. (a) Mean annual night temperature and high relative humidity (percentage of measurements ≥ 90% relative humidity); (b) mean annual precipitation on windward and leeward slopes; (c) annual frequency of afternoon cloud-base formation by elevation; and (d) annual frequency of air temperatures ≤ 2°C and ≤ 3°C 1 m above the ground by elevation.

ground frosts. January and February ground frosts occurred most nights at our 2600-m campsite. The lower boundary of regular ground frosts (defined as a temperature of 2°C at 1 m height) occurred between 2350 and 2760 m (Fig. 3d). We occasionally observed ground frosts as low as 1850 m. Minimum air temperatures recorded 1 m above the ground were: 3.6°C at 1530 m, 2.7°C at 1850 m, 1.4°C at 2350 m, and 0.1°C at 2760 m.

Forest composition elevational patterns

Visual inspection of elevational trends in tree-species density (Fig. 4a) and non-pine tree-species regeneration (seedlings and saplings; Fig. 4b) suggests vegetation discontinuities at 2300 and 2600 m, as the rate of decline in species number increased notably at these elevations. From around 1100 to 1500 m, mean tree-species density increased steadily, levelling off at mid-elevations. Of the 15 tree species still present above 2100 m, however, 12 reach their elevational maximum at or below 2350 m (Fig. 5); only two non-pine tree species occur above 2350 m, namely *Garrya fadyenii* (Hooker) and *Weinmannia pinnata* L.

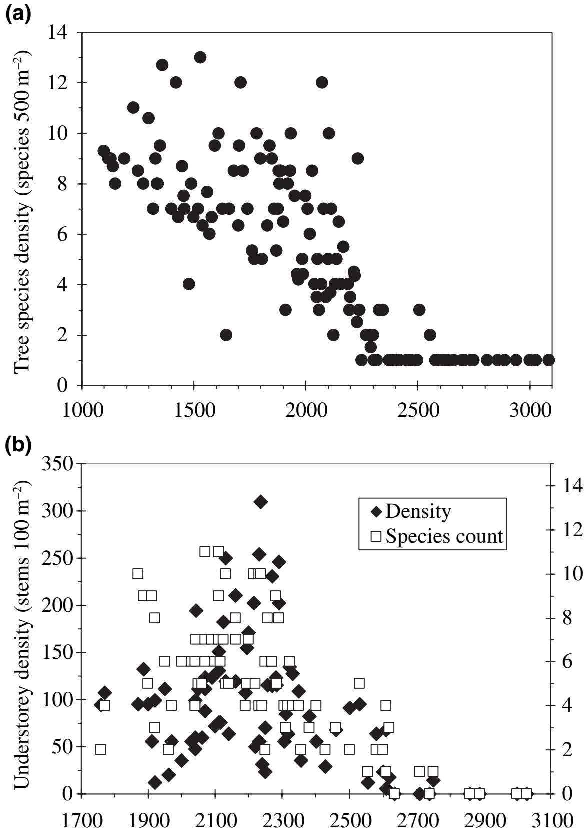

Figure 4 (a) Number of tree species (92 species total) by elevation in the Cordillera Central, Dominican Republic. (b) Understorey density and species counts of non-pine tree-species regeneration (seedlings and saplings) in pine plots by elevation. Pine plots were defined by overstorey pine importance values ≥ 70% (relative basal area + relative density/2). Only pine plots were used in order to enable consistent comparisons over the full elevation range, as cloud-forest plots were confined to below *c.* 2300 m.

Statistical analysis of these patterns (the aggregation of species' distributional limits with elevation, developed by Shipley & Keddy, 1987) showed significantly higher rates of species turnover in two elevational bands when data from a given elevational band were included (standard analysis SS_1, controls for the effects of differences in total species richness) or excluded (jackknife analysis SS_2) (Table 1). According to this analysis, the shift from cloud forest to monodominant pine forest at 2200–2300 m and the shift from monodominant to monospecific pine forest at 2500–2600 m are accompanied by statistically significant higher rates of compositional turnover.

Ecotone landscape patterns

The ecotone boundary, as mapped with the photomosaic, was 124 km in length with a mean elevation of 2007 m (± 164 m standard deviation) (Figs 2 & 6a). This mean elevation is lower than detected in the Shipley–Keddy test because the mapped data examined a different feature of the ecotone, namely the spatial pattern of the visually evident ecotone boundary between cloud forest and monodominant pine forest. It is noteworthy that fundamentally different methods provide a similar result.

