

Tropical montane vegetation dynamics near the upper cloud belt strongly associated with a shifting ITCZ and fire

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Summary

1. Tropical montane forests house unusual and diverse biota and are considered highly vulnerable to climate change, particularly near the trade wind inversion (TWI) – the upper end of the cloud belt that defines tropical montane cloud forest (TMCF). The upper cloud belt has two possible futures: one hypothesis postulates a ‘lifting cloud base’, raising both the upper and lower ends of the cloud belt; the other expects the upper end of the cloud belt will change independently, with a ‘shifting TWI’.

2. We used a ~5900-year-long palaeorecord of vegetation and fire from a small forest hollow at 2455 m in the Cordillera Central, Dominican Republic. The site sits near the upper limit of TMCF taxa and the TWI and allows us to evaluate the relationship between vegetation dynamics and two potential drivers of TWI elevation – the Intertropical Convergence Zone (ITCZ) and the El Niño/Southern Oscillation (ENSO).

3. Vegetation changed from cloud forest (~5900–5500 cal. years BP) to alpine grassland (~4300–1300 cal. years BP), to pine savanna (~1300–600 cal. years BP) and finally to closed pine forest (after ~600 cal. years BP). Habitat distribution models for TMCF and pine forest taxa show that these state changes were strongly associated with position of the ITCZ (cloud forest $xR^2 = 0.63$; pine forest $xR^2 = 0.53$), providing support for the shifting TWI hypothesis.

4. We find a negative relationship between fire and TMCF and a hump-shaped relationship between fire activity and pine.

5. *Synthesis.* Shifts up- and downslope of the upper limit of the cloud belt over the last 5900 years produced major vegetation changes. Fire also played a significant role, in particular when pine occupied the site after ~1300 years ago and from 1965 AD when fire suppression led to a rapid return of cloud forest taxa. Our results strongly suggest that latitudinal shifts in the ITCZ position have controlled the upper limit of cloud forest in the Caribbean and understanding how the ITCZ will respond to climate change will be critical for tropical montane conservation strategies.

Key-words: charcoal analysis, Cordillera Central, Dominican Republic, ecotone, Intertropical Convergence Zone, palaeoecology and land-use history, *Pinus occidentalis*, pollen analysis, shifting TWI hypothesis, tropical montane cloud forest

Introduction

Tropical montane cloud forests (TMCFs) have long been recognized for their unique floristic composition and are among the world’s biodiversity hotspots with high levels of endemism (Grubb & Whitmore 1966; Hamilton, Juvik & Scatena 1995; Bruijnzeel *et al.* 2010). The geographic extent of

TMCFs encompasses areas amid ~20° S and 20° N latitude, above ~1000 m elevation and, most importantly, above where cloud formation becomes regular (Stadtmüller 1987; Churchill *et al.* 1995; Webster 1995; Bruijnzeel 2001). Frequent and persistent cloud immersion defines these forests, though they exist in a fairly broad range of climatic conditions and elevations otherwise (Oliveira *et al.* 2014). At higher elevations, TMCF reaches its limit where the cloud zone dissipates or is capped and where freezing temperatures occur, restricting the

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distribution of many tropical montane tree species (Martin, Sherman & Fahey 2007). This band of clouds that limits TMCF distribution is expected to be affected by climate change, with reduced cloudiness overall and altered elevational boundaries (Foster 2001).

The lower end of the cloud belt is determined by the lifting condensation level (LCL), where relative humidity approaches 100% as the air cools with adiabatic lifting. Generally, vegetation composition and structure turns over gradually with elevation across the LCL as well as within the TMCF zone (e.g. Lieberman *et al.* 1996; Vázquez & Givnish 1998; Martin, Sherman & Fahey 2007). The upper end of the cloud zone is set by the trade wind inversion (TWI) in many montane regions of the tropics. The TWI is a temperature inversion that results from the rising moist air of the trade winds encountering the dry descending air of the Hadley circulation (see Stadtmüller 1987; Shubert *et al.* 1995; Cao *et al.* 2007). The change in moisture conditions across the TWI represents one of the steepest climate gradients in the world (e.g. Loope & Giambelluca 1998). On tropical mountains tall enough to breach the TWI, TMCF reaches its upper limit at this elevation and vegetation often transitions to a new state (e.g. subalpine shrubland or grassland; Kitayama & Mueller-Dombois 1992; Kitayama 1995; Martin, Sherman & Fahey 2007; Crausbay & Hotchkiss 2010; Martin, Fahey & Sherman 2011; Crausbay *et al.* 2014).

Because of the remarkable gradients in both climate and biotic composition at the upper end of the cloud zone, the highest TMCFs are considered exceptionally vulnerable to climate change, particularly if future climate changes alter the position of the TWI (Loope & Giambelluca 1998). The height of the TWI at any one location varies on multiple time scales (diurnal to millennial) and is determined by many drivers and feedbacks, including strength of the Hadley subsidence. However, a clear geographic pattern shows that the mean TWI elevation slopes upwards with increased proximity to the Intertropical Convergence Zone (ITCZ; Shubert *et al.* 1995; Cao *et al.* 2007). The ITCZ is the broad area around the tropics where trade winds from each hemisphere meet at the warmest surface waters, creating a band of high rainfall. The ITCZ migrates north or south over long-time scales, responding to changes in temperature and insolation that are driven by Earth's orbital variations (Haug *et al.* 2001), presumably also affecting the mean TWI elevation. In addition, the El Niño-Southern Oscillation (ENSO) influences the TWI, with El Niño events causing a lower and more persistent TWI (Cao *et al.* 2007). When the TWI moves to a lower elevation, it creates a sudden, sharp decline in relative humidity that greatly increases evapotranspiration and water stress, suggesting ENSO-TWI interactions may set the upper distributional limits of TMCF in some locations (Crausbay *et al.* 2014).

Despite a well-documented and comparatively rapid warming trend in tropical mountain regions (Bradley 2006; Giambelluca, Diaz & Luke 2008; Thompson *et al.* 2011), the influence of global change on the climatic conditions (especially cloud formation) in TMCFs remains highly uncertain.

There are conflicting possibilities for the upper end of the cloud zone. The lifting cloud base (LCB) hypothesis maintains that a rise in sea surface temperature (SST) will result in a higher elevation for the LCL and thus the cloud base that defines the lower TMCF boundary (Still, Foster & Schneider 1999). It is often assumed that the LCB hypothesis includes an elevational increase in the upper bound of the cloud belt (e.g. Benning *et al.* 2002). Such a scenario threatens the alpine communities which occur only on the tops of mountains, but allows for TMCF taxa at lower elevations to migrate upslope.

Another hypothesis is that the upper end of the cloud belt will respond independently to global change than the lower end of the cloud belt. The shifting TWI hypothesis suggests the upper end of the cloud belt could shift with changes in the TWI elevation due to a latitudinal shift of the ITCZ, a change in the frequency/intensity of ENSO and/or variation in the strength of Hadley circulation (Loope & Giambelluca 1998; Sperling, Washington & Whittaker 2004). If this upper level of the cloud belt lowers – for a Northern Hemisphere example, if climate change shifted the ITCZ southward – alpine flora adapted to drier conditions above the upper cloud belt could potentially expand downslope (if not strongly temperature limited). However, cloud-dependent flora in TMCFs would likely be squeezed between a 'lifted' cloud base at lower elevations and lower TWI at higher elevations.

This study investigates the shifting TWI hypothesis in the mountains of the Caribbean – one of the hottest of biodiversity hotspots with high levels of endemism richness in plants, vertebrates, amphibians, reptiles and birds (Myers *et al.* 2000; Kier *et al.* 2009). We use palaeorecords from a site at the modern TWI that chart vegetation shifts and fire frequency in the Cordillera Central, Dominican Republic, combined with palaeorecords of ENSO (Moy *et al.* 2002) and ITCZ (Haug *et al.* 2001) from the region. We built habitat distribution models out of these paleorecords to test whether these two drivers of TWI elevation (the ITCZ and ENSO) are associated with past vegetation shifts.

