Ruth E. Sherman, Patrick H. Martin, Timothy J. Fahey and Steve D. Degloria

Fire and Vegetation Dynamics in High-elevation Neotropical Montane Forests of the Dominican Republic

In March and April 2005, severe fires burned over 1000 km^2 of tropical montane forests in the Cordillera Central, Dominican Republic. The fire burned through our network of permanent vegetation plots, which were established in 1999 to examine interactions among environment, vegetation, and disturbance. We used QuickBird satellite imagery combined with field surveys to map the extent and severity of the fire across the landscape. The fire burned through 96% of the pine forest but quickly extinguished at the pine–cloud forest boundary along most of the ecotone. Topographic factors and fire severity had no influence on fire behavior at the ecotone. These observations support our original hypothesis that fire maintains the abrupt boundary between the pine and cloud forest vegetation in these mountains. Vegetation structure and composition played a direct role in regulating fire spread and behavior in this landscape.

INTRODUCTION

Tropical montane forests (TMFs) have traditionally been classified into two distinct altitudinal floristic zones, a lower and upper montane forest, which differ markedly in composition, physiognomy, and structure (1–4). While environmental changes associated with elevation provide the overarching control on vegetation zonation patterns, the nature of these controls and the corresponding patterns of vegetation change are not uniform across tropical regions nor are they well understood. Species changes with elevation on tropical mountains can be continuous and individualistic (5–9), or abrupt shifts in the composition between the upper and lower montane forests can occur (2, 9–13). The environmental changes that accompany the elevation gradient vary among mountain ranges, owing to such influences as latitude, continental versus island locations, and broad atmospheric circulation patterns. Moreover, local variation in disturbance regimes can have a pronounced influence on vegetation patterns. An understanding of the ways in which vegetation, natural disturbance, and complex environmental gradients interact can provide valuable insights into controls of tropical montane vegetation organization.

On the windward slopes of the Cordillera Central of the Dominican Republic, a discrete ecotone between a species-rich cloud forest and monodominant pine forests occurs at about 2200 m elevation (Fig. 1a) (13, 14). Forest structure and physiognomy change dramatically from a compositionally and structurally diverse cloud forest of stunted trees covered in a thick blanket of bryophytes to a tall, pine forest with an open understory above the ecotone. Our previous work has suggested that this abrupt transition in composition is controlled primarily by fire (13). In 2000, all pine stands showed evidence of previous fires, whereas only a small percentage of the cloud forest stands showed any fire evidence. While the elevation of the cloud forest is associated with the position of the trade wind inversion (TWI), the sharply delineated character of the ecotone suggests that contrasting fire disturbance histories across the ecotone provide the direct control on this abrupt vegetation shift (13).

In March–April 2005, a severe fire burned through the Cordillera Central of the Dominican Republic, resulting in patchy, yet landscape-scale mortality (Fig. 2). The fire escaped from a farmer's field adjacent to the southern, leeward side of the park. The fire burned for 28 d, eventually spreading through most of the high-elevation pine forests on both the leeward and windward slopes of the Cordillera Central and burning over 1000 km^2 of mostly virgin forest. The fire occurred after a pronounced drought that was coincident with an El Niño–Southern Oscillation event in late 2004 and early 2005. This was the first extensive fire in the study area since 1965. The fire burned through many of the permanent plots established in 1999–2000 to study the vegetation dynamics of these mountains (13–15). The recent fire provided a direct test of our hypothesis that fire interacts with vegetation to form the discrete pine–cloud forest ecotone. In this paper, we address three main objectives. First, we examine the spatial heterogeneity of burn severity across the mountain landscape using high-resolution satellite imagery. Second, we examine the relationship of prefire stand and site characteristics to the patterns of fire-induced mortality. Third, we analyze vegetation and landscape characteristics that influence fire behavior along the fire border of the pine–cloud forest ecotone. We hypothesize that intense fires burn through most of the high-elevation pine forest but extinguish at the cloud forest boundary.

STUDY AREA

This study was conducted in the 766 km^2 Armando Bermúdez National Park and adjacent 679 km^2 Carmen Ramírez National Park of the Dominican Republic, located in the central mountain range on the island of Hispaniola (Fig. 3). The study area encompassed approximately 85 km^2, extending from the community of La Ciénaga de Manabáo at the eastern park entrance at 1100 m elevation to the top of Pico Duarte, the highest point in the Caribbean at 3087 m, and spanning the windward (northeastern) and leeward (southwestern) slopes of the central massif (Fig. 1a). 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) experience regular below-freezing temperatures (13, 16). Climatic patterns on the island reflect the influence of the prevailing northeast trade winds and exhibit a marked rain shadow. Annual precipitation on the windward slopes averages about 1900 mm, but only about 1300 mm y^{-1} fall on the leeward slopes, with less than 31 mm mo^{-1} falling during the dry season (14). The geology of these mountains is complex and is dominated by Cretaceous volcanic, metamorphic, and plutonic rocks, which contrast with the rest of the island, where Tertiary and Quaternary rocks are dominant at the surface (17). The topography is rugged, with steep and sharply dissected slopes.