Landscape variation in the ecotone was analysed using every fifth sample (i.e. 250 m apart) because spatial autocorrelation dropped to zero at ecotone lengths > 200 m, as indicated by the autocorrelation function analysis. The elevation of the ecotone showed no significant patterns with slope angle or aspect. However, the mean ecotone elevation in the eastern zone was significantly (*t*-test, $P < 0.0001$) higher than that in the western zone – on average 150 m higher. This difference was largely the result of the extensions of monodominant pine forest to elevations as low as 1570 m in the western zone vs. a low elevation of 1893 m in the eastern zone. In contrast, the maximum elevation of the cloud forest did not differ significantly between zones (*t*-test, $P < 0.91$; Fig. 6a). Ridge-and-drainage topography also affected the elevation of the ecotone, which was on average significantly (*t*-test, $P < 0.0005$) lower on ridges than on drainage gullies (Fig. 6b).

Vegetation and disturbance at the ecotone

Forest composition and structure differed significantly between paired plots (Tables 2 and 3). Mean canopy height ($P < 0.0001$) and bole volume ($P < 0.005$) were almost twice as high in the pine plots, while tree-species richness (no. species^{-1} 500 m^2; $P < 0.0001$) and dead tree density ($P < 0.009$) were about twice as high in cloud-forest plots. Arborescent ferns (Cyatheaceae) dominated the cloud-forest paired plots, as was the case throughout the cloud forest (Sherman *et al.*, 2005); they were also the second most abundant taxon in pine plots. *Brunellia comocladifolia* H&B and *Garrya fadyenii* were also notably abundant in both plot types. Three dominant cloud-forest species (*Podocarpus aristulatus* Parl., *Antirhea oligantha* Urb., and *Ditta maestrensis* Borhidi) were very rarely observed in the pine plots, while the shrub *Myrica picardae* Krug & Urb. was found only in pine plots.

Indicators of disturbance also differed significantly between plot types (Table 3). The incidence of all fire indicators (charcoal, charred trunks, and fire scars) was significantly

Table 1 Number of species reaching elevational limits (E) vs. the number of species present not reaching elevational limits in each elevational band (N) on the windward slopes of the Cordillera Central (Shipley & Keddy, 1987; adapted from Vázquez & Givnish, 1998). Standard scores $[(X_i-\mu)/\sigma]$ for E/N are given for all elevational bands (SS_1), and a jackknife analysis excluding the elevational band in question from the mean μ and the standard deviation σ of E/N (SS_2). If the absolute value of the score exceeds 1.96, this indicates an elevational band with significant aggregation of species distributional limits (denoted with an asterisk '*'). Note: the same elevation bands remained statistically significant if the analysis included only those elevations up to the start of mono-specific pine forest (2500–2600 m) or elevations up to the top of the gradient (3000 m).

Elevation (m)	E	N	E/N	SS_1	SS_2
1300–1400	7	21	0.33	−0.06	−0.06
1400–1500	3	26	0.12	−0.42	−0.44
1500–1600	7	25	0.28	−0.15	−0.15
1600–1700	3	28	0.11	−0.44	−0.45
1700–1800	1	26	0.04	−0.55	−0.57
1800–1900	4	23	0.17	−0.32	−0.34
1900–2000	4	21	0.19	−0.30	−0.31
2000–2100	5	17	0.29	−0.13	−0.13
2100–2200	4	14	0.29	−0.14	−0.14
2200–2300	9	5	1.80	2.37*	3.09*
2300–2400	2	3	0.67	0.49	0.51
2400–2500	0	3	0.00	−0.61	−0.64
2500–2600	2	1	2.00	2.71*	3.88*
2600–2700	0	1	0.00	−0.61	−0.64
2700–2800	0	1	0.00	−0.61	−0.64
2800–2900	0	1	0.00	−0.61	−0.64
2900–3000	0	1	0.00	−0.61	−0.64