Materials and methods

STUDY SITE

The Cordillera Central is an extensive massif that occupies the central region of the island of Hispaniola, with extensive areas above 2500 m and several peaks over 3000 m including the highest mountain in the Caribbean (Pico Duarte, 3087 m), and it supports an unusual community rich in endemics. The study site occurs in the Cordillera Central, northeast of Pico Duarte within Armando Bermúdez National Park near the upper limit of TMCF taxa (Figs 1 and 2). Montane vegetation above 1000 m on the windward slopes was classified with an ordination (Sherman, Martin & Fahey 2005) wherein vegetation communities include the following (Fig. 2): (i) broadleaf montane forest from 1100 to 1550 m, (ii) mixed pine-broadleaf forest from 1550 to 1900 m, (iii) small-statured cloud forest that lacks pine and is dominated by tree ferns (Cyathaceae), epiphytic bryophytes, and filmy ferns (Hymenophyllaceae) from 1900 m up to 2200 m, (iv) monodominant Hispaniolan pine (*Pinus*

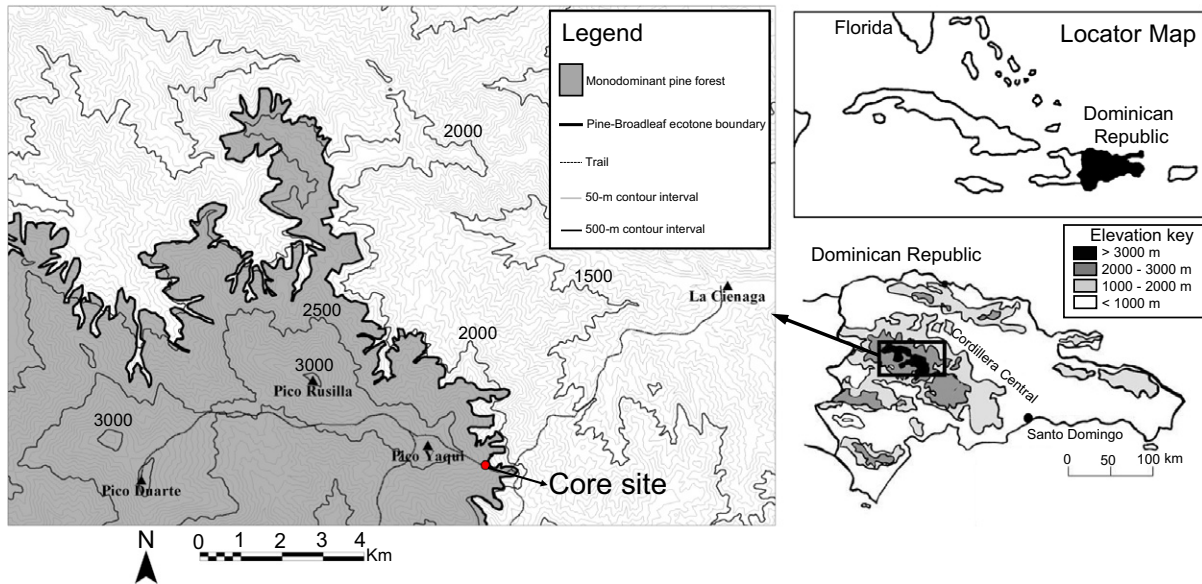


Fig. 1. Location of the coring site, the small hollow named Arrepentimientos, at 2455 m elevation in the Cordillera Central, Dominican Republic.

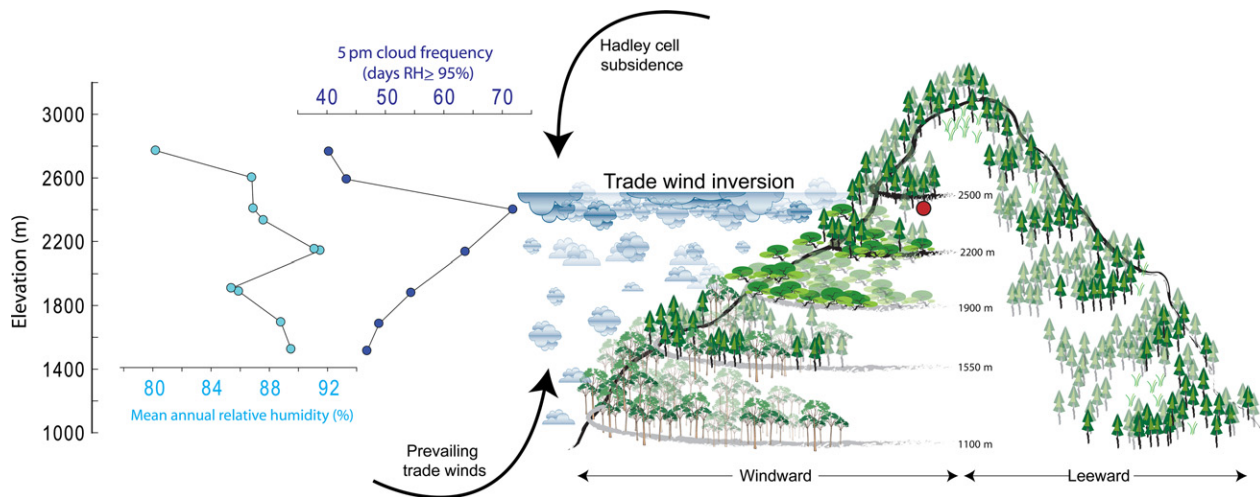


Fig. 2. Vegetation zonation, cloud and humidity patterns along the elevation gradient in the Cordillera Central, Dominican Republic. The left side shows the elevational patterns of mean annual relative humidity and cloud cover frequency at 5 PM (from Martin & Fahey 2014). The cloud patterns at 5 PM are similar throughout the afternoon. The right side shows vegetation zonation patterns (drawn from data in Sherman, Martin & Fahey 2005 and Martin, Sherman & Fahey 2007) by elevation: broadleaf montane forest (1100–1550 m), mixed pine-broadleaf forest (1550–1900 m), cloud forest (1900–2200 m), monodominant pine forests with cloud forest elements (2200–2500 m) and monospecific pine forest covering the highest windward elevations (2500–3087 m) and all leeward slopes. Grey contour lines denote areas with continuous turnover in vegetation composition, and black contour lines denote statistically discontinuous turnover in composition; that is discrete ecotones at 2200 m and 2500 m. The small forest hollow named Arrepentimientos is depicted as a red circle near the ecotone boundary at 2500 m.

occidentalis Swartz) forests from ~2200 to 2500 m with varying degrees of colonization by cloud forest tree species and (v) a mosaic of monospecific pine forest and pine savanna that lacks cloud forest taxa above 2500 m, with ground cover dominated by endemic grasses (*Danthonia domingensis* Hack & Pilger and *Agrostis hiemalis* (Walt.) B.S.P; Sherman, Martin & Fahey 2005). Vegetation change across these zones is gradual, except for a two discrete ecotones – one between the diverse cloud forest and the monodominant pine forest just above it at 2200 m and the other at the upper limit of cloud forest taxa where the monospecific pine forest begins to

dominate at 2500 m, coincident with the mean TWI elevation (Fig. 2; Sherman, Martin & Fahey 2005; Martin, Sherman & Fahey 2007; Martin & Fahey 2014). The pine-cloud forest ecotone is remarkably consistent at 2000–2200 m elevation across the entire northern and eastern slopes of the Cordillera Central, with a mean elevation of 2125 m (max = 2366 m, min = 1893 m; Martin, Sherman & Fahey 2007). However, some TCMF species thrive in the monodominant pine forests above this boundary and are located either in the understorey, in gullies or in small isolated islands that occur in wet concave depressions that are likely protected from fire

(Martin, Fahey & Sherman 2011). By 2500 m, 12 of the 14 cloud forest tree species reach their elevational limit, above which *P. occidentalis* is the only arborescent plant (two cloud forest tree species occur as small-statured shrubs up to ~2700 m), forming a monospecific pine forest. The coring site is located at 2455 m on the windward slopes within a concave depression that hosts a small patch of cloud forest (consisting of *Ilex repanda* Griseb., *Ilex impressus* Loes. & Ekm., *Weinmannia pinnata* L., *Garrya fadyenii* Hooker, *Miconia* sp. and *Cyathea* sp.) surrounded by monodominant Hispaniolan pine forest (Figs 1 and 2). This depression remains wet in the dry season, and at a ~10 m in diameter, it likely has a small catchment, similar to forest hollows of temperate forests (e.g. Calcote 1998). This location is ideally situated to detect historical changes in the maximum elevation of the cloud forest, because its relatively high elevation (for cloud forest taxa) reflects the more fundamental control on distribution and range limits.

