Are We Losing the Best Parts of Our Protected Areas in Tropical Mountains?

Shauna-Lee Chai[1] and **Edmund Tanner**

Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK

ABSTRACT

Protected areas (PAs) on tropical mountains undergo greater forest destruction in their lower altitudes. We compared the extent of forested, nonforested, and fragmented areas between lowland (< 1000 m asl) and montane zones of the Blue Mountains inside the Blue and John Crow Mountains National Park established in Jamaica in 1993. We found that in 2008, inside the montane zone, only 4 percent of forest was cleared, and forest fragmentation was minimal. In the lowland zone, however, the percentage of forest cleared was seven times as high, and the density of fragments was 11-fold higher. We established twenty-five 0.04 ha lowland plots; ordination of tree species composition in these plots reflected a rainfall gradient, showing that plots on the wetter northern side of the Blue Mountains were floristically different from those on the drier southern side. The conservation value of the remaining lowland forest is high because of its high endemism (18% of species in our plots) and beta diversity. In addition, IUCN Red List data show that about 71 percent of threatened tree species in the Blue Mountains grow in the lowland region, 92 percent of which are endemic. From these findings, we identify a 'protected area hotspot zone', which lies between the PA boundary and the core high-altitude zone, and which should be instituted in IUCN categories I and II PAs.

Key words: endemism; hotspot; Jamaica; lowland forest; national park; zonation.

Most of the world's tropical forest protected areas (PAs) include mountains. Emerging patterns in the placement of PAs toward higher elevations, steeper slopes, and longer distances to roads and cities (Joppa & Pfaff 2009) as well as the increasing isolation of PAs due to deforestation outside PAs (DeFries *et al.* 2005) have already been recognized. There is also an elevation bias within PAs, because the lowland portions undergo higher rates of deforestation than the higher elevation zones (Green & Sussman 1990, Kinnaird *et al.* 2003, Curran *et al.* 2004, Southworth *et al.* 2004). This elevation bias within PAs has largely been ignored as a wide-scale pattern evident across much of the tropics. Because of the geometry of mountains, most *montane* PAs have a significant portion of forest at lower altitudes that may be classified as lowland or lower montane, the precise altitudes of which vary according to the Massenerhebung effect (Richards 1952, Grubb 1974). Within these lower altitudes, where tropical forests still exist, they are often in the form of isolated fragments (Turner & Corlett 1996) which occupy only a small fraction of their historical range, and are surrounded by shifting cultivation and/or invasive alien species monocultures. Maintaining the few remaining elevation gradients in tropical forest habitats is essential for species conservation (Hall *et al.* 2009), and is especially important for PAs, which often contain the last remaining strongholds for endemic species.

With increased awareness of tropical deforestation as the second highest anthropogenic contributor of atmospheric carbon dioxide, which accounted for approximately 12 percent of CO_2 emitted in 2008 (Le Quéré *et al.* 2009), the issue of tropical forest protection is heightened in the global arena. If PAs, especially those in the Caribbean and Southeast Asia, are to become more successful in preventing deforestation and species loss (as studies have shown them not to be, *e.g.*, Gaveau *et al.* 2007, Chai *et al.* 2009), conser-

vation planners should focus on threatened lowland forests, as montane areas appear to be relatively protected *de facto*. With an estimated 11 percent of the original vegetation of the Caribbean remaining (Myers *et al.* 2000), this region is projected to lose the most endemic species of all 25 biodiversity hotspots (Brooks *et al.* 2002), and this is despite 100 percent of the remaining Caribbean hotspots being under some sort of legal protection (Myers *et al.* 2000).

The Blue and John Crow Mountains National Park (BJCMNP) in Jamaica provides a particularly good example of the bias in emphasizing higher elevations in what are commonly referred to as 'montane parks'; some 50 percent of the total area of this park is < 800 m elevation, yet protection of these lowland areas has been marginalized (Fig. S1). Like other tropical PAs that contain mountains, the lowland area in the BJCMNP undergoes considerably higher deforestation and forest degradation pressures (mainly due to clearance for agriculture) than its largely inaccessible high-altitude counterpart (Eyre 1987, Kelly 1988, Chai *et al.* 2009). In 1953, Asprey and Robbins reported that no 'typical' rain forest remained below 300 m altitude in Jamaica, and while the higher altitude forests of the BJCMNP have received keen scientific attention (Shreve 1914; Grubb & Tanner 1976; Tanner 1977, 1986), the composition of forests over the geographical range of the lower altitudes has not been described, although there is an account of the flora of two plots 100 × 25 ft at 1800 and 2500 ft in the south eastern part of what became the BJCMNP in Asprey and Robbins (1953). A Rapid Ecological Assessment (Muchoney *et al.* 1994) also described nine 20 × 20 m plots < 1000 m elevation in (unspecified) locations within the park boundary.