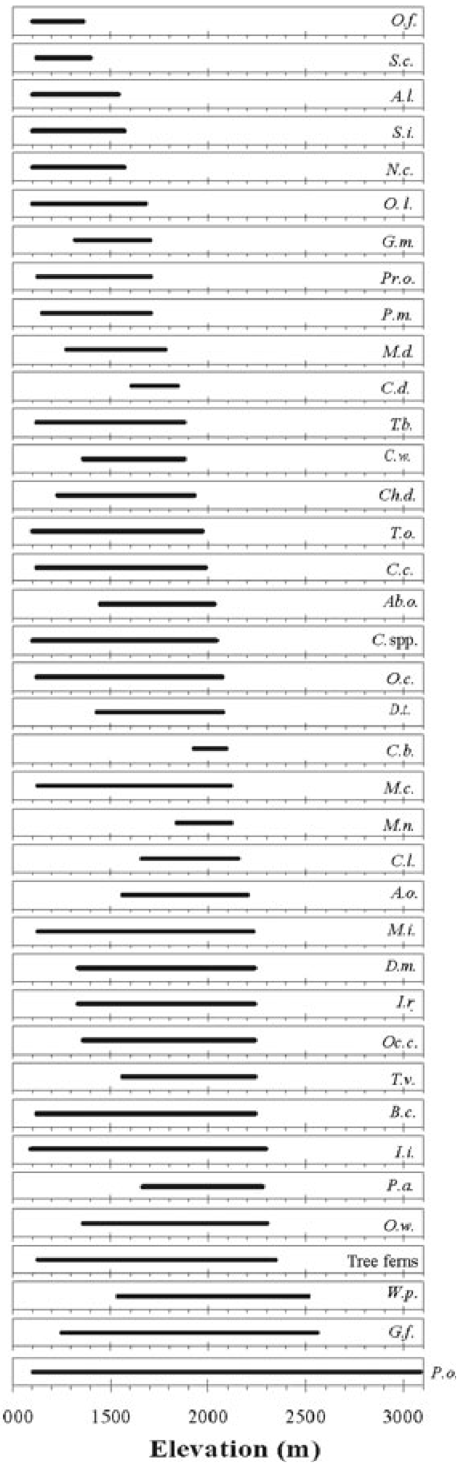

Figure 5 Elevation ranges of 38 tree species in a montane forest in the Cordillera Central, Dominican Republic. For tree species with a maximum elevation below 1800 m, only species with > 10 individuals sampled are shown. Species codes are as follows: *O.f.*, *Ocotea floribunda* (Sw.) Mez; *S.c.*, *Sideroxylon cubense* (Griseb.) T. Pennintong; *A.l.*, *Alchornia latifolia* Sw.; *S.i.*, *Sloanea ilicifolia* Urb.; *N.c.*, *Nectandra coriacea* (Sw.) Griseb.; *O.l.*, *Ocotea leucoxylon* (Sw.) Mez; *G.m.*, *Gyrotaenia myriocarpa* Griseb.; *Pr.o.*, *Prunus occidentalis* Swartz; *P.m.*, *Prestoea montana* (R. Graham) Nichols; *M.d.*, *Myrcia deflexa* (Poiret) DC.; *C.d.*, *Chaetocarpus domingensis* G. Proctor; *T.b.*, *Tabebuia berterii* (DC) Britton; *C.w.*, *Coccoloba wrightii* Lindau; *Ch.d.*, *Chionanthus domingensis* Lam.; *T.o.*, *Turpinia occidentalis* (Sw.) G. Don; *C.c.*, *Clusia clusioides* (Griseb) D'arcy; *Ab.o.*, *Abarema oppositifolia* (Urban) Barneby & Grimes; *C.* spp., *Citharexylum* spp.; *O.c.*, *Oreopanax capitatus* (Jacq.) Decne. & Planch.; *D.t*, *Didymopanax tremulus* Krug & Urb.; *C.b.*, *Cleyera balleana* (O.C. Schmidt) Kobuski; *M.c.*, *Myrsine coriacea* (Sw.) R.Br; *M.n.*, *Myrsine nubicola* Liogier; *C.l.*, *Calypthrantes limoncillo* Liogier; *A.o.*, *Antirhea oligantha* Urb.; *M.i.*, *Meliosma impressa* Krug & Urb.; *D.m.*, *Ditta maestrensis* Borhidi; *I.r.*, *Ilex repanda* Griseb.; *Oc.c.*, *Ocotea cicatricosa* C.K. Allen; *T.v.*, *Tabebuia vinosa* A.H. Gentry; *B.c.*, *Brunellia comocladifolia* H&B.; *I.i.*, *Ilex impressus* Loes. & Ekm.; *P.a.*, *Podocarpus aristulatus* Parl.; *O.w.*, *Ocotea wrightii* (Meissn) Mez.; Tree ferns, Cyatheaceae; *W.p.*, *Weinmannia pinnata* L.; *G.f.*, *Garrya fadyenii* (Hooker); *P.o.*, *Pinus occidentalis* Swartz.