Annual rainfall in the Caribbean basin is largely bimodal, with two rainfall maxima (May–June and September–October) separated by a winter dry season drought (January–March) and a weaker ‘mid-summer’ drought (July–August) due to the expansion of the North Atlantic subtropical high-pressure cell (Gamble, Parnell & Curtis 2008). Caribbean climate is also driven by north-easterly trade winds, which are influenced by the proximity of the ITCZ. The ITCZ is generally south of Hispaniola, and in the boreal summer when the ITCZ migrates to its northernmost position, trade winds weaken, promoting convective activity and rainfall, and the TWI rises (Martin & Fahey 2014). In the boreal winter, trade winds strengthen as the ITCZ shifts southward and further away from Hispaniola, inhibiting convective activity and lowering the TWI. Precipitation is also affected by El Niño events, with up to 50% lower rainfall during El Niño dry seasons (Martin & Fahey 2006; Jury, Malmgren & Winter 2007).

In this high-elevation study area, annual precipitation on the windward slopes averages about 1900 mm but only 80 mm month⁻¹ during the winter dry season (Sherman, Martin & Fahey 2005). Atmospheric humidity declines gradually from 1500 to 2300 m and abruptly from 2300 to 2710 m due to the TWI (Martin, Sherman & Fahey 2007; Martin & Fahey 2014). Peak cloud cover occurs at 2400 m and peak relative humidity occurs at 2100 m (Fig. 2; Martin & Fahey 2014). The lower boundary of regular ground frosts (defined as a temperature of 2 °C at 1 m height) occurred between 2350 and 2760 m (Martin, Sherman & Fahey 2007).

SEDIMENT CORING AND CHRONOLOGY

We recovered a 0.95-m-long sediment sequence from a small forest hollow, Arrepenimientos (a local name), at 19.028° N, 70.924° W and 2455 m with a modified large-diameter Livingstone piston corer. Sediment was recovered in two drives, and drives were extruded and wrapped in plastic and aluminium foil and sealed in PVC tubes. Cores were sent to LacCore, the National Lacustrine Core Facility, hosted by the Limnological Research Center at the University of Minnesota (Minneapolis, MN, USA), where they were split longitudinally into working and archived halves, photographed and subjected to magnetic susceptibility analysis. The working halves of each drive were sliced into contiguous 0.5-cm intervals.

Dating control was provided by nine accelerator mass spectrometer (AMS) ¹⁴C measurements on pollen/spore concentrates obtained with heavy liquid (density = 2.3) separation (Table 1). Radiocarbon dates were calibrated with IntCal09, converted to cal. years before present (BP), where ‘present’ is 1950 C.E., and age-depth models were

Table 1. Accelerator mass spectrometry ¹⁴C ages from sediment sequence recovered from a small forest hollow at 2455 m (‘Arrepenimientos’) in the Cordillera Central, Dominican Republic. The age followed by an asterisk, and a 4.5-cm section of the surrounding sediment sequence, was deleted from the age-depth model

Sample depth (cm)	Laboratory ID	Material dated	¹⁴ C age
6.0–7.0	UGAMS-12125	Pollen/spores	120 ± 20
12.2–13.3	UGAMS-12126	Pollen/spores	670 ± 25
17.9–19.0	UGAMS-12127	Pollen/spores	1270 ± 20
24.2–25.3	UGAMS-12128	Pollen/spores	2300 ± 25
30.0–31.2	UGAMS-12129	Pollen/spores	3830 ± 25
36.1–37.0	UGAMS-12130	Pollen/spores	4500 ± 25
42.0–43.0	UGAMS-12131	Pollen/spores	2030 ± 25*
48.0–49.0	UGAMS-12132	Pollen/spores	4780 ± 30
54.5–56.0	UGAMS-11703	Pollen/spores	5160 ± 40

UGAMS, The University of Georgia, Center for Applied Isotope Studies.

constructed using the Bayesian techniques in the P_Sequence algorithm in OXCAL 4.2 software with $k = 10$ cm (Bronk Ramsey 2009).

POLLEN AND SPORES

We subsampled 1 cm³ of sediment to concentrate pollen/spores using standard techniques including acetolysis (Faegri & Iversen 1989). Samples were taken in alternating 0.5-cm sections (i.e. every 1 cm) and were processed at LacCore. To reconstruct pollen accumulation rates, each sample was spiked with a known concentration of polystyrene microspheres (diameter ~16 µm, $\rho = 1.3$ g cm⁻³) before chemical preparation of sediments. Pollen/spore residues were mounted in silicone oil and all pollen and fern spores were quantified at 400× and sometimes 1000× until we reached a sum of at least ~300 pollen grains (average = 346; range 297.5–1028.5). Pollen and spore identification was aided by a freeware Neotropical pollen data base (Bush & Weng 2007) and a Neotropical reference book (Roubik & Moreno 1991). Pollen and spore percentages were then calculated from raw counts after all fern spores (which can be easily overrepresented in tropical montane systems; Crausbay & Hotchkiss 2012) were excluded from the sum. The average number of fern spores counted in each sample was 710 (range = 51–9284).

CHARCOAL

Influx of small fragments of charcoal records the occurrence of past fires, and both theoretical and empirical studies demonstrate that macroscopic charcoal > 125 µm provides the best indication of local fires in lakes and small hollows (Whitlock & Larsen 2001 and references therein; Higuera, Sprugel & Brubaker 2005). We quantified macroscopic charcoal particles > 125 µm in contiguous 0.5-cm increments of the sediment core. For each sample, we processed 1 cm³ of sediment by treating with hot 10% KOH, sieving, transferring material > 125 µm to a Petri dish and ‘bleaching’ the sample with 30% H₂O₂ in a drying oven at 60 °C for 24 h. We counted charcoal particles at 30×–60× magnification on a dissecting microscope.

DATA ANALYSIS – POLLEN AND SPORES

We identified vegetation zones over time with hierarchical agglomerative clustering (McCune & Grace 2002), using stratigraphically

unconstrained data. We used a flexible beta = -0.25 linkage method based on a quantitative Sørensen distance matrix $2w/(a + b)$, where a and b are the sums of abundances in individual sample units and w is the sum of shared abundances.

We quantified the difference in species composition among different vegetation zones with multiresponse permutation procedure (MRPP), a nonparametric method for testing multivariate differences among pre-defined groups. We used a Sørensen distance measure and a weighting option for each item in the group = $n_i/\text{sum}(n_i)$, where n_i = number of items in group i . MRPP provides a chance-corrected within-group agreement value A , which is independent of sample size. $A = 0$ when heterogeneity within groups equals expectation by chance; $A = 1$ when all items are identical within groups, the highest possible value for A . In community ecology, values for A are commonly below 0.1 and an $A > 0.3$ is considered fairly high (McCune & Grace 2002).

We identified the taxa that were significantly associated with a particular group with indicator species analysis (ISA) based on Dufrêne & Legendre's (1997) method. Cluster analysis, MRPP and ISA were performed in PC-ORD™ 6.0 (MjM Software Designs, Glenden Beach, OR, USA).