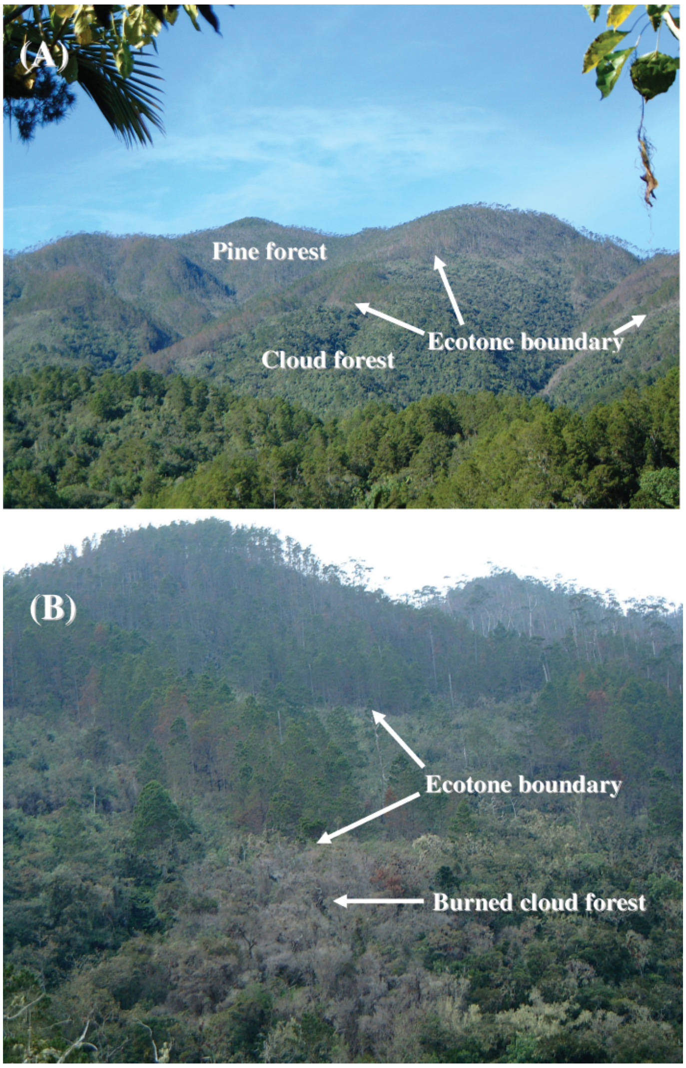

Figure 1. (A) The pine–cloud forest ecotone on the windward slopes of the Cordillera Central, Dominican Republic. Higher elevations have monodominant forest of *Pinus occidentalis*, in which brown and gray burned areas are visible. In the foreground, lower-elevation mixed broadleaf–pine forest can be seen. (B) Close-up of the pine–cloud forest ecotone. A gray area of burned cloud forest is visible where the fire burned comparatively far into the cloud forest. In the area of this photograph, the fire burned down through the pine forest primarily as a moderately intense surface, though some smaller overstory pines were killed. (Photo: P. Martin)

A network of 245 permanent sample plots (0.05 or 0.1 ha) was established in 1999–2000, and all trees >10 cm diameter at breast height (d.b.h.) were identified and tagged (Fig. 3). Plots were placed at random locations along several hiking trails that varied in elevation and aspect (14). We classified the forest vegetation across the study area into five major associations assembled along an elevational gradient on the windward slopes (14): *i*) low-elevation riparian forests (18); *ii*) low-to-mid-elevation evergreen broadleaved forests of tall stature and high diversity; *iii*) mixed broadleaf–pine forests with varying degrees of dominance by the endemic Hispaniola pine (*Pinus occidentalis* Swartz); *iv*) stunted cloud forests of the upper montane zone; and *v*) open and closed-canopy monodominant and monospecific Hispaniola pine forests at the highest elevations. The forest composition transition from lower to upper montane forest is gradual; in contrast, at high elevations, a visibly and quantitatively discrete ecotone occurs on the windward slopes at ~2100 m elevation (13). Below the ecotone, there is the compositionally and structurally diverse cloud forest, and above the ecotone, there is a monodominant pine forest. Monospecific pine forests dominate the drier, leeward slopes at all elevations, although patches of broadleaf forest occur in protected coves at 1500–1800 m elevation.

Figure 2. An El Niño–Southern Oscillation (ENSO)–triggered fire in 2005 caused landscape-scale overstory mortality and created a complex matrix of burn and mortality patterns. (Photo: P. Martin)

Fire Regime

A dendrochronological reconstruction of (200 y) fire history using fire-scarred pines indicates that these forests experience frequent surface fires and occasional crown fires, where the most severe fires are synchronized with El Niño–triggered droughts (15). The mean fire return interval (FRI) for the entire study area is 31.5 y. However, mean FRI varies markedly with elevation and aspect. Mean FRI is much longer on more moist windward slopes (42.1 y) than on the dry, leeward slopes (16.7 y). On windward slopes, FRI is notably shorter at higher elevations (2400–3000 m; 26.4 y) than at mid-elevations (2000–2400 m; 74.5 y) and at low elevations (1600–2000 m; 63.9 y) (15). Significant increases in fire frequency were detected between 1900–1965 in both leeward and windward areas, coincident with an increase in human settlement in the area, but fire frequency subsequent to 1965 declined to values similar to pre-1900, presumably owing to the creation of the two national parks in the late 1950s, which offer more protection for these forests. Paleoecological evidence indicates that fires were common in these mountains thousands of years prior to permanent human settlement of Hispaniola (about 4000 y BP) (19).

METHODS

Field Assessment of Postfire Vegetation

We classified the severity of fire into five categories defined by the degree of damage to overstory and understory vegetation:

i) crown fire—needles of canopy trees completely consumed, 100% stand mortality;
ii) severe burn—needles of canopy trees not completely consumed, 90–100% stand mortality;
iii) severe understory burn—canopy trees still have green needles but significant scorching of stems occurs, usually less then 40% mortality of canopy trees, saplings, and smaller trees consumed by the fire;
iv) light surface fire—little to no mortality of canopy trees, saplings mostly survive, slight scorching of bark near the base of some trees; and
v) unburned.