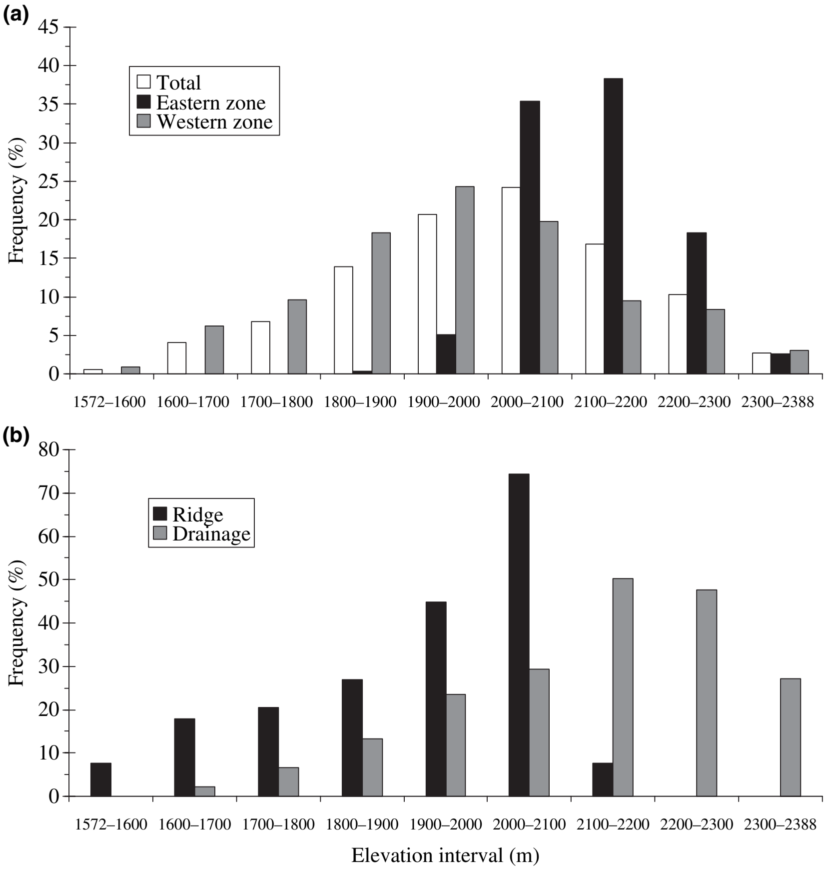

Figure 6 (a) Elevation distribution of the pine–cloud forest ecotone in the Cordillera Central, Dominican Republic. Elevation estimates were made from a georeferenced photomosaic every 250 m along the 124-km length of the mapped ecotone boundary. Categories include the total ecotone, and eastern and western sections of the ecotone bisected by a major north–south ridge *c.* 2100 m in elevation (see Fig. 2). Summary statistics for each category are as follows. *Total boundary*: mean = 2007 m (± 164 SD); *Eastern zone*: mean = 2125 m (± 83 SD), max = 2366 m, min = 1893 m; *Western zone*: mean = 1967 m (± 172 SD), max = 2388 m, min = 1572 m. (b) Elevation distribution of the pine–cloud forest ecotone by ridge and drainage topography. Summary statistics for each category are as follows. *Ridges*: mean = 1902 m (± 154 SD), max = 2125 m, min = 1572 m; *drainages*: mean = 2110 (± 171 SD), max = 2388 m, min = 1673 m.

higher in pine plots ($P < 0.0001$ for all types, Fisher's exact test). Charcoal was found in 100% of the pine plots and in 22% of the cloud-forest plots. Fire-scar evidence indicated that 40% of the pine plots recruited after a single fire, while the remaining 60% experienced two or more fires that repeatedly burned out at the cloud-forest boundary. Conversely, abundant growth of fire-sensitive bryophytes occurred in significantly higher frequencies in cloud-forest plots ($P = 0.035$, Fisher's exact test). Recent wind damage was also significantly more frequent in cloud-forest plots ($P = 0.04$, Fisher's exact test); however, 35% of recent wind damage consisted of tip-ups and snap-offs of pine trees felled during Hurricane George in September 1998, converting sections of the ecotone into cloud forest. Older wind disturbance – probably associated with Hurricane David and Hurricane Frederick in 1979 – was observed in many of the paired plots, but it did not vary significantly across the ecotone ($P = 0.625$, Fisher's exact test; Table 3).