To identify the rate of compositional change in vegetation, we conducted rate-of-change analysis on adjacent pollen/spore percentages. Rate of change (ROC) was determined by calculating the Sørensen dissimilarity between consecutive pollen/spore samples and dividing by the time elapsed between samples. This analysis was performed in PAST™ 2.17c (Hammer, Harper & Ryan 2001; available at <http://folk.uio.no/ohammer/past>).

DATA ANALYSIS – CHARCOAL

The charcoal analysis identified peaks in the charcoal series that most likely represented high-severity fires burning within 100 m from the site ('local'). We interpolated charcoal counts, sample volume and sample depths to a sample interval of 15 years and smoothed using a LOWESS that is robust to outliers with a window width of 800 years in the CharAnalysis program (Higuera *et al.* 2009; available at <https://sites.google.com/site/charanalysis/>). Charcoal accumulation (CHAR) curves were separated into (i) a low frequency 'background' component, which includes charcoal integrated from distant fires, secondary deposition and noise and (ii) a high frequency 'peak' component, assumed to represent local fires. Peaks were identified in CharAnalysis as $C_{\text{peak}} = C_{\text{interpolated}} - C_{\text{background}}$, with a locally defined threshold level. Only peaks $> 99.9\%$ of the noise distribution and with a $< 5\%$ chance of coming from the same Poisson distribution as the maximum peak were retained for calculation of fire return intervals.

DATA ANALYSIS – DRIVERS OF VEGETATION DYNAMICS

We used nonparametric multiplicative regression (NPMR) in HYPERNICHE 2.0 (MjM Software Designs) to build habitat distribution models and relate vegetation dynamics (the accumulation rate of pollen from pine forest taxa and cloud forest taxa; 80-year median resolution) to variation in fire (charcoal accumulation; 15-year interpolated resolution), the latitudinal position of the ITCZ (Haug *et al.* 2001, 5-year resolution) and El Niño frequency (Moy *et al.* 2002, 100-year resolution). Multiple high-resolution palaeorecords of ENSO have recently become available, and they provide coherent evidence of maximum ENSO frequency, magnitude and duration between ~2000 and 1000 years ago (Conroy *et al.* 2008). Here we use the Laguna Pallacocha record from the southern Ecuadorian Andes (Moy *et al.*

2002), because of its proximity to our site. For the NPMR analysis, we standardized each record to 80-year intervals to conform to the median resolution of the response variable (pollen data).

NPMR builds multiple response models from different combinations of predictors, using a forward stepwise approach and a leave-one-out cross-validation procedure. Models were selected based on the best goodness-of-fit with the lowest number of predictor variables and additional predictor variables were retained only if they improve the correlation by $> 5\%$. Fit was evaluated with a leave-one-out cross-validation procedure, a cross R^2 (xR^2). Importance of predictor variables is measured by sensitivity, expressed as a proportion of the range of the response variable. Sensitivity is the mean absolute difference resulting from nudging predictor values up and down by 5% of the range of individual predictors and calculating the resulting change in the estimate for that point (McCune 2006). Sensitivity measures are independent of variable units and higher sensitivities represent more important predictor variables.

Results

LITHOLOGY AND CHRONOLOGY

The sediment sequence from the Arrepentimientos forest hollow consists of an organic-rich silty clay for the upper 56.0 cm with a gradual transition to the parent material below. The organic-rich upper sediment sequence is interrupted by an intrusion of sediment at 42.0–46.5 cm depth characterized by a copious large roots (> 1 cm) and fern-derived macrofossils; a darker, finer sediment texture; sharp contacts on upper and lower bounds; and an anomalously young radiocarbon date (Table 1). We removed this 4.5-cm 'intrusion' from the age-depth model and did not analyse this section of the sediment sequence for pollen and charcoal. As a result, the sediment sequence analysed was 51.5 cm in length. The age-depth model shows ~5900 cal. years BP accumulated in the basin over these 51.5 cm (Table 1, Fig. 3), resulting in a mean sedimentation rate across the record of 115 years cm^{-1} (range = 20–425 years cm^{-1} , median = 90 years cm^{-1}). Sedimentation rate was the slowest in the middle of the record from ~4000 to 2000 cal. years BP, at ~300 years cm^{-1} .

POLLEN ANALYSIS

Pollen analysis showed a highly dynamic vegetation history at this site, with clear changes in composition and structure as vegetation shifted between grassland, pine savanna, pine forest and cloud forest over the last 5900 years (Table 2; Figs 4 and 5a). We term such fundamental shifts in community type a 'state change'. Seven vegetation zones, characterized by significant patterns in the abundance and frequency of different taxa, were defined by the cluster analysis (Fig. 5a). Multiresponse permutation procedures (MRPP) show significantly distinct composition between groups, with a high degree of within-group homogeneity ($A = 0.62$, $P < 0.0001$).

In zone 7, from ~5900 to 5525 cal. years BP TCMF taxa were abundant, including *Ilex*, the filmy ferns (Hymenophyllaceae) and the epiphytic fern *Lepisorus* (Table 2; Fig. 4). Most

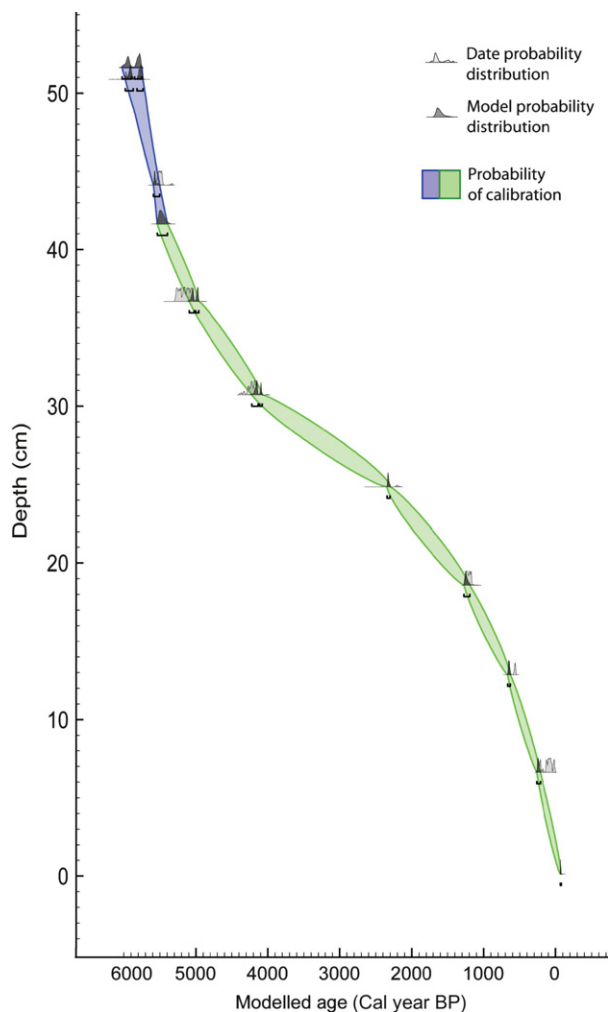


Fig. 3. Age-depth model from a small forest hollow, Arrepentimientos, located at 2455 m elevation in the Cordillera Central, Dominican Republic. The model was constructed using ^{14}C dates of pollen/spore concentrates, calibrated and modelled in OXCAL v4.2.2 (Bronk Ramsey 2009). Probability of calibration shows the 95.4% highest posterior density range.