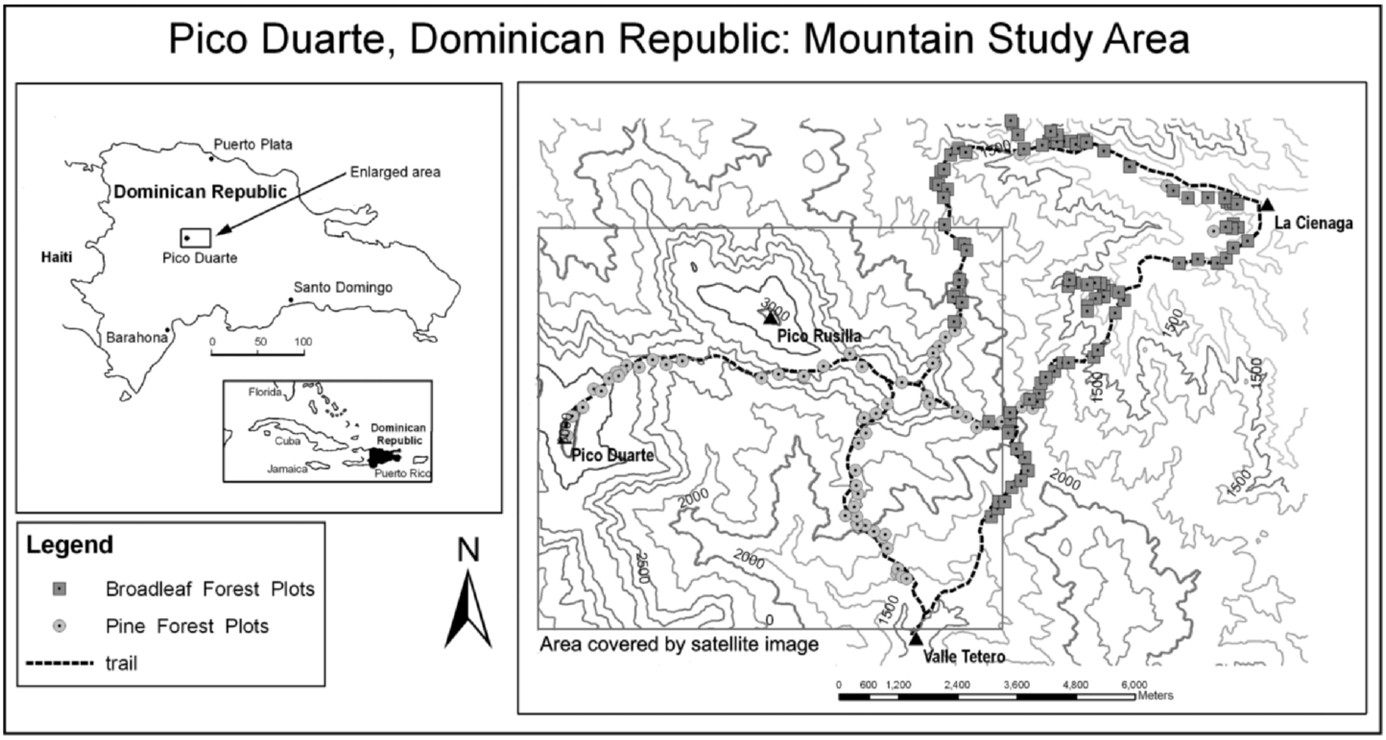

Figure 3. Map of the study area in the Bermúdez and Ramírez National Parks, Cordillera Central, Dominican Republic, showing the location of the permanent vegetation plots established in 1999–2000. The area covered by the QuickBird satellite image is indicated on the map.

Postfire vegetation was surveyed in the field during December 2005–January 2006 and January–March 2007. Fire severity was assessed by visual observation of burn damage using these five categories, and the location of the observation was recorded with a Garmin Map 60CSx GPS.

Field surveys were conducted in January 2006 at 47 reasonably accessible points along the pine–cloud forest ecotone to analyze vegetation factors and landscape characteristics that influenced fire behavior at the ecotone. An additional 16 surveys were conducted on the leeward side of a 2000 m saddle along the main 3000 m ridge where a similar pattern was observed: the fire went out near the edge of lower-elevation broadleaved forest patches (~1700 m elevation) adjacent to the burned over pine forest matrix. This area leeward of the saddle receives precipitation similar to windward areas (unpubl. data), but, as it occurs at lower elevations, it has different tree species composition than the cloud forest. At these 63 points, species and d.b.h. were recorded for all trees $\geq$10 cm d.b.h., and the level of fire damage to each individual tree was recorded (dead, severe, low, none) along 5-m-wide belt transects that extended from burned to unburned areas. Transects were started in the burned pine forest at least 10 m from the unburned fire edge. In addition, the number of saplings ($>$1 m tall and $<$10 cm d.b.h.) were recorded and identified in a 2-m-wide transect along the same transect length. The slope gradient and slope aspect were measured, and epiphyte (bryophytes, lichens, and filmy ferns) abundance was estimated visually every 5 m along each transect.

Sixty-two of the 245 prefire permanent study plots were within the area covered by the high-resolution, multispectral satellite data set. Seven of these plots were in the broadleaf forest, and the remaining 55 were in pine forest plots. We revisited these plots in 2007 to assess the burn severity and relate burn severity to prefire stand characteristics of each plot. All tagged trees ($\geq$10 cm d.b.h.) were located, and the d.b.h. was measured if the tree was alive; for dead trees, we recorded how the tree was killed, either by fire or dead before the fire (based on indicators like foliage loss and decay). Multiple regression analysis was used to test whether plot-level burn severity could be explained by prefire stand and site characteristics, including density, basal area, elevation, slope gradient, slope aspect, canopy height, and the convexity or concavity of the landscape (based on the terrain shape index [20]). Aspect was converted into two uncorrelated measures of aspect, eastness and southness, for the analysis (both values range from +1.0 to −1.0) (14).