Ring counts from the largest pines at the ecotone indicated a large range in stand age (35–150 years). In a section of the ecotone near Pico Yaqui (Fig. 2), many dominant pines aged to *c.* 1965, which corresponds to the last major fire year in that part of the study area (Martin & Fahey, 2006). Structural variation was high in the cloud-forest paired plots, where tree density ranged from 120 to 1680 stems ha^{-1}, and basal area ranged from 2.7 to 74.3 m^2 ha^{-1}. Structural variation in pine paired plots was much narrower: density ranged from 200 to 960 stems ha^{-1}, and basal area ranged from 12.2 to 49.6 m^2 ha^{-1}.

Invasion of the pine paired plots by cloud-forest species varied along the ecotone: basal area of cloud-forest tree species ranged from 0 to 18 m^2 ha^{-1} in pine stands. In decreasing importance, the significant predictors (Stepwise regression, $F_{3,23} = 7.12$, adjusted $R^2 = 0.42$, $P = 0.0016$) of increased density of cloud-forest trees in pine plots were decreasing pine density ($R^2 = 0.22$, $P = 0.005$), the presence of abundant epiphytic bryophytes ($R^2 = 0.21$, $P < 0.05$), and greater evidence of old windthrow ($R^2 = 0.03$, $P < 0.01$). Sapling density of cloud-forest tree species in the pine-forest understorey ($F_{2,23} = 13.0$, adjusted $R^2 = 0.49$, $P = 0.0002$) was best predicted by the presence of abundant epiphytic bryophytes ($R^2 = 0.44$, $P < 0.0007$) and a lower maximum DBH of pine ($R^2 = 0.22$, $P < 0.038$). On average, sapling density of cloud-forest tree species was twice as high when epiphytic bryophytes were abundant on overstorey pine trees.

DISCUSSION

Overview

A discrete ecotone between species-rich cloud forest and monodominant pine forest occurred at *c.* 2200 m on the

Table 2 Composition of live trees (DBH ≥10 cm) from 50 plots (0.05 ha^{-1}) paired along the pine–cloud-forest ecotone in the Cordillera Central, Dominican Republic. Importance values (IV) were calculated by averaging the relative density and relative basal area of each species. Species with an IV of < 1% were pooled as miscellaneous.

Species	Density (no. ha^{-1})	Relative density (%)	Basal area (m^2 ha^{-1})	Relative basal area (%)	Importance value (%)
Pine forest plots					
Pinus occidentalis	419	64	20.2	83	74
Cyathea spp.	71	11	1.0	4	8
Brunellia comocladifolia	28	4	0.5	2	3
Garrya fadyenii	24	4	0.3	1	2
Weinmannia pinnata	13	2	0.2	1	2
Ilex impressus	13	2	0.2	1	1
Didymopanax tremulus	11	2	0.3	1	1
Tabebuia vinosa	13	2	0.2	1	1
Clusia clusioides	9	1	0.3	1	1
Ocotea wrightii	10	2	0.2	1	1
Myrica picardae	11	2	0.1	1	1
Alsophila sp.	7	1	0.1	0	1
Misc (12 spp.)	**26**	**4**	**0.6**	**3**	**3**
	657	100	24.1	100	100
Cloud-forest plots					
Cyathea spp.	375	45	6.8	29	37
Brunellia comocladifolia	76	10	2.8	12	11
Podocarpus aristulatus	32	4	4.2	18	11
Antirhea oligantha	51	6	1.4	6	6
Garrya fadyenii	56	7	1.0	4	6
Ditta maestrensis	30	4	0.6	3	3
Didymopanax tremulus	6	1	1.1	5	3
Ocotea wrightii	17	2	0.8	3	3
Alsophila sp.	25	3	0.4	2	2
Weinmannia pinnata	14	2	0.6	3	2
Tabebuia vinosa	22	3	0.4	2	2
Meliosma impressa	18	2	0.4	2	2
Ocotea cicatricosa	9	1	0.6	3	2
Misc (26 spp.)	**78**	**9**	**2.0**	**9**	**9**
	810	100	23.0	100	100