TMCF taxa had declined by the beginning of zone 6 at 5525 cal. years BP, except for the TMCF shrub *Piper* which was co-dominant with Poaceae until 4323 cal. years BP. In zone 5, from 4323 to 1269 cal. years BP, Poaceae maintained clear dominance. Zone 4 begins after 1269 cal. years BP when the abundance of *Pinus* began to increase sharply. During this time, Poaceae remained abundant and Tubuliflorae types increased, suggesting a pine savanna. In zone 3, beginning at 586 cal. years BP, *Pinus* continued to increase in abundance, with a concurrent decline in Poaceae, indicating the formation of a more closed pine forest. Zone 3 lasted until 85 cal. years BP and also includes pollen from pine-dependent mistletoes (Loranthaceae) and the disturbance-dependent fern genus *Pteridium* (Sherman, Martin & Fahey 2005; Martin, Sherman & Fahey 2007), suggesting a forest similar to drier leeward monospecific pine forests found in the area today (Kennedy, Horn & Orvis 2005). After 85 cal. years BP, zone 2 remained a monospecific pine forest and there was an

increase in the ferns *Lophosoria* and *Hypolepis*, suggesting a wetter forest similar to windward monospecific pine forests of today (Kennedy, Horn & Orvis 2005). Zone 2 ended recently, at -11 cal. years BP, with a sudden increase in TMCF taxa – characteristic of zone 1 – suggesting a recent return of cloud forest taxa, including *Ilex* and *Weinmannia* within a matrix of monodominant pine forest.

Rate of change (ROC, % dissimilarity per decade) was very low throughout the record, but ROC peaked at around 15% (dissimilarity decade $^{-1}$) in the very recent past, at -34.5 cal. years BP coincident with the recent increase in TMCF taxa (Fig. 5b). Otherwise, ROC had values up to 5% (dissimilarity decade $^{-1}$) from ~ 5900 to 5000 cal. years BP and again from ~ 1300 cal. years BP to the present.

Pollen influx – suggestive of vegetation's degree of closure (e.g. Bunting *et al.* 2004) – was highest during periods when taxa associated with either cloud forest or pine forest were abundant, and was particularly low between ~ 4300 and 1300 cal. years BP, when vegetation was dominated by Poaceae, strongly suggesting the presence of a grassland (Fig. 4). Magnetic susceptibility, which indicates increased erosion into the basin, is generally the inverse of pollen influx. Susceptibility was highest between ~ 4300 and 1000 cal. years BP when the area was likely a grassland, lowest from ~ 1000 cal. years BP to the present, except for a short-lived peak in magnetic susceptibility at 1048 cal. years BP, and most variable from ~ 5900 to 4300 cal. years BP (Fig. 4).

CHARCOAL ANALYSIS

Charcoal samples were taken contiguously, but because of changes in sedimentation rates (Fig. 3), the amount of time in each sample varied from 15.5 to 198.5 years. Charcoal accumulation rates (CHAR) interpolated to 15 years ranged from 0.29 to 35.54 pieces cm $^{-2}$ year $^{-1}$ (mean = 3.91 pieces cm $^{-2}$ year $^{-1}$, median = 2.22 pieces cm $^{-2}$ year $^{-1}$). CHAR was highest from 5900 to 5430 cal. years BP and ~ 1830 to 20 cal. years BP and lowest from 5430 to 1830 cal. years BP and 20 to 60 cal. years BP, Fig. 5c). Ten local charcoal peaks were identified: six between 5600 and 4200 cal. years BP and four between 800 and 10 cal. years BP (Fig. 5c).

DISTRIBUTION MODELS

We built distribution models to relate the accumulation rate of different forest types to charcoal accumulation (Fig. 5c), position of the ITCZ (Fig. 5d) and El Niño event frequency (Fig. 5e). The accumulation rate of cloud forest pollen types is best modelled with just the ITCZ ($xR^2 = 0.63$, sensitivity = 1.06, Fig. 6). The accumulation rate of pine forest pollen types is most associated with charcoal (sensitivity = 0.88) and ITCZ position (sensitivity = 0.77), with a minor association with El Niño event frequency (sensitivity = 0.03) ($xR^2 = 0.53$, Fig. 7). These distribution models show that cloud forest taxa were highest during times of a more northerly ITCZ – which promotes convective activity,

Table 2. Chronology of vegetation zonation, described by a stratigraphically unconstrained cluster analysis of pollen assemblages from the small forest hollow Arrepentimientos, at 2455 m elevation in the Cordillera Central, Dominican Republic

Zone	Age (cal. years BP)	Likely vegetation type	ISA angio	ISA ferns
(1)	–11 to –60	Monodominant pine forest w/TMCF elements	<i>Ilex</i> , <i>Garrya</i> , <i>Weinmannia</i>	<i>Dryopteris</i> , Monolete #1
(2)	85 to –11	Windward monospecific pine forest	Cyperaceae	<i>Lophosoria</i> , <i>Hypolepis</i>
(3)	586–85	Leeward monospecific pine forest	Loranthaceae	<i>Pteridium</i> , <i>Lycopodium</i>
(4)	1269–586	Pine savanna	Tubuliflorae	Trilete #6
(5)	4323–1269	Grassland	Poaceae	–
(6)	5525–4323	Poaceae- <i>Piper</i>	–	–
(7)	5900–5525	Cloud forest	<i>Piper</i>	Hymenophyllaceae, <i>Lepisorus</i> , <i>Pteris</i>

Composition of these seven groups was significantly different (MRPP, $A = 0.62$, $P < 0.0001$). Significant ($P < 0.05$) angiosperm and fern/fern ally indicators are shown. ISA, indicator species analysis.

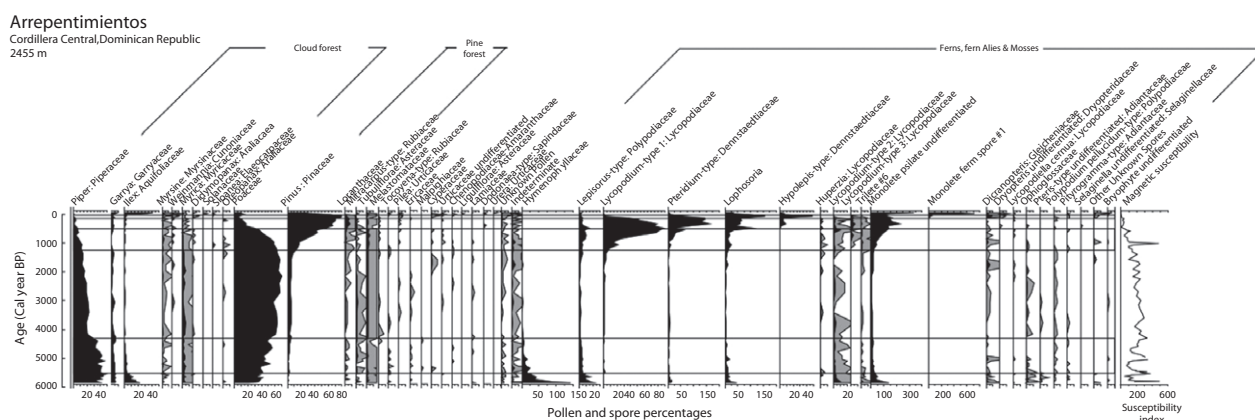


Fig. 4. Pollen and spore percentages over time from the small hollow, Arrepentimientos, at 2455 m near the upper limit of cloud forest taxa on windward Cordillera Central, Dominican Republic. Exaggeration curves of 10% are shown in grey. Seven vegetation zones based on cluster analysis (Table 2) are demarcated. On the far right, magnetic susceptibility is reported as a susceptibility index.

increases rainfall and raises the elevation of the TWI. In contrast, pine forest taxa were highest during times of a more southerly ITCZ which lowers the TWI (Figs 6 and 7).

Discussion

HIGH-ELEVATION VEGETATION DYNAMICS

This high-elevation site in the Cordillera Central experienced dramatic changes in structure and composition of vegetation over the past 5900 years, alternating between cloud forest, grassland, pine savanna and pine forest. In contrast, a pollen record from the nearby Valle de Bao (~12 km away, ~650 m lower in elevation and slightly more leeward) found a 4300-year record of continuous pine dominance (Kennedy, Horn & Orvis 2006). The divergent history between these two sites corresponds with the pattern observed in a compilation of Andean and Amazonian palaeorecords of greater vegetation dynamics with increasing elevation (Urrego *et al.* 2009). The

state changes in vegetation composition and structure at this high-elevation site are clear indications of up- and downslope movement of ecotone boundaries (Fig. 8; Table 2) and offer strong evidence of the fundamental sensitivity of high-elevation ecosystems to climate variability.