Jamaican plants have been described in a modern flora (Adams 1972), which includes their elevation limits and distribution in 13 parishes (or administrative zones). Their distribution is notably complex and often so narrowly localized that some species are confined to a single wooded hilltop, cliff face, mossy woodland, or

---

other such peculiarly narrow locales (Proctor 1982). This means that plant beta diversity—the difference in species composition among sites in an area—is high, but an investigation of the environmental factors influencing this beta diversity has never been carried out. Plant beta diversity probably led to the high plant endemism for which Jamaica is noted; Jamaica has the fifth highest percentage of floral endemism among islands of the world (Davis *et al.* 1997). Montane plots in the Blue Mountains of Jamaica have, for example, a 41 percent tree species endemism (Tanner 1986).

Our research uses Landsat ETM+ data to quantify the extent of forested, nonforested, and fragmented areas in the relatively intact high-altitude forest with that of the threatened lower altitude forests in the BJCMNP. Remote sensing analysis comparing deforestation and fragmentation in the BJCMNP across time scales (1983–2002) has already been carried out (Chai *et al.* 2009); in this paper, we quantify elevation patterns in deforestation and fragmentation using 2008 imagery. We compared the total tree diversity in lowland vs. montane regions of the park by tallying the potential flora of these two areas using Adams flora of Jamaica, and we investigated the implications for biodiversity conservation of disappearing low-altitude forests using the IUCN Red Data books. We established 25 permanent plots throughout the geographic range of lowland forest to describe the tree species composition, and examined patterns in the tree species distribution. Specifically, our research answers the following questions: What is the extent of forested, nonforested, and fragmented area in lowlands vs. montane sections in the BJCMNP? How do tree species richness, endemism, and threatened species vary between lowlands and montane forests? What is the current tree species composition in the lowlands of the park, and are they still relevant for conservation? What environmental factors influence species spatial turnover? And finally, we applied our findings to the way national parks and strict nature reserves on mountains are zoned, to draw the attention of PA managers to areas that require most conservation effort.

METHODS

STUDY AREA.—The study was conducted in the tropical forests of the Blue Mountains (18° N, 76° W) that form a major part of the BJCMNP (IUCN category II) established in Jamaica in 1993. The Blue Mountain park is *ca* 32,550 ha and runs mainly west to east for about 39 km along the major axis (Fig. S1). The Grand Ridge forms the backbone of the range and reaches 2256 m, the highest elevation in the country. The mountains possess steep-sided valleys with deeply gorged rivers and igneous geology unlike most of the rest of the island, which is limestone. They span three parishes in the eastern section of the island: Portland, St. Thomas, and St. Andrew. Our lowland plots are located in the parishes of Portland (on the northern slopes of the Blue Mountains), which receives *ca* 3075 mm/yr rainfall (30 yr average, Meteorological Service of Jamaica 2009), and St. Thomas (on the southern slopes), which receives *ca* 1970 mm/yr rainfall (30 yr average, Meteorological Service of Jamaica 2009). This marked rainfall differentiation is caused by the moisture-laden north-east trade winds that originate

from the Atlantic Ocean blowing inland over the eastern parts of Jamaica and rising up the northern slopes of the Blue Mountains, causing precipitation as the air cools. This causes the northern slopes and the wind corridor of the Rio Grande Valley between the Blue and John Crow mountain ranges, which include Cunha Cunha Pass, to receive high rainfall. The mean annual rainfall (over 70 yr) in the vicinity of Cunha Cunha Pass is 6401 mm at 220 m elevation (Jamaica Rainfall for the year 1942, 1945). The southern side of the Blue Mountains in the rain shadow receives considerably less rainfall.