windward slopes of the Cordillera Central. Below the ecotone, the elevational distributions of tree species support the individualistic hypothesis, as species composition varied continuously (Table 1, Fig. 5). Around 2200 and 2500 m, however, our results indicate that compositional discontinuities occurred, with the Shipley & Keddy (1987) test finding significantly higher rates of turnover at these elevations. Clearly, the discreteness of this ecotone results primarily from fire. What otherwise might be a gradual transition, as species drop out as a result of frost and moisture stress, is a sharply delineated ecotone whose boundary coincides with many separate fires. In this regard, the elevational consistency of the ecotone across the Cordillera Central (Figs 2 & 6a) is notable, because the conditions (e.g. ignition, drought, wind) associated with many separate fires surely varied. Pronounced mesoclimatic gradients, which are strongly associated with the elevational patterns of fire frequency (Martin & Fahey, 2006), override the particularities of fire behaviour. Declining temperature and precipitation combine with the average position of the TWI (frequently observed at 2000–2300 m in the Caribbean; Schubert *et al.*, 1995) to create a narrow climatic zone where most fires extinguish, enabling fire-sensitive and fire-tolerant taxa to abut.

Climate and topography

Climatic variation is expected to influence the position of ecotones through its effects on fitness and competitive interactions (e.g. Stevens & Fox, 1991; Grau & Veblen, 2000). In this study, the key climatic influence is the interaction between the orographic uplift of trade winds and the TWI. As noted, the TWI creates a relatively narrow humid–dry boundary, above which humidity deficits restrict humidity-sensitive species. The TWI creates similar discontinuities in mesoclimates throughout the Tropics on mountains high enough to breach the inversion (Stadtmüller, 1987; Kitayama & Mueller-Dombois, 1994a; Fernández-Palacios & de Nicolás, 1995; Hamilton *et al.*, 1995; Davis *et al.*, 1997), and hence its effects are more commonly seen on subtropical mountains, where the inversion occurs at lower elevations (Stadtmüller, 1987).

Low temperatures and frosts are also important influences on vegetation patterns on tropical mountains, where they limit the elevational maxima of most tropical cloud-forest tree species, in effect creating a high-elevation ‘tropical–temperate’ boundary (Ohsawa, 1995; Ashton, 2003). The influence of temperature in the Cordillera Central is best

Table 3 Forest structure, tree-species counts, and disturbance and vegetation indicators in 50 plots (0.05 ha^{-1}) paired on the pine–cloud-forest ecotone in the Cordillera Central, Dominican Republic. Patterns of statistical significance for structure and species counts were analysed with a one-way ANOVA; disturbance and vegetation presence–absence frequencies were analysed with a contingency table (Fisher's exact test). Fire disturbance includes all evidence of prior fires (charcoal, trunk charring and number of fire scars). Wind disturbance was categorized by visual evidence of the age of windthrown logs, tip-ups and snaps. When *highly* abundant in a plot, the presence of two climbing fern species (*Gleichenia revoluta* and *Pteridium aquilinum*; indicators of recent disturbance; Walker *et al.*, 1996) and of epiphytic and forest-floor bryophytes (indicators of a fire-free stand; Kessler, 2000) were noted. Asterisks (*) denote a statistically significant difference (familywise $\alpha < 0.05$).

Structure and species counts	Cloud forest	Pine forest
Density – living (stems 0.1 ha^{-1})	81.0	65.7
Density – dead (stems 0.1 ha^{-1})	17.4*	10.0*
Basal area – living (m^2 ha^{-1})	23.1	24.1
Basal area – dead (m^2 ha^{-1})	8.1	6.4
Canopy height (m)	10.8*	18.0*
Standing bole volume (m^3 0.1 ha^{-1})	24.9*	44.5*
Tree species counts (spp. 0.05 ha^{-1})	10.3*	4.2*
Disturbance and vegetation indicators (%)		
Charcoal	22*	100*
Trunk charring	0*	52*
1 fire scar	0*	22*
2–3 fire scars	0*	37*
Wind damage – recent	40*	15*
Wind damage – old	61	63
Gaps	39	48
Ferns	26	19
Moss	45*	22*

observed in drainage gullies, where the cloud forest unvaryingly attains its maximum elevation (Figs 2 & 6b), a pattern seen on other tropical mountains (Troll, 1973; Ashton, 2003). In gullies, fire likelihood and moisture stress are correspondingly low, enabling the cloud forest to reach a maximum elevation that is set in part by low temperatures. The elevation of this temperature threshold is suggested by the fact that 12 of 14 cloud-forest tree species reach their maximum elevation between *c.* 2200 and 2350 m (Fig. 5), the zone where temperatures begin to drop discontinuously and frost frequency increases markedly (Fig. 3). Above this zone, pine forest forms a climatic climax, even dominating gullies. Similarly, the lowest elevations of the monodominant pine forest closely track ridges. Ridges are predisposed to rapid drying and are comparatively likely to carry fires (Johnson & Miyanishi, 2001). Where present, other topographic features (e.g. cliffs) protect the cloud forest by creating firebreaks, and in some locations set the ecotone boundary.