At the start of this palaeorecord at 5900 cal. years BP, the site was comprised largely of TMCF taxa, including a classic cloud forest indicator (e.g. Proctor 2003; Krömer & Kessler 2006), the moisture-sensitive epiphytic ferns of the Hymenophyllaceae (Table 2; Fig. 4). At this time, TMCF taxa were already on a negative trajectory. Most TMCF taxa dropped to very low abundances within ~400 years (Fig. 4) and the abundance of all TMCF taxa continued a steady decline until only very recently (Fig. 5a). After ~5500 cal. years BP when most TMCF taxa had declined, the vegetation was co-dominated by Poaceae and *Piper* (a TMCF shrub taxon), seemingly without a modern analogue (Kennedy, Horn & Orvis 2005; Sherman, Martin & Fahey 2005). By ~4300 BP, grasses came to clearly dominate the site and remained domi-

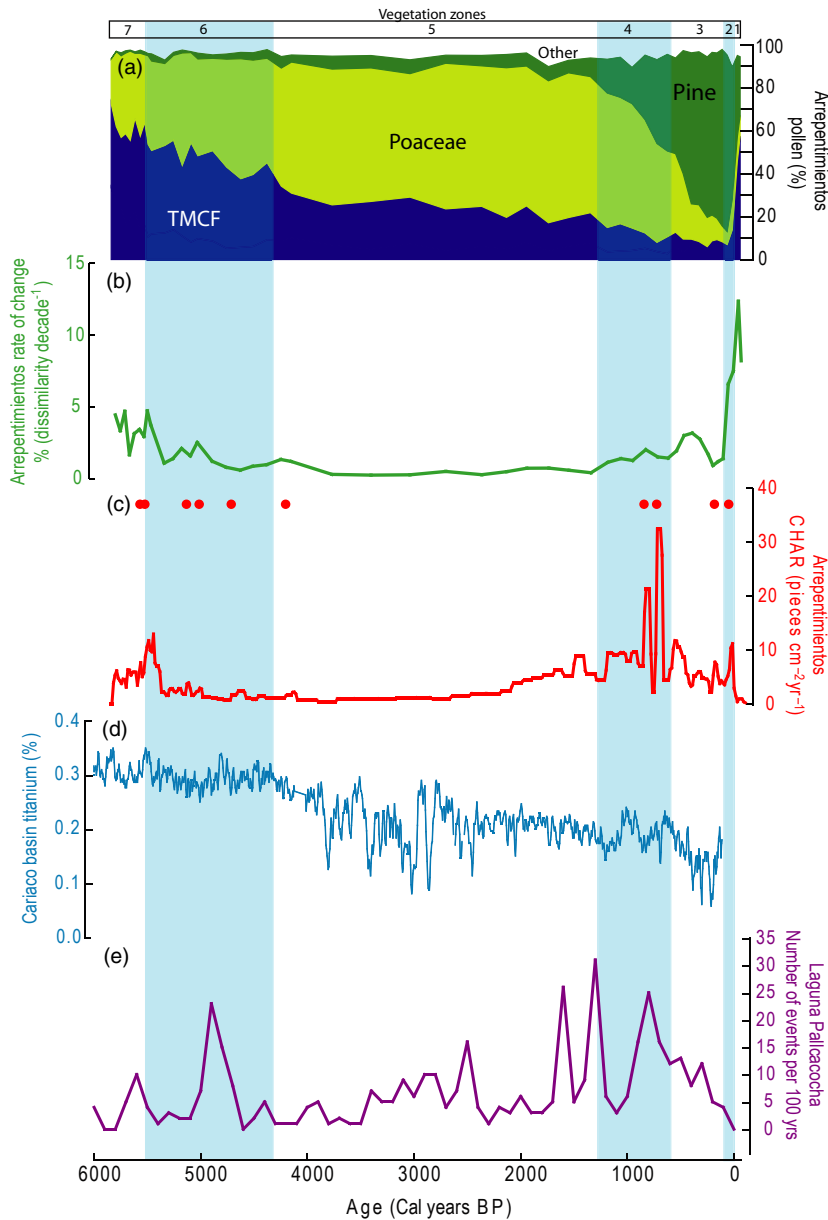


Fig. 5. Data from the small hollow, Arrepenimientos, at 2455 m elevation in the Cordillera Central, Dominican Republic showing a time series of (a) pollen percentages of select taxa with seven vegetation zones (Table 2) illustrated at top. Cloud forest pollen types include *Didymopanax*, *Garrya*, *Ilex*, *Myrica*, *Myrsine*, *Oreopanax*, *Piper*, *Solanaceae*, *Sloanea* and *Weinmannia*; pine forest pollen types include *Pinus* and *Loranthaceae*, (b) rate of change in pollen/spore assemblages and (c) interpolated charcoal accumulation, with charcoal peaks, representing local fires, as circles above the graph. The remaining panels are from other sites: (d) ITCZ latitudinal position, per the Cariaco Basin Titanium percentage, where lower percentages indicate a more southward ITCZ (Haug *et al.* 2001) and (e) El Niño events per 100 years from the colour intensity in the sediment sequence from Laguna Pallcacocha (Moy *et al.* 2002).

nant for the next 3000 years, suggesting an alpine grassland habitat (Fig. 5a). Yet today in the Cordillera Central, grasslands (dominated by *D. domingensis* Hack. & Pilg.) occur only as relatively small patches (up to 1 ha) within a pine-dominated landscape and a tree line is not reached. This record shows clear, progressive downslope movement of vegetation from ~5900 to 1300 cal. years BP as the site changed from TCMF to apparent alpine grassland. Several records across the Caribbean, including the nearby Valle de Bao (Kennedy, Horn & Orvis 2006), suggest a drying trend over this time frame since ~6000 years ago, particularly at ~4000–1000 years ago (Hodell *et al.* 1991; Curtis & Hodell 1993; Hodell, Curtis & Brenner 1995; Curtis, Brenner & Hodell 1999; Bernal *et al.* 2011; Lane *et al.* 2011; Lane & Horn 2013).

The percentage of *Pinus* during this time was remarkably low (< 5% until ~4300 cal. years BP and < 10% until

~1300 cal. years BP; Figs 4 and 5a). This pattern is in strong contrast to modern surface samples from high elevations nearby in the Cordillera Central that report high percentages (generally well over 20%) of *Pinus* pollen even where Hispaniolan pine is not locally abundant, because pine is regionally dominant and its pollen is well dispersed over long distances (Kennedy, Horn & Orvis 2005). Taken together, this suggests that pine forests were absent from the high elevations of the Cordillera Central until relatively recently. Yet today Hispaniolan pine is extraordinarily dominant across virtually all of the highest elevations. The apparent absence of pine above ~2400 m in the past may help explain the two types of vegetation with no apparent analogue – Poaceae-*Piper* assemblage (zone 6) and Poaceae-dominated assemblage (zone 5) – from ~5500 to 1300 years ago (Fig. 8).

The advent of pine-dominated vegetation at 1269 cal. years BP was another strong state change in vegetation and

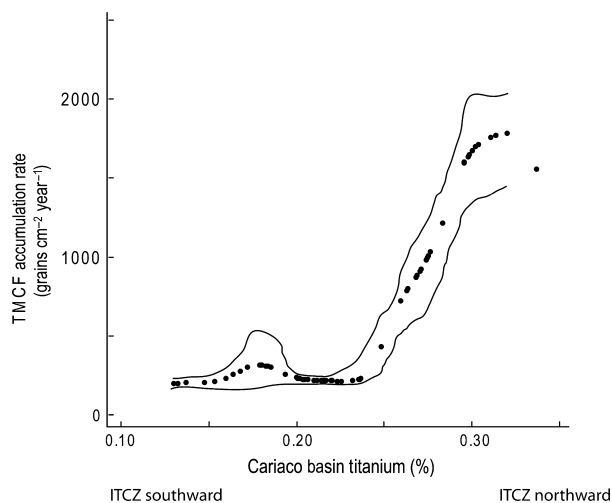


Fig. 6. Fitted relationship between cloud forest taxa accumulation rate from Arrepenimientos, Dominican Republic, and the ITCZ latitudinal position, with 5th and 95th percentile variability bands. The distribution model began with three predictor variables (CHAR, ITCZ and ENSO), but the accumulation rate of cloud forest pollen types is modelled with just the ITCZ ($xR^2 = 0.63$, sensitivity = 1.06). Cloud forest pollen types include *Didymopanax*, *Garrya*, *Ilex*, *Myrica*, *Myrsine*, *Oreopanax*, *Piper*, *Solanaceae*, *Sloanea* and *Weinmannia*.