Jamaica was almost entirely forested in the pre-Columbian era (Kelly 1988), and forests of the Blue Mountains probably did not undergo significant disturbance until the late 1780s when the first coffee plantations were established (Delle 1998). Native forest communities include lowland forest, lower and upper montane rain forest, high-altitude scrub forest, and montane summit savannah (Muchoney *et al.* 1994), and are a mixture of old growth (*ca* 50%) and secondary vegetation (*ca* 25%) (Muchoney *et al.* 1994). The other major land cover types include *Pinus caribaea* plantations (7%) and agriculture (18%) (Muchoney *et al.* 1994). Much of the forest conversion evident in the Blue Mountains today occurred before 1993, when the area was designated as a national park; about 27 percent of the area had already been converted by 1992; however, the rate of forest clearance post park establishment is still high at 1.4 percent/yr (Chai *et al.* 2009). Land tenure is mostly by the government of Jamaica, but includes lands leased to private individuals. The forests are threatened by conversion to agriculture, both small-scale shifting cultivation and large-scale coffee cultivation, invasion of alien species (*e.g.*, *Pittosporum undulatum* [Bellingham *et al.* 2005], *Hedychium gardneranum, and Bambusa vulgaris*), and selective logging.

QUANTIFYING FORESTED, NONFORESTED, AND FRAGMENTED AREAS ACCORDING TO ELEVATION.—We classified two Landsat ETM+ images taken in January and October 2008 and created an image mosaic to fill in missing scan lines using the January image to fill the October image (due to the scan line detector defect in the Landsat sensor after 2003, which produced gaps in the image data). The images were geometrically, atmospherically, and topographically corrected and classified into forest and nonforest categories using Erdas Imagine v.8.7 software. Accuracy assessment of images was carried out by ground truthing 50 locations. Grid files were configured in ArcGIS v.9.2, and fragmentation metrics were calculated using FRAGSTATS v.3.3 (see Chai *et al.* 2009 for details on image processing, classification, and accuracy assessment). A 6 m digital elevation model obtained from the Jamaica National Works Agency was used to create contour lines for elevation mapping.

POTENTIAL TREE FLORA AND THREATENED SPECIES.—We used Adams (1972) *Flowering Plants of Jamaica* supplemented with Proctor's (1982) additions to the flora to tally the potential tree flora of the Blue Mountain study area. Using data from the parishes of Portland, St. Thomas, and St. Andrew, as the Blue Mountains span sections of these three parishes, upper and lower altitudinal limits, geographic ranges, and habitat were recorded. World Conservation

Union (IUCN) Red Data books (IUCN 2009) were used to tally the threatened tree species: IUCN categories of critically endangered, endangered, vulnerable, or near threatened. We included species classified as near threatened in our tally of threatened trees because the IUCN Red List assessment for Jamaican trees was carried out in 1998, and as deforestation has been ongoing since this time, the likely status of these near-threatened trees has probably escalated over the past 12 yr.

TREE AND ENVIRONMENT SAMPLING.—Below 1000 m elevation, we established 25 permanent 20 × 20 m plots located randomly within 300 m of access trails, and rivers to determine tree species composition in lowland forest fragments. Many of the areas sampled were probably disturbed relict secondary forest (Muchoney *et al.* 1994). Randomness in choosing plots was restricted by accessibility, and proximity to forest and nonforest boundaries. If a random plot location chosen was inaccessible, or if it was within 30 m of a forest/nonforest boundary, the location was abandoned and another location was selected. With no clear-cut boundary between lowland and montane forests, 1000 m was chosen as the elevation limit for lowland forest (Brooks *et al.* 1999), and plots were at 146–960 m elevation. Because of the high diversity of lowland tropical forests, and the difficulty of identifying some species, only large trees with a minimum diameter of 24 cm were enumerated. Fieldwork was carried out from August 2008 to January 2009. Trees were tagged, identified, their heights were estimated, and their diameter at breast height (dbh at 1.3 m) was measured. Importance values were calculated by averaging the relative density and the basal area. Nomenclature follows Adams (1972) and Proctor (1982) except where authorities are given.

Environmental characteristics measured in the plots were altitude, surface soil pH (measured using an electronic pH meter by bringing soil sample into a paste with distilled water), aspect, soil depth, and slope in degrees. We also estimated the percent canopy cover and collected parent rock material to determine the geology. Rainfall data for specific sites were obtained either from historical 70 yr mean data (1872–1942) (Jamaica Rainfall for the year 1942 1945) or from the Meteorological Service of Jamaica (mean rainfall for 2007 and 2008).