Disturbance and vegetation switches

The vegetation and ecotone in our study area are clearly influenced by disturbance. The sharpness and composition of the ecotone is primarily the result of fire patterns, as all pine stands showed evidence of fire. A paradigm of fire-controlled treelines has often been applied in tropical mountains, particularly where influenced by human activities (e.g. Ellenberg, 1979; Corlett, 1987; Lægaard, 1992; Young, 1993; Cavalier *et al.*, 1998); our results demonstrate that fires can create ecotones between TMF associations as well (see also Kowal, 1966; Unwin, 1989; Ohsawa, 1995; Grau & Veblen, 2000; Ashton, 2003; Hemp, 2005). The pronounced influence of fire in this site is not surprising, given the juxtaposition of fire-sensitive cloud-forest flora (e.g., May, 1997) and the fire-tolerant *P. occidentalis* (Darrow & Zanoni, 1990; Martin & Fahey, 2006). The elevational consistency of a fire-generated ecotone is, however, noteworthy. Discontinuities in mesoclimate (Fig. 3) around the ecotone, particularly atmospheric humidity and cloud formation, presumably play a key role in establishing the elevational consistency of the ecotone. Elsewhere, climatic patterns are known to influence the position of ecotones through their influence on fire regimes (Gardner *et al.*, 1996). Today, the extent of the ecotone may in part reflect anthropogenic influences on fire frequency, which increased in *c.* 1900 with the onset of permanent settlement in the region until active fire suppression began in the late 1960s (Martin & Fahey, 2006).

Asymmetric wind damage also played a role in ecotonal vegetation patterns, as evidenced by the effects of Hurricane George in 1998 (Table 3). The contrast in tree height at the ecotone makes the pines more prone to wind damage, converting pine to cloud forest. In general, hurricanes do more damage to conifers (e.g. Foster, 1988; Boucher *et al.*, 1990) than to tropical montane cloud forests (e.g. Brokaw & Walker, 1991; Bellingham *et al.*, 1995). Hurricanes may also reduce the small-scale elevational heterogeneity of the ecotone associated with topography, as ridges are more likely to be damaged by hurricanes (Bellingham, 1991; Boose *et al.*, 1994). At higher elevations, the effects of hurricanes on composition are minor, in part because interior pine stands are better protected from wind, but primarily because pine is the lone arborescent species available to recolonize blow-downs. Hurricanes may also interact with fire severity, dramatically increasing fuels and drying the understorey by opening the canopy (e.g. Goldammer & Price, 1998).

Once established, vegetation patterns probably reinforce the spatial pattern of the fire regime. Pine stands, with comparatively high light understories and well-aerated, combustible needle litter, are fire-prone (Mutch, 1970). Conversely, the structure and physiognomy of the cloud forest should reduce fire likelihood, as epiphytic bryophytes are well known to 'strip' substantial quantities of moisture from clouds even during the dry-season (Bruijnzeel & Proctor, 1995). Because the growth of epiphytic bryophytes is strongly determined by moisture availability (Proctor, 1982), the TWI probably restricts most epiphytic bryophytes below a general elevation: the presence–absence of bryophytes then feedbacks on stand moisture levels and fire likelihood. The role of contrasting vegetation composition and structure in reinforcing spatially segregated fire frequency is well documented in other subtropical and tropical locations (Kalisz & Stone, 1984; Kellman & Meave, 1997; Biddulph & Kellman, 1998).

An appreciation of the importance of disturbance in TMFs has grown considerably, but studies that integrate disturbance into studies of ecotones have lagged (but see Vázquez & Givnish, 1998; Grau & Veblen, 2000). The importance of disturbance in this site contrasts with the exclusive emphasis placed on environmental controls in some TMFs (Grubb & Whitmore, 1966; Stadtmüller, 1987; Kitayama & Mueller-Dombois, 1994b; Hamilton *et al.*, 1995). Certainly, the frequency of catastrophic disturbance in our study area is higher than in most equatorial TMFs, where small gaps and landslides are the principal mechanism of canopy turnover (Brokaw & Walker, 1991). However, hurricanes are important in TMFs in the broader Caribbean, eastern Central America and northern South America (e.g. Brokaw & Walker, 1991; Lugo & Scatena, 1996; Waide *et al.*, 1998; Arriaga, 2000), and tropical East Asia and the western Pacific (e.g. Whitmore, 1989; Herwitz & Young, 1994; Hamilton *et al.*, 1995). As noted, fire is also commonly acknowledged as an important driver of high-elevation vegetation patterns in TMFs (e.g. Smith & Young, 1987; Herwitz & Young, 1994; Vázquez & Givnish, 1998; Ashton, 2003), but more quantitative study is required to elucidate its long-term influence on vegetation patterns.