Satellite Imagery

Postfire imagery of our study area was acquired on 20 March 2006, one year after the fire, with the Ball Global Imaging System 2000 high-resolution, multispectral sensor (http://www.satimagingcorp.com/satellite-sensors/quickbird.html) on the QuickBird Earth-orbiting satellite (DigitalGlobe, Longmont, CO, USA). There were no archived satellite images of the study area having spectral and spatial resolution similar to the QuickBird images; thus, no prefire image data were available for multitemporal, comparative analyses as described by Brewer et al. (21). The 81 km^2 image covered all of the burned area of our study site (Fig. 3). The image was collected at 18° off-nadir angle with a resulting resolution of 2.69 m for the multispectral image. All image processing and analysis were performed using ERDAS Imagine 8.0 software (Leica Geosystems LLC). We orthorectified the image using a 20 m digital elevation model and the QuickBird Rational Polynomial Coefficients geometric correction model in ERDAS (http://gi.leica-geosystems.com/) to the Universal Transverse Mercator coordinate system and projection, Zone 19, North American Datum of 1927. The positional accuracy of the rectified image was assessed by computing the root mean square error (RMSE) using 23 independent ground control points (GCPs) collected in the field using a Trimble GeoXT global positioning system (GPS) combined with a Trimble Hurricane Antenna. Ground control points were collected along the major trail system at sites that

Table 1. Summary of fire-severity map accuracy using supervised classification of a single-date, multispectral QuickBird satellite image.

Fire class	Producer's accuracy (%)	User's accuracy (%)	Kappa coefficient
Severe	88.2	88.2	0.781
Moderate	87.3	86.3	0.759
Unburned	90.0	94.7	0.941

Overall accuracy = 88.0%. Overall kappa = 0.797.

could be identified on the satellite image. The number of GCPs collected was limited because very few features on the landscape were both clearly distinguishable on the satellite image and accessible in the field. The overall RMSE for the multispectral image was 5.4 m, or approximately two QuickBird multispectral pixels.

Principal component analysis (PCA), a spectral enhancement technique, was applied to the image to reduce redundancy among the four spectral bands. Our visual interpretation showed that the enhanced image using the PCA transformation improved discrimination over the nonenhanced image of different burn categories. We then performed a supervised classification of the five fire-severity categories using maximum likelihood discriminant analysis. The set of 202 GPS-positioned points collected in the field in January 2006 was used to develop spectral models of each fire-severity category ("training classes") for use by the maximum likelihood image classification model. Only points that were located fully within a fire-severity category were used as spectral training sites. Eighteen points, located in the transition zone between fire-severity categories, were not used to develop spectral training classes. An independent set of 184 GPS points collected in January 2007, which included 62 permanent plots (described previously), was used for assessing the accuracy of the resulting map of fire severity. A neighborhood smoothing technique, using a 7 pixel × 7 pixel spatial filter, was applied to the map of predicted fire severity after the accuracy assessment was conducted to eliminate the "salt and pepper" appearance by converting the fire-severity value of each pixel in the center of the moving spatial filter based on a majority rule. The classified and smoothed fire-severity map was imported into ArcScene in ArcGIS to create a three-dimensional image for visualization purposes.

Fire-severity patterns were examined in relation to the topographic variables, slope gradient and slope aspect, using ArcGIS 9.0. Slope aspect (as measured in arc-degrees of azimuth from north) was grouped into eight 45° classes corresponding to the major compass directions: N, NE, E, SE, S, SW, W, and NW. Slope gradient was grouped into four classes based on ranges of percent slope: 0–15, 15–30, 30–60, and >60. The area of the different fire-severity classes was then calculated for each slope gradient or slope aspect class. A chi-square analysis was used to test whether the observed frequency of area burned in each slope gradient or slope aspect class was significantly different than expected, assuming the proportion burned in each fire-severity category was equal. The mean elevation of the fire perimeter was quantified on the windward slopes by recording the elevation of several hundred points along the fire edge on the map of fire-severity categories produced by satellite image classification.

RESULTS

The initial classification based on five fire-severity categories had a high error rate. Misclassification errors resulted from spectral confusion between severity categories 1 and 2 and the spectral signatures of fire severity categories 3 and 4. Thus, class 1 and class 2 were combined into a "severe" fire severity category (crown fire), and classes 3 and 4 were combined into a "moderate" fire severity category (understory fire) for a total of three classes including the "unburned" class. The cloud forest was either unburned or severely burned and did not experience moderate fires. The spectral signature of the severely burned cloud forest could not be reliably distinguished from the severely burned pine forest.

An accuracy assessment performed on the classified map based on the three fire severity categories had an overall kappa coefficient of 0.80 and an overall classification accuracy of 88.0% (22). All three fire-severity categories (severe, moderate, unburned) had both high producer and user accuracy (Table 1).

Fire Patterns

The fire-severity map illustrates that the fire burned throughout most of the pine forest but tended to extinguish at the pine–cloud forest ecotone (Fig. 4). The mean elevation of the fire perimeter on the windward slopes measured from the satellite image was 2073 ± 156 m, which was similar to the prefire elevation (2007 m) of the pine–cloud forest ecotone measured on aerial photographs (13). Fire-severity patterns were spatially heterogeneous across the landscape. Thirty-six percent of the monodominant pine forest as mapped by the satellite image classification was burned severely, 60% burned moderately, and only 4% escaped the fire. Slope gradient had a limited affect on fire patterns. Pine forest hillslopes at ≤30% gradient experienced significantly less burn than the expected proportion, but these slopes comprised only 5% of the landscape. Also, steep slopes (>60%), accounting for 12% of the landscape, experienced greater than expected severe burn and less than expected unburned areas. Slope aspect had a significant relationship to fire patterns, with a greater than average proportion of SE-, S-, and SW-facing slopes experiencing severe and moderate fire severity in the pine forest, and slopes with NE, N, and NW aspects experiencing less than average severe burns. Conversely, unburned areas were significantly more common on N and NW slopes and less common on slopes with SE, S, and SW aspects. None of the other landscape variables was significantly correlated with fire extent and severity.