TREE DATA ANALYSIS.—Nonmetric multidimensional scaling (NMDS), an unconstrained method of ordination in the R package 'vegan' (Oksanen *et al.* 2005), was used to identify gradients in tree species composition. NMDS is based on ecologically relevant measures of community dissimilarity and is a nonparametric method (Clarke 1993) that makes relatively few assumptions about the data being analyzed. We used the Bray–Curtis (Sørensen) dissimilarity distance to compute plot locations in the ordination based on raw plot data of species density, and an analysis of similarities (ANOSIM) to test the significance of observed trends in the ordination (Clarke 1993). The variation explained by the ordination axes was calculated using function 'stressplot' as $1-stress^2$ (Oksanen *et al.* 2005). We interpreted axes from NMDS by correlating them (Kendall's τ) with species richness, and the environmental data collected (slope, altitude, rainfall, pH, elevation, canopy cover, geology, aspect, and soil depth).

RESULTS

FORESTED, NONFORESTED, AND FRAGMENTED AREAS ACCORDING TO ELEVATION.—In 2008, at > 1500 m elevation, forest was unfragmented and was one contiguous area of 3100 ha between 1500 and 2000 m, and 246 ha at > 2000 m elevation (Table 1). Below 1500 m, however, forest was fragmented into 190 fragments and 21 percent of the area had been cleared. Below 1000 m (the lowlands), 28 percent of land was cleared, which is seven times as high as the 4 percent cleared at > 1000 m (Fig. 1). The density of fragments in lowlands (1.3 fragments/100 ha) is 11 times that of montane forest (0.12 fragments/100 ha). Of the total area under nonforest cover, 92 percent was at elevations < 1000 m. The overall classification accuracy was 92 percent ($\kappa = 0.826$).

POTENTIAL TREE FLORA AND THREATENED SPECIES FOR THE EASTERN PARISHES OF JAMAICA ACCORDING TO ADAMS FLORA (1972) AND IUCN RED LIST (2009).—The potential tree species pool in the Blue Mountain study area includes 449 native species belonging to 72 families, plus 61 introduced species (Table 2). Of these, 165 species (37% of native species) are endemic to Jamaica. Almost all (99%) of the endemics were recorded as inhabiting forests, woodlands, or thickets (1% was found growing in pastures) (Adams 1972); this underscores the importance of forests as habitat for endemic tree species. It is well documented that tree species diversity in tropical forests decreases with altitude (*e.g.*, Gentry 1992), and the distribution of tree species from Adams (1972) follows this trend, as 62 percent of native tree species recorded from the three eastern parishes in Adams flora were recorded at only < 1000 m elevation.

Of the 449 native tree species recorded in Adams flora (in the three eastern parishes), 19 percent (85 species) are threatened according to the IUCN (2009). The lowland forests have a higher percentage threat than the montane forests; 53 species (21%) of lowland species are threatened (92% are endemic), while 22 species (14%) of montane species are threatened (68% endemic). Overall, 71 percent of threatened tree species in the Blue Mountains grow only in the lowlands. The altitudinal range of ten threatened species is unknown.

TREE SPECIES COMPOSITION AND STRUCTURE FROM PLOT DATA.—In the 25 lowland plots, 216 trees (dbh ≥ 24 cm) of 58 different species

TABLE 1. *The distribution of forest fragments according to elevation in the Blue Mountains in 2008.*