Biogeography

This study is germane to elevational vegetation patterns in subtropical montane forests, which have received limited attention. Between 15° and 25° latitude there are extensive high-elevation forests influenced by fire and frost that transition from speciose tropical cloud forest to monodominant tree species of temperate lineage, usually from the Pinaceae or Fagaceae (Troll, 1968; Sarmiento, 1986; Frahm & Gradstein, 1991; Ashton, 2003). In particular, the pattern in this study is similar to tropical–temperate transitions in Mexico and Central America (e.g. Rzedowski, 1978; Kappelle & Zamora, 1995; Arriaga, 2000), the Lauraceae–*Pinus* ecotone in South-east Asia (Ohsawa, 1990), a Laurel forest–*Pinus* ecotone in the Canary Islands (Fernández-Palacios & de Nicolás, 1995), forest ecotones in South America (Sarmiento, 1986; Grau & Veblen, 2000; Kessler, 2000), and fire-created ecotones in Australia and Tasmania (e.g. Ash, 1988; Unwin, 1989). Several areas bear a striking similarity to that of our study. In the subtropical Himalayas, the maximum elevation of subtropical tree species is between 2500 and 2800 m, the zone where high-elevation fires and frosts lead to dominance by north-temperate conifers (*Tsuga*, *Abies* and *Picea*) (Ohsawa, 1995; Ashton, 2003). In the Philippines, a pine–cloud forest ecotone occurs, of which Kowal (1966) notes: 'It is… at the border where pine forest and montane forest meet, that one can clearly observe the role of fire in determining the balance. The boundaries… are rather distinct, the ecotone being very narrow. Fires burn up to the nonflammable montane forest and are extinguished.' As in our site, conifers in these studies are typically distributed over a large elevation range, occurring as early successional species at lower elevations and as climax species at high elevations. Montane 'climate-physiognomic' ecotones may be more common in the northern subtropics, where a comparatively abrupt shift occurs from aseasonal to seasonal temperature regimes at 18–20°N (Ohsawa, 1990).

The future of TMFs is uncertain. Human encroachment (Hamilton *et al.*, 1995) and global climate change may exert profound changes on TMF vegetation patterns and the elevational extent of tropical cloud forests, particularly where fire mediates a dynamic between climate and vegetation. The projected rise in tropical temperatures and the 'lifting cloud-base' hypothesis under a doubling of CO_2 concentrations are expected to raise the elevational optima of TMF tree species by several hundred metres (Hamilton *et al.*, 1995; Hotchkiss & Juvik, 1999; Foster, 2001). Other climate-change scenarios, however, project a high-elevation drought on tropical mountains (Loope & Giambelluca, 1998) owing to a general reduction in the cloudiness that envelopes tropical cloud forests (Foster, 2001), a lower elevation of the TWI, and an increased frequency of the El Niño–Southern Oscillation (Timmermann *et al.*, 1999; Hemp, 2005). Increases in fire frequency owing to more frequent or severe El Niño events would probably lower the extent of cloud forest. Vegetation dynamics in this system will be fascinating to follow and present a complex challenge for modelling future forest patterns.

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BIOSKETCHES

Patrick Martin's research focuses on landscape ecology and the dynamics of vegetation communities, including quantifying controls on landscape vegetation patterns by integrating environmental gradients and disturbance regimes, and understanding the long-term effects of exotic species on native plant communities and ecosystem function.

Ruth Sherman's research focuses on understanding processes that control the structure and function of ecosystems, including forest patterns and productivity in tropical mangroves and in tropical montane forests in the Dominican Republic and southwest China. Her goal is to apply scientific methodologies to conservation within an adaptive management framework.

Timothy Fahey conducts research into temperate forests in New Hampshire, examining the effects of soil calcium depletion on sugar maple, and in New York, studying invasive earthworm impacts on the nutrient cycles of forests, and into tropical montane forests in the Dominican Republic, studying the interactions of fire, topography and climatic factors on vegetation pattern and process.

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