Field surveys along the fire perimeter indicated that the fire usually was extinguished at the pine–cloud forest boundary. Field inventory data showed that the fire burned on average 15.1 ± 1.1 m into the cloud forest along 90% of the transects before being extinguished. The point at which the fire extinguished in the cloud forest often coincided with the occurrence of a dense cover of epiphytes and bryophytes on the trees and ground (Fig. 5). A similar pattern was observed in the leeward saddle area: the fire extinguished near the edge of small broadleaf forest patches within the burned-over pine forest matrix. In the 16 leeward transects, the fire penetrated on average 15.3 ± 1.7 m into the broadleaf forest. Slope gradient, slope aspect, and slope curvature had no influence on the location at which the fire extinguished in either the cloud or broadleaf forests. In six of the cloud forest transects, the fire burned comparatively far into the cloud forest (70–145 m distance from the ecotone), consuming the deep accumulations of the mossy peat as well as the canopy trees (Fig. 1b). Four of these six transects had evidence of previous hurricane damage (Fig. 5). The severity of the fire in the pine forest adjacent to the cloud forest or broadleaf forest patches had no relationship to the distance that the fire penetrated into the hardwood stands.

Mortality in the 55 pine forest permanent plots ranged from 0% to 100%, whereas none of the seven broadleaf forest plots burned within the fire zone as mapped using the satellite image.

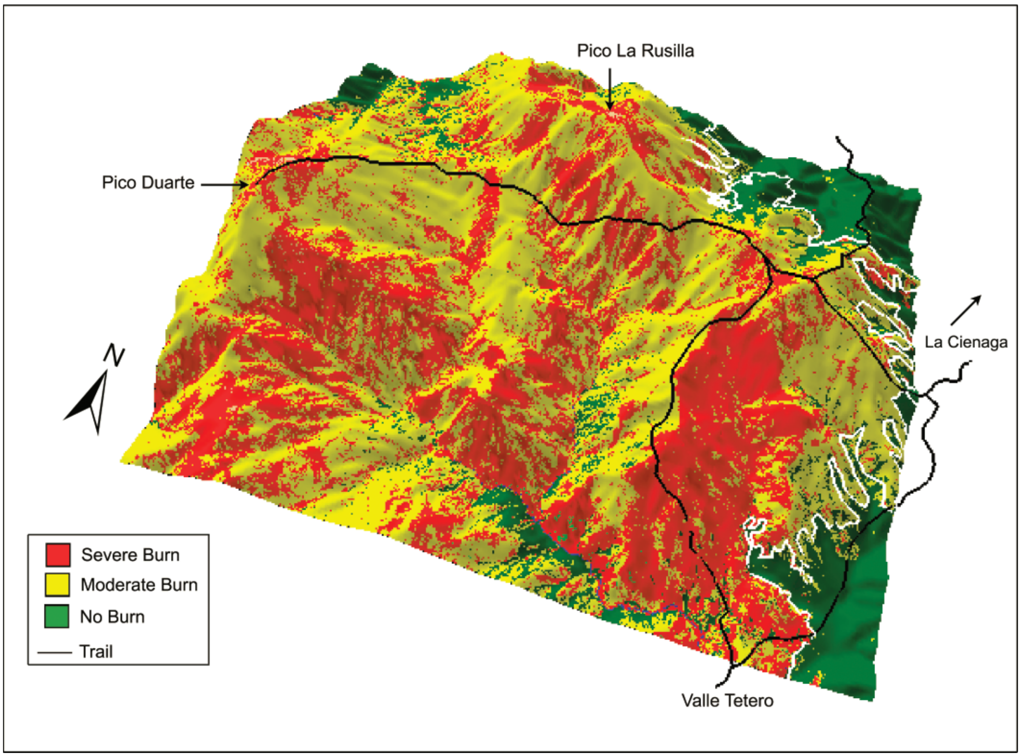

Figure 4. Extent and severity of the March 2005 fire in the Bermúdez and Ramírez National Parks, Cordillera Central, Dominican Republic, based upon interpretation and supervised classification of a March 2006 QuickBird satellite image. Also indicated are the prefire pine–cloud forest boundary (white line) mapped from aerial photographs (13) and trail (black line) used to acquire GPS-referenced field data.

There was a significant positive linear relationship between the percent of trees in a plot killed by the fire and stand density ($r^2 = 0.18$, $p = 0.002$) and southness ($r^2 = 0.14$, $p = 0.007$), and a negative linear relationship with elevation ($r^2 = 0.28$, $p < 0.001$). No significant correlations were found between fire mortality and other prefire stand characteristics.

DISCUSSION

The 2005 fire burned over approximately 96% of the monodominant pine forest in our study area but mostly failed to burn into the adjacent cloud forest. These observations support our hypothesis that fire maintains the abrupt boundary between the pine and cloud forest vegetation (13). Similarly, the fire tended to extinguish at the edge of lower-elevation broadleaf forest patches that occur in moist coves adjacent to the monodominant pine forest matrix leeward of the 2000 m saddle. These findings suggest that the mechanisms regulating the pine–cloud forest ecotone (e.g., mosses abundance) are not unique: fire behavior at the lower-elevation pine–broadleaf forest boundary appears to be regulated by similar processes.