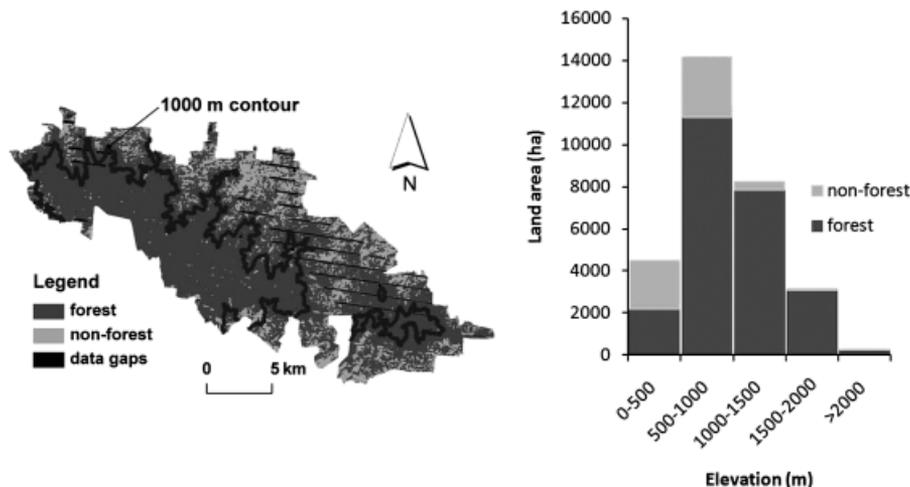| Elevation (m)	Number of fragments ≥ 0.36 ha	Total area (ha)
0–500	59	2177
500–1000	120	11,308
1000–1500	11	7859
1500–2000	1	3100
> 2000	1	246

FIGURE 1. Land area in the Blue Mountains under forest and nonforest cover (based on an image composite of two classified 2008 Landsat ETM+ images) inside the Blue and John Crow Mountains National Park (BJCMNP) according to elevation.

belonging to 31 families were enumerated, including five that were unidentified (Table 2). The species accumulation curve showed that species richness was still increasing after 1 ha was sampled, indicating high beta diversity (Fig. 2). Both individual-based and plot-based species accumulation curves showed a similar pattern, which suggests that species were distributed randomly over plots, rather than being clustered. Tree species in our plots demonstrated a continuous variation in their elevation range; the mean range was 913 m (range 156–1069 m; 49 species; Table 3).

Many of the plots were located in degraded forests with signs of logging and agriculture nearby. In some areas, few or no large trees (dbh ≥ 24 cm) were observed. The mean canopy cover was 84 percent, and the tree canopy cover of all plots was > 60 percent, which is in agreement with internationally accepted definitions of 'forest'.

Our plots had nine species that are endemic to Jamaica (18% endemic) and 49 native species (84% native) plus nine introduced species. The mean tree height was 19 m, the mean dbh was 35.6 cm,

and the total basal area was 25.7 m^2/ha. The three most common species were *Clethra occidentalis*, *Matayba apetala*, and *Calophyllum calaba*. The largest families were Lauraceae (with eight species) and Moraceae (with six species) (Table 3). The commonest introduced species were *P. caribaea*, *Mangifera indica*, and *Syzygium jambos*. *Pinus caribaea* was by far the most frequently occurring introduced species in the lowlands, as it was planted in pure stands over hundreds of hectares in the 1970s by the Forest Industries Development Company.

Twenty-seven percent of the trees recorded in Asprey and Robbins (1953) as belonging to the 'lower shale hills' and 'lower

TABLE 2. *Potential tree flora of the Blue Mountains in lowland and montane areas based on an analysis of the species distribution in Adams (1972) flora of Jamaica for the three eastern parishes. The altitudinal range for an additional 38 species which includes 33 native species, 17 endemics, and five introduced species is unknown. Data for twenty-five 0.04 ha plots (dbh ≥ 24 cm) in the lowland forest (< 1000 m) are also shown. 'Lowland' species are those which grow only below 1000 m asl; 'Montane' species have an altitudinal range over 1000 m asl.*

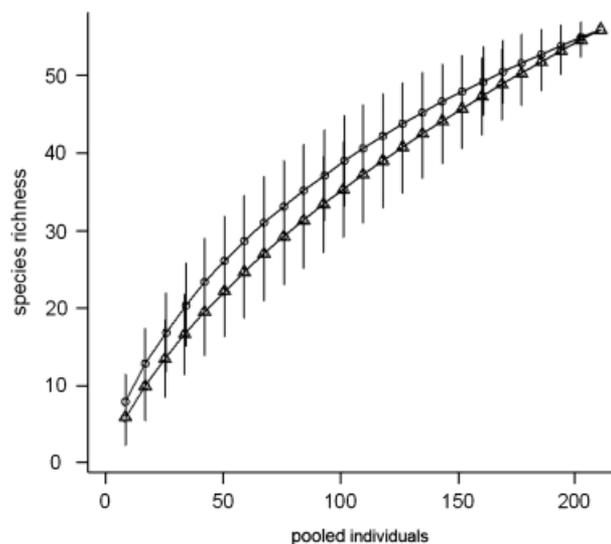| Number of | Potential tree flora | | Total | Plot data |
	Lowland	Montane		
Native species	256	160	416	49
Endemic species	77 (30%)	71 (44%)	148	9
Introduced species	40 (14%)	16 (9%)	56	9
Native families	56	53	–	31