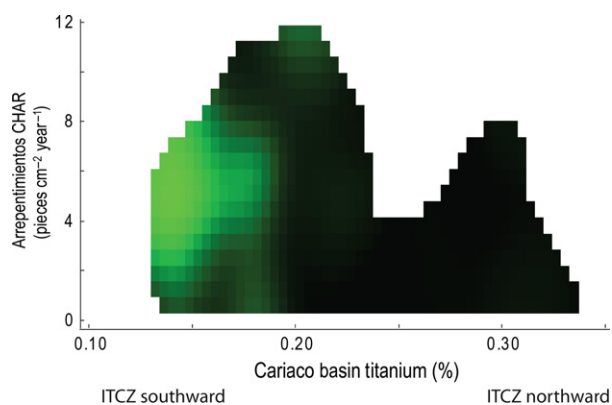


Fig. 7. Response contour map from a nonparametric multiplicative regression (NPMR) model of the accumulation rate of pine forest taxa from Arrepenimientos, Dominican Republic. The distribution model began with three predictor variables (CHAR, ITCZ and ENSO). The accumulation rate of pine forest pollen types is modelled ($xR^2 = 0.53$) with all three predictor variables, but primarily by charcoal (sensitivity = 0.88) and ITCZ position (sensitivity = 0.77), with only a minor association with El Niño event frequency (sensitivity = 0.03). Sensitivity measures of predictor variables describe relative importance (highest = most important). The gradient from black to green shows accumulation rates, with the brightest green shade indicating the most favourable space for high accumulation rates of pine forest taxa, which include *Pinus* and *Loranthaceae*.

suggests the beginning of upslope vegetation movement. After the dramatic increase of *Pinus*, the pine-dominated vegetation changed through time, moving from a pine savanna to a monospecific pine forest with *Pteridium* to the present monospecific pine forest with *Lophosoria* (Table 2; Fig. 4). Kennedy, Horn & Orvis (2005) show from modern surface samples in the area that *Pinus-Pteridium* assemblages are

common in leeward, drier pine forests, whereas *Pinus-Lophosoria* assemblages are common in wetter windward pine forests. These changes in the type of pine forest suggest a wetter environment over time and are coincident with palaeoclimatic evidence from Haiti for increased moisture since ~1000 cal. years BP (Curtis & Hodell 1993). This trend towards a wetter environment over the last millennium culminates with the very recent, rapid rise of TMC F taxa at this site (Fig. 5a,b).

FIRE AND VEGETATION DYNAMICS

Fire played an important role in the vegetation dynamics in this study. Perhaps most clearly, an abrupt reduction in fire on the landscape was associated with the most rapid vegetation change over the entire record (Fig. 5b,c) – the recent return of TMC F within a wider pine-dominated matrix (Fig. 5a). This reduction in fire is well-documented, with a clear decline in charcoal accumulation at this site in the last few decades (Fig. 5c) and a sudden drop in frequency of tree-ring fire scars from the area at around 1965 AD, when park protection and active fire suppression began (Martin & Fahey 2006). This rapid increase in TMC F abundance is notable in the light of the common observation that TMC F taxa are particularly slow-growing (e.g. Bruijnzeel *et al.* 2010) and demonstrates that some TMC Fs can quickly colonize an area once environmental conditions are right – in this case, a wetter environment protected from predominantly human-ignited fires.

Humans play an important role in the fire regime in the Cordillera Central today, but fire has been a natural component of the highlands landscape for at least 40 000 years (Horn *et al.* 2000) and anthropogenic impacts have been largely confined to the last ~100 years when the highlands were first cleared and permanently settled (Martin & Fahey 2006). Our palaeorecords show that the prehistoric fire regime played an important role in vegetation dynamics before widespread anthropogenic influence. The end of the cloud forest vegetation type at ~5500 cal. years BP (Zone 7; Fig. 5a) is associated with two on-site fire events (5610 and 5565 cal. years BP; Fig. 5c). These fires and the moderately high charcoal accumulation rates around this time fit in with the general Neotropical pattern of increased high-elevation fires between ~6000 and 5000 years ago (Power *et al.* 2010). As fire peaked in the greater Neotropical region, most TMC F taxa were driven from this site and may have been driven from high elevations across the wider landscape of the Cordillera Central.

When the site was dominated by pine (after 1269 cal. years BP), charcoal accumulation rates were particularly high indicating that, in contrast to TMC F, pine dominance is maintained or even increased by some fire regimes. Positive pine-fire relationships, with widespread burning during times of high pine abundance, have been observed in other Neotropical montane forests palaeorecords, including the nearby Valle de Bao (Kennedy, Horn & Orvis 2006; Figueroa-Rangel, Willis & Olvera-Vargas 2008). Our distribution models for pine

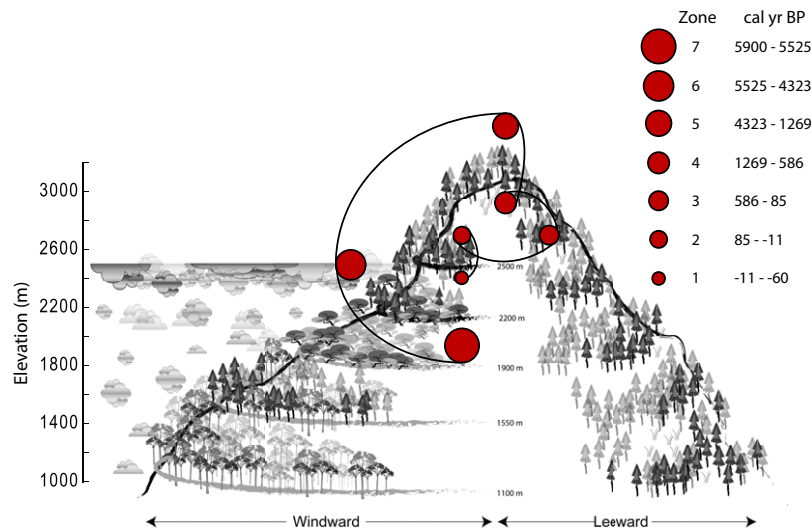


Fig. 8. Conceptual diagram of vegetation dynamics over time from the small hollow, Arrepentimientos, at 2455 m elevation in the Cordillera Central, Dominican Republic. Red circles represent the seven different vegetation types (defined by cluster analysis) that occupied Arrepentimientos over the last 5900 years (Table 2). The size of circles identifies the time period and zone number. The location of circles is used to show the modern vegetation type that each palaeo-vegetation type is most similar to, based on a qualitative comparison of the vegetation data in Sherman, Martin & Fahey (2005) and with the modern pollen data in Kennedy, Horn & Orvis (2005). Circles that are placed off of the mountain have no obvious analogue in today's vegetation. The lines connecting the circles show the path of vegetation through time.

forest taxa find a hump-shaped relationship between fire activity and pine, with peak pine at moderate fire activity (Fig. 7). Charcoal accumulation was most abundant early in the history of pine, when the site was a more open monospecific pine savanna (Fig. 5a,c). When charcoal accumulation began to decline ~585 cal. years BP to moderate levels, the pine forest appeared more closed with more *Pinus* pollen, fewer grasses and abundant *Pteridium* (Figs 4 and 5c). This decrease in fire also coincides with broader trends in Neotropical fire patterns that show a decline in fire frequency around 500 years ago (Power *et al.* 2012). Modern ecological data suggest that the Hispaniolan pine is increased by fire – both as a post-fire colonist and as a fire-tolerant species (e.g. with thick bark) – and fire presence-absence data strongly predict *P. occidentalis* occurrence on the landscape today (Sherman, Martin & Fahey 2005). Our longer record, however, reveals a more nuanced pine-fire relationship.