Clearly, contrasting vegetation characteristics and environmental conditions influence fire likelihood across the pine–cloud forest ecotone. The high-light understory environment of the pine stands has well-aerated, combustible needle litter that favors fire spread (23). In contrast, the dense canopy and deeply shaded understory of the broadleaf forest stands maintain a moist environment that reduces flammability (24). This effect is reinforced in the cloud forest by the blanket of bryophytes and filmy ferns, which covers the canopy, stem, and ground surface, and which traps and retains moisture from clouds and rain (25). Once established, positive feedbacks between the vegetation and microenvironment would reinforce the spatial pattern in the fire regime and sharpen the ecotone over time, as has been observed in other tropical and subtropical ecosystems (26–28). It is notable that even where an intense crown fire occurred in an adjacent pine forest stand, the fire did not penetrate any deeper into the cloud forest or broadleaf forests than it did in forest stands experiencing lower-intensity surface fires. Surprisingly, topographic factors, such as slope angle and shape (27), also did not influence fire behavior at the ecotone. Clearly, vegetation structure and composition play the primary role in regulating fire spread in this landscape, at least for the 2005 fires. The pronounced influence of fire on vegetation patterns in this site is not surprising given the juxtaposition of fire-sensitive cloud forest flora and the fire-tolerant pine. The elevational consistency of the ecotone, however, is noteworthy. Discontinuities in mesoclimate around the ecotone, particularly atmospheric humidity and cloud formation associated with the TWI, presumably play a complementary role in establishing the elevational consistency of the ecotone over such a large area. Elsewhere, climatic patterns are known to influence the position of ecotones through their influence on fire regimes (29).

Cloud forests rarely burn, but when they do, cloud forest fires can be highly destructive (24, 30). Wet humid forests are

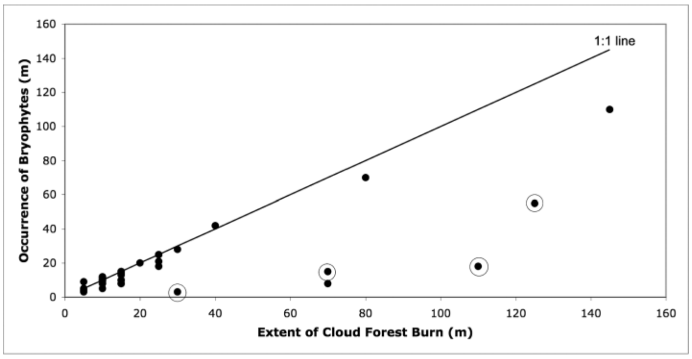

Figure 5. The distance the fire burned into the cloud forest in relation to the occurrence of a dense cover of epiphytes and bryophytes on the trees and ground within the cloud forest. Points on the 1:1 line indicate the fire extinguished when it encountered the bryophyte-laden forest, whereas points below the line indicate the distance the fire penetrated the cloud forest beyond the point at which bryophytes were encountered. The circled points are plots that had evidence of earlier hurricane damage.

more vulnerable to fire than drier forests because trees have thin bark and so suffer high mortality rates from fire (31). In addition, most species have little or no ability to resprout from fire-caused mortality, so recovery is slow (30). Fires burned extensively into the cloud forest in a few locations (Fig. 1b), resulting in high mortality of the canopy trees and, in some locations, consuming the deep accumulations of mossy peat. The thick organic soil horizons in cloud forests provide additional fuel that can sustain slow-burning fires, causing large reductions in belowground biomass and contributing to overstory tree mortality (24). Wind damage from earlier hurricane disturbance (Hurricanes David in 1979 and Georges in 1998) and resultant large accumulations of woody fuels and open understories may have contributed to the severity of the fire in these locations by favoring fire spread. These intense burns also coincided with two exceptionally windy days on 22 and 23 March 2005 (F. Peralta pers. comm., Dominican Park Service). Although we can only speculate as to why the cloud forest burned extensively at these locations, long-term monitoring of their recovery will provide invaluable insights into the dynamics of the pine–cloud forest ecotone.

Factors that mediated patterns of burn severity in the pine forest across the landscape were prevailing wind direction, slope gradient, slope aspect, and forest stand density. As noted, much of the severe burning occurred on two exceptionally windy days that produced strong upslope winds, resulting in widespread mortality on the leeward slopes. Although wind was the principal influence on fire behavior, other patterns also emerged: tree survivorship tended to be higher in low-tree-density stands on gentler slopes with more northerly exposures. Higher-elevation ($>$2800 m) pine forests in the study area have more open canopies and lower tree densities (linear regression: $r^2 = 0.15$, $p = 0.004$); thus, fire-induced mortality declined with increasing elevation in part because of this forest structure pattern.

A paradigm of fire-controlled treelines has been often applied in tropical mountains, particularly where influenced by human activities (32–34); our results demonstrate that fires can create and maintain ecotones between TMF associations as well (9, 12, 35–38). This study is germane to broader vegetation patterns in subtropical montane forests. Between 15° and 25° latitude, there are extensive montane forests influenced by fire and frost that transition at high elevations from speciose tropical cloud forest to monodominant forests of temperate lineage tree species, usually from the Pinaceae or Fagaceae. Specifically, the pattern in this study is similar to other fire-influenced or fire-created TMFs ecotones in Mexico (39, 40); a Lauraceae–*Pinus* ecotone in Southeast Asia (41); a Laurel forest–*Pinus* ecotone in the Canary Islands (42); forest ecotones in South America (38, 43); a narrow pine–cloud forest ecotone in the Philippines (35); ecotones in Australia and Tasmania (36, 44); and the subtropical Himalayas, where fires and frosts above 2500 m lead to dominance by north temperate conifers (*Tsuga*, *Abies*, and *Picea*) (9, 37).