FIGURE 2. Plot-based (triangle) and individual-based (circle) species accumulation curves for twenty-five 0.04 ha lowland plots. Points plotted are mean pooled species richness for all plots/individuals based on 100 random subsamples of the data, error bars are ± 2 SD. The horizontal axis is scaled by the mean number of accumulated individuals.

TABLE 3. *Tree species composition and elevation ranges of trees in 25 lowland (< 1000 m) forest plots (dbh ≥ 24 cm) in the Blue Mountains. Relative density was calculated as a percentage of the density of each species divided by the total number of individuals. Relative basal area was calculated as a percentage of the basal area of each species divided by the total basal area of all species. Importance values were calculated by averaging relative density and relative basal area for each species. Species with an importance value of < 1 percent were omitted. *indicates endemic species.*

Species	Elevation range (m)	Density (no./ha)	Relative density (%)	Basal area (m²/ha)	Relative basal area (%)	Importance value (%)
Clethra occidentalis	122–1615	45	21	4.2	16	18
Matayba apetala	213–1311	18	8	2.1	8	8
Calophyllum calaba	0–762	16	7	1.6	6	7
Nectandra patens	—	9	4	1.5	6	5
Hibiscus elatus	0–1219	9	4	1.3	5	5
Nectandra sp.	0–914	10	5	1.1	4	4
Dendropanax arboreus	76–1829	9	4	1.2	4	4
Ocotea leucoxylon	244–1219	6	3	1.2	4	4
Sapium jamaicense	37–671	6	3	0.6	2	3
Ficus maxima	15–1067	2	1	1.0	4	2
Cecropia peltata	15–884	6	3	0.5	2	2
Ficus aurea	0–975	2	1	0.8	3	2
Cyrilla racemiflora	457–1890	2	1	0.8	3	2
Plumeria sp.	0–914	4	2	0.5	2	2
Eugenia sp.	—	5	2	0.3	1	2
Mangifera indica	0–1372	4	2	0.3	1	2
Nectandra coriacea	0–914	2	1	0.5	2	1
Garcinia decussata*	457–1189	3	1	0.3	1	1
Coccoloba longifolia*	0–914	3	1	0.3	1	1
Prunus occidentalis	518–1067	2	1	0.4	2	1
Cordia macrophylla*	152–701	3	1	0.3	1	1
Cleyera theaeoides	701–2225	3	1	0.3	1	1
Alchornea latifolia	76–1707	2	1	0.4	1	1
Pinus caribaea	—	2	1	0.3	1	1
Guarea glabra Vahl	152–1707	3	1	0.2	1	1
Nectandra antilliana	15–853	3	1	0.2	1	1
Miconia tetrandra	457–1311	1	0.5	0.4	2	1
Tabernaemontana rendlei*	—	1	0.5	0.4	2	1

montane rain forest' of the Blue Mountains were also found in our plots. Our most similar plots—those in the Cunha Cunha Pass area—shared 42 percent (Sørensen's index) of species with those recorded in Asprey and Robins' Cunha Cunha Pass plots. The low overlap in tree species composition implies high beta diversity. The commonest large trees recorded from Muchoney *et al.* (1994) in a comparable altitudinal range were similar to those recorded in our plots: *M. apetala*, *C. calaba*, and *C. occidentalis*, but also included *Pouteria multiflora* which was only found once in our plots. This species, however, inhabits mostly limestone substrates and was probably common in the John Crow Mountains; Muchoney *et al.* (1994) measured plots in the John Crow Mountains as well as in the Blue Mountains. The canopy heights of 25 m recorded in Asprey and Robbins (1953) and of 18–27 m recorded in Muchoney *et al.* (1994) were similar to the mean tree height of 19 m in our plots. A maximum dbh of 97 cm was recorded by Muchoney *et al.* (1994), and our maximum recorded dbh was 95 cm.