Interestingly, fire began to increase here in the Cordillera Central's high elevations at ~1800 cal. years BP, several centuries before pine's dramatic rise in abundance (Fig. 5a,c) and around the time of a peak in Neotropical fires ~2000 years ago (Power *et al.* 2010). During this time period, the site was a grassland, which for the previous 2500 years (4300–1800 cal. years BP) had apparently not supported an active fire regime (Fig. 5a,c). This change in the fire regime at ~1800 cal. years BP initially had little effect on grassland species assemblage and more than 600 years passed before the rise of pine. Overall, the records show that vegetation–fire relationships in a high-elevation tropical montane site can be nonlinear or negative and that fire can (i) maintain a vegetation type but alter species abundance, as in the pine forest, (ii) convert one vegetation type to another, as in the cloud forest or (iii) have very little

effect on vegetation, as in the grassland. These data illustrate the complexity of fire–vegetation relationships in tropical montane systems and demonstrate the need for long ecological records to understand fire–vegetation–climate dynamics.

ITCZ POSITION AND VEGETATION DYNAMICS

Our distribution models show that high-elevation ecotone dynamics in the Cordillera Central are related to the prevailing position of the ITCZ, likely through its effects on the elevation and strength of the TWI. We modelled two forest types: TMCF, which occurs at lower elevations generally below the TWI, and pine forest, which occurs at higher elevations, generally above the TWI (Fig. 2). The accumulation rate of pine forest pollen types peaked when the ITCZ was in more southerly positions and the TWI was at lower elevation (Fig. 7). In our pine forest model, the proxy for ITCZ position is nearly as important as our proxy for fire. In contrast, the peak accumulation rate of TMCF taxa occurs when the ITCZ was more northerly, suggesting the probability of TMCF at this elevation is highest with increased moisture and a higher TWI (Fig. 6). TMCF taxa continued a slow decline over the length of our palaeorecord, suggesting steady down-slope movement of vegetation, coincident with the long-term southerly shift in the ITCZ (Fig. 5a,d). The very recent rise in TMCF taxa also comes after a clear northward shift in the ITCZ since the end of the 'Little Ice Age' (Fig. 5a,d; Haug *et al.* 2001; Sachs *et al.* 2009).

There was a 3000-year period (~4300–1300 cal. years BP) between these two forest types, when the site was more similar to an alpine grassland. During this time, the ITCZ shifted to its most southerly positions during the Holocene (Fig. 5a,d; Haug *et al.* 2001). This strong southerly shift in the ITCZ likely

caused a marked drying of high-elevation areas in the Cordillera Central as the TWI shifted to its lowest elevation. Our record indicates there was increased aridity during this period with lower pollen influx, lower sedimentation rate and higher magnetic susceptibility (Figs 3–5a). Overall, our data provide support for the shifting TWI hypothesis, with clear state changes in vegetation indicative of up- and downslope movement that are significantly associated with the ITCZ. Other palaeorecords have suggested that vegetation dynamics in upper montane tropical forests relate to vertical shifts of the TWI (Selling 1948; Hooghiemstra *et al.* 1992; Burney *et al.* 1995), perhaps in relation to the ITCZ (Lane *et al.* 2011; Lane & Horn 2013). To be sure, the drivers of mean TWI elevation over the Holocene were likely complex. Despite the complexity in TWI controls and the potential for drivers we did not consider, our distribution models indicate that ITCZ-forced changes in the TWI's elevation have fundamental consequences for tropical montane vegetation in the Caribbean.

Movement of the cloud belt up- or downslope causes stark changes in cloud cover and high-humidity cloud immersion over short distances. Cloud immersion reduces water stress through fog–water interception (Burgess & Dawson 2004), and cloud cover reduces water stress by lowering net radiation and temperatures, dampening temperature extremes and reducing evapotranspirative losses (Fischer, Still & Williams 2009; Carbone *et al.* 2013). These kinds of changes in cloud cover and immersion frequency may ultimately affect ecotone position and TMCF distribution by strongly altering drought stress and mortality risk, as in other cloud-affected ecosystems such as coastal forests (e.g. Fischer, Still & Williams 2009). In the Cordillera Central, peak cloud cover occurs near the TWI at 2400 m (Fig. 1). This pattern suggests that a downward shifting TWI could have a very strong effect on vegetation nearest the TWI because this area would be exposed to both reduced cloud cover and reduced humidity.

This study highlights the pivotal role that future changes in cloud formation will play in tropical montane vegetation dynamics. In particular, our results demonstrate how in the Caribbean, the elevation where the upper end of the cloud belt forms is strongly linked to latitudinal variation in the ITCZ's position. Palaeoclimate records show that on long-time scales, the ITCZ is forced by orbital precession and the resulting variation in temperature and seasonality (Haug *et al.* 2001). The ITCZ's palaeohistory suggests it may move northward with future climate warming, because it was further north during the Holocene thermal maximum (Haug *et al.* 2001), and further south during the last glacial maximum (Chiang, Biasutti & Battisti 2003). However, there is no widely accepted explanation for the drivers behind the prevailing latitude of the ITCZ and its position has a complex relationship with temperature. The ITCZ tends to shift southward whenever the cross-equatorial SST gradient is diminished, which can occur with warming in the eastern Pacific, or cooling the north Atlantic, as during the 'Little Ice Age' (Sachs *et al.* 2009). Therefore, the effects of future warming on the ITCZ, the TWI and the upper limit of clouds in the

Caribbean remain highly uncertain. Our data show we cannot rely on an assumption that the lifting cloud base phenomenon will extend to higher elevations. Instead, an improved understanding of the ITCZ's sensitivity to CO₂-induced warming will help determine whether the upper cloud zone will rise or fall in future climates, with profound implications for the outlook of tropical montane ecosystems in the Caribbean.

Conclusions

Vegetation was highly variable at this tropical high-elevation site, ranging from TMCF to grassland to pine forest, indicative of up- and downslope movement of vegetation. Our distribution models provide support for the shifting TWI hypothesis by showing that these strong state changes in vegetation were associated with the prevailing position of the ITCZ. A clear example is the long decline of TMCF taxa from 5900 years ago until only the last few decades, and its association with the ITCZ's steady southward migration until a recent northward trajectory. Modern ecological research from this area has hypothesized the pine-cloud forest ecotone, and the upper limit of cloud forest taxa is controlled partially by moisture balance associated with the TWI and El Niño-driven droughts, as well as fire (Martin, Sherman & Fahey 2007; Martin, Fahey & Sherman 2011). Our distribution models confirm the role of moisture and fire, but provide no support for El Niño driving long-term changes in vegetation near the TWI. Instead, the predominant position of the ITCZ and its comparatively slower dynamics plays an overarching role in Caribbean montane ecosystems over long-time scales.

This research further highlights how distinguishing between a lifting vs. lowered cloud belt has important implications for conservation strategies aimed at protecting tropical mountain ecosystems. High-elevation areas of tropical mountains are important as an upslope 'escape route' for lower elevation biota as temperatures warm, but only if they remain moist. Our study points to the ITCZ and its sensitivity to future climate change as a fruitful direction for anticipating the future of tropical montane vegetation. The ITCZ is relevant to far more than montane ecosystems in the Caribbean because it determines the location and length of the rainy season across the tropics, which in turn governs the subsistence of more than a billion people. Understanding the ITCZ's sensitivity to climate change is a research priority.

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Data accessibility

Data from this study are available from the Neotoma Paleocology Database (Crausbay, Martin & Kelly 2015).

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