An El Niño event in 2004–2005 produced drought conditions across the region that coincided with the March 2005 fire. Similarly, severe fires in the past have also coincided with strong El Niño years (15). Under future climate change scenarios, the frequency and strength of El Niño–Southern Oscillation events are expected to increase (12, 45), which could lead to more frequent droughts and fires. Adult trees of *P. occidentalis* have two adaptations that favor their survival to fire—thick bark and self-pruning of lower branches (46), but seedlings do not have adaptations to survive severe fire events. In order for pine to persist at a given site, the interval between at least some fires needs to be long enough to allow seedlings to become large enough to survive future fires. Areas that experience more frequent burns may be maintained as savannas dominated by the endemic, fire-tolerant tussock grass, *Danthonia domingensis* Hack. & Pilger. Cloud forests also are susceptible to fire under conditions of extreme drought and may be exceptionally vulnerable to fire damage (24). Severe or repeated fires in the cloud forest could create conditions that allow pines or other species to become established, altering the microenvironment and fire regime and inhibiting the regeneration of cloud forest species. Once tropical moist forests burn, they become increasingly susceptible to fire under normal dry-season weather conditions, and recurrent fires can cause greater damage than the initiating fire (47).

The tight coupling of fire dynamics with the position of the pine–cloud forest ecotone raises concern over the future of these unique forests of the Cordillera Central. Climate change models predict an increase in wildfires in tropical forests due to an increase in droughts, El Niño events, hurricane frequency, and lightning (45, 48). Moreover, changes in the elevation of the TWI and reduced cloudiness have been predicted to occur (49), which also would influence the fire regime. The narrow zone occupied by cloud forests makes them particularly susceptible to disruptions in disturbance regimes and climate. Our continued monitoring of these montane tropical forests should provide valuable insights on the stability of ecotones in the face of global environmental change.

References and Notes

1. Richards, P.W. 1952. *The Tropical Rain Forest*. Cambridge University Press, London, UK, 450 pp.
2. Grubb, P.J. and Whitmore, T.C. 1966. A comparison of montane and lowland rain forests in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. *J. Ecol. 54*, 303–333.
3. Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica, 206 pp.
4. Grubb, P.J. 1974. Factors controlling the distribution of forest-types on tropical mountains: new facts and a new perspective. In: *Altitudinal Zonation in Malesia. Transactions of the 3rd Aberdeen-Hull Symposium on Malesian Ecology*. Flenley, J.R. (ed). Department of Geography, University of Hull, Hull, UK, pp. 13–46.
5. Hartshorn, G. and Peralta, R. 1988. Preliminary description of primary forests along the La Selva–Volcan Barva altitudinal transect, Costa Rica. In: *Tropical Rainforest: Diversity and Conservation*. Almeda, F. and Pringle, C.M. (eds). California Academy of Sciences, San Francisco, CA, pp. 281–295.
6. Lieberman, D., Lieberman, M., Peralta, R. and Hartshorn, G.S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol. 84*, 137–152.
7. Vasquez, J.A. and Givinish, T.J. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *J. Ecol. 86*, 999–1020.
8. Lovett, J.C. 1998. Continuous change in Tanzanian moist forest tree communities with elevation. *J. Trop. Ecol. 14*, 719–722.
9. Ashton, P.S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Persp. Plant Ecol. Evol. System. 6*, 87–104.
10. Kitayama, K. 1992. An altitudinal transect study of the vegetation of Mount Kinabalu, Borneo. *Vegetatio 102*, 149–171.
11. Kitayama, K. and Mueller-Dombois, D. 1994. An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian island mountain: (2) vegetation zonation. *Phytocoenologia 24*, 135–154.
12. Hemp, A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Glob. Change Biol. 11*, 1013–1023.
13. Martin, P.H., Sherman, R.E. and Fahey, T.J. 2007. Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *J. Biogeogr. 34*, 1792–1806.
14. Sherman, R.E., Martin, P.H. and Fahey, T.J. 2005. Vegetation-environment relationships in forest ecosystems of the Cordillera Central, Dominican Republic. *J. Torr. Bot. Soc. 132*, 293–310.
15. Martin, P.H. and Fahey, T.J. 2006. Fire history along environmental gradients in the subtropical pine forests of the Cordillera Central, Dominican Republic. *J. Trop. Ecol. 22*, 289–302.
16. Pederson, A. 1953. Frost damage in the pine forest. *Carib. For. 14*, 93–96.
17. Lewis, J.F. 1980. Cenozoic tectonic evolution and sedimentation in Hispaniola. In: *Transactions of the 9th Caribbean Geology Conference, Volume 1*. Santo Domingo, Dominican Republic, pp. 65–73.
18. Martin, P.H., Sherman, R.E. and Fahey, T.J. 2004. Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. *Biotropica 36*, 297–317.
19. Horn, S.P., Orvis, K.H., Kennedy, L.M. and Clark, G.M. 2000. Prehistoric fires in the highlands of the Dominican Republic: evidence from charcoal in soils and sediments. *Carib. J. Sci. 36*, 10–18.
20. McNab, W.H. 1989. Terrain shape index: quantifying effect of minor landforms on tree height. *For. Sci. 35*, 91–104.
21. Brewer, C.K., Winne, J.C., Redmond, R.L., Opitz, D.W. and Mangrich, M.V. 2005. Classifying and mapping wildfire severity: a comparison of methods. *Photogramm. Eng. Rem. Sens. 71*, 1311–1320.
22. Congalton, R.G. and Green, K. 1999. *Assessing the Accuracy of Remotely Sensed Data: Principles and Practices*. Lewis Publishers, New York, 137 pp.
23. Mutch, R.W. 1970. Wildland fires and ecosystems—a hypothesis. *Ecology 50*, 1046–1051.

24. Asbjornsen, H., Velazquez-Rosas, N., Garcia-Soriano, R. and Gallardo-Hernandez, C. 2005. Deep ground fires cause massive above- and below-ground biomass losses in tropical montane cloud forests ion Oaxaca, Mexico. *J. Trop. Ecol. 21*, 427–434.
25. Bruijnzeel, L.A. and Proctor, J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? In: *Tropical Montane Cloud Forests*. Hamilton, L.S., Juvik, J.O. and Scatena, F.N. (eds). Ecological Studies, Vol. 110. Springer-Verlag, New York, pp. 38–78.
26. Kalisz, P.J. and Stone, E.L. 1984. The longleaf pine islands of the Ocala National Forest, Florida: a soil study. *Ecology 65*, 1743–1754.
27. Kellman, M. and Meave, J. 1997. Fire in the tropical gallery forests of Belize. *J. Biogeogr. 24*, 23–34.
28. Biddulph, J. and Kellman, M. 1998. Fuels and fire at savanna–gallery forest boundaries in southeastern Venezuela. *J. Trop. Ecol. 14*, 445–461.
29. Gardner, R.H., Hargrove, W.W., Turner, M.G. and Romme, W.H. 1996. Climate change, disturbances and landscape dynamics. In: *Global Change and Terrestrial Ecosystems*. Walker, B. and Steffen, W. (eds). Cambridge University Press, Cambridge, UK, pp. 149–172.
30. May, T. 2000. Five years of post-fire vegetation succession in a Caribbean cloud forest (Cordillera Central, Dominican Republic). *Ecotropica 6*, 117–127.
31. Uhl, C. and Kaufmann, J.B. 1988. Fire in the Venezuelan Amazon: 2. environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos 53*, 176–184.
32. Ellenberg, H. 1979. Man's influence on tropical mountain ecosystems in South America: the second Tansley lecture. *J. Ecol. 67*, 401–416.
33. Young, K.R. 1993. Tropical treelines: changes in forest structure and regeneration between two Peruvian treeline margins. *Arct. Alp. Res. 25*, 167–174.
34. Cavalier, J., Aide, M.T., Santos, C., Eusse, A.M. and Dupuy, J.M. 1998. The savannization of moist forests in the Sierra Nevada de Santa Marta, Colombia. *J. Biogeogr. 25*, 901–912.
35. Kowal, E.K. 1966. Shifting cultivation, fire, and pine forest in the Cordillera Central, Luzon, Philippines. *Ecol. Monogr. 36*, 389–419.
36. Unwin, G.L. 1989. Structure and composition of the abrupt rainforest boundary in the Herberton Highland, north Queensland. *Austral. J. Bot. 37*, 413–428.
37. Ohsawa, M. 1995. The montane cloud forest and its gradational changes in Southeast Asia. In: *Tropical Montane Cloud Forests*. Hamilton, L.S., Juvik, J.O. and Scatena, F.N. (eds). Ecological Studies, Vol. 110. Springer-Verlag, New York, pp. 254–265.
38. Grau, H.G. and Veblen, T.T. 2000. Rainfall variability, fire and vegetation dynamics in neotropical montane ecosystems in north-western Argentina. *J. Biogeogr. 27*, 1107–1121.
39. Rzedowski, J. 1978. *Vegetación de México*. Arcos de Belén, Editorial Lumisa, México City, México, 432 pp.
40. Arriaga, L. 2000. Types and causes of tree mortality in a tropical montane cloud forest of Tamaulipas, Mexico. *J. Trop. Ecol. 16*, 623–636.
41. Ohsawa, M. 1990. An interpretation of latitudinal patterns of forest limits in south and east Asian mountains. *J. Ecol. 78*, 326–339.
42. Fernández-Palacios, J.M. and de Nicolás, J.P. 1995. Altitudinal pattern of vegetation variation on Tenerife. *J. Veget. Sci. 6*, 183–190.
43. Kessler, M. 2000. Altitudinal zonation of Andean cryptogam communities. *J. Biogeogr. 27*, 275–282.
44. Ash, J. 1988. The location and stability of rainforest boundaries in north-eastern Queensland, Australia. *J. Biogeogr. 15*, 619–630.
45. Timmermann, A., Oberhuber, J., Bacher, J., Esch, M., Latif, M. and Roeckner, E. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature 398*, 694–696.
46. Darrow, W.K. and Zanoni, T. 1990. Hispaniolan pine (*Pinus occidentalis* Swartz): a little known subtropical pine of economic potential. *Commonw. For. Rev. 69*, 133–146.
47. Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M. Jr., Nepstad, D.C., Lefebvre, P. and Davidson, E.A. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science 284*, 1832–1835.
48. Goldhammer, J.G. and Price, C. 1998. Potential impacts of climate change on fire regimes in the tropics based on MAGICC and a GISS GCM-derived lightning model. *Clim. Change 39*, 273–296.
49. Loope, L.L. and Giambelluca, T.W. 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawai'i. *Clim. Change 39*, 503–517.

Ruth Sherman is an ecosystems ecologist in the Department of Natural Resources, Cornell University. She has been a member of the research staff since 1998. Her general scientific interests are in vegetation-environment interactions in both temperate and tropical systems. Her address: Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA.
E-mail: res6@cornell.edu

Patrick Martin is an Assistant Professor. His 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 climate change and exotic species on native plant communities and ecosystem function. His address: Department of Horticulture and Landscape Architecture, 215 Shepardson Building, Colorado State University, Fort Collins, CO 80523, USA.
E-mail: Patrick.Martin@colostate.edu

Timothy Fahey is a forest ecologist in the Department of Natural Resources, Cornell University. He has been a member of the Cornell faculty since 1982. His general scientific interest is in better understanding forest ecosystems, both tropical and temperate. His address: Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA.
E-mail: tjf5@cornell.edu

Steve DeGloria is a professor of Environmental Information Science in the Department of Crop and Soil Science, Cornell University. His areas of expertise are in resource inventory, mapping, and analysis; remote sensing; geographic information systems; environmental information science; and soil survey, interpretations, and conservation. His address: Department of Crop and Soil Science, Rice Hall, Cornell University, Ithaca, NY 14853, USA.
E-mail: sdd4@cornell.edu