Environmentally, our lowland plots had surface soil pH values ranging from 5.1 to 8.9 (Table S1). These were higher than the pHs (3.0–4.3) in montane plots in the Blue Mountains (Tanner 1977). The geology of plots was quite variable and ranged from granodiorite–diorite (generally deeply weathered and altered), limestone, volcanoclastic sediments (coarse, gritty sandstone), siltstone and mudstone (medium to fine grained), and andesite. Slopes were generally steeper in our plots (mean slope 41°) than in montane plots recorded by Tanner (1977) (30°). Soils were generally > 50 cm deep, with only three plots having soil 13–15 cm deep.

TREE SPECIES DISTRIBUTION AND ENVIRONMENT.—Axis 1 of the ordination separated plots located mostly on the northern side of the Blue Mountains as well as those in the Cunha Cunha Pass area from those on the southern side (Fig. 3). The ANOSIM test showed that the plots with high rainfall in the northern and Cunha Cunha Pass areas were more similar than either of these groups of plots was to
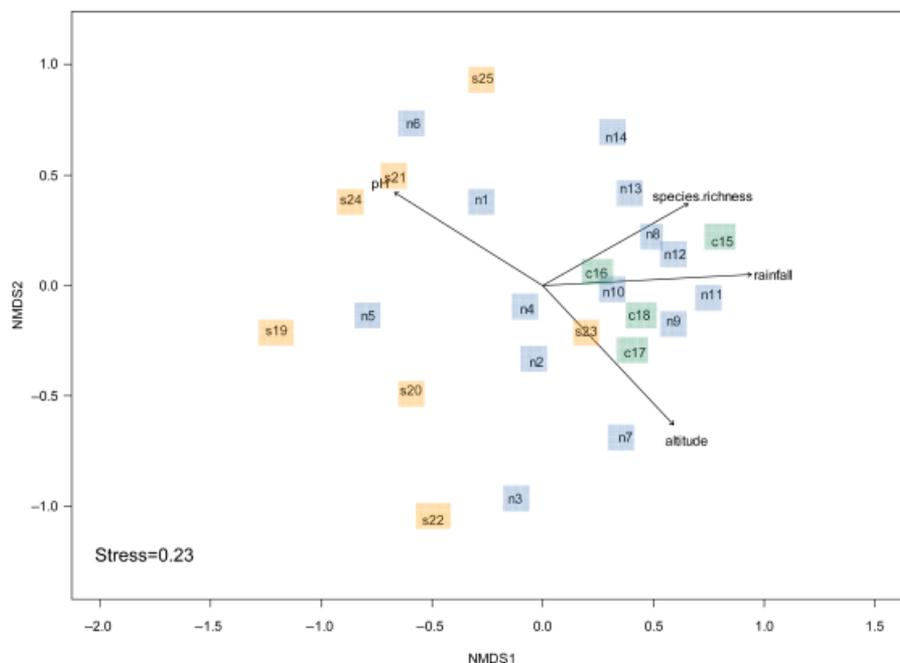
FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordination of twenty-five 0.04 ha lowland plots. Plot location (n, northern; s, southern; c, Cunha Cunha Pass) and plot number (1–25) are given for each plot.

plots in the drier south ($r = 0.36$, $P < 0.05$). Axes 1 and 2 explained 55.3 percent of the variance in species composition, and the stress or badness of fit of ordination distances with their empirical dissimilarity indices was 0.23. The Cunha Cunha Pass area is located at the eastern end of the Blue Mountains between the northern and the southern plots (Fig. S1); it receives high rainfall similar to the northern side of the Blue Mountains because it is a wind corridor. Rainfall data at the parish level indicate that the northern side of the Blue Mountains receives about one-third (1000 mm/yr) more rainfall per year than the southern side. Axis 1 of the NMDS was positively correlated (Kendall's τ) with rainfall ($r = 0.41$, $P < 0.01$) and species richness ($r = 0.26$, $P < 0.1$), and was negatively correlated with pH ($r = -0.32$, $P < 0.05$). Axis 2 was negatively correlated with altitude ($r = -0.25$, $P < 0.1$).

The tree species composition is different in the northern and the southern areas probably due to one or a combination of the following factors: the steep rainfall gradient, the physiological barrier posed by the 'high' ridge on this tropical mountain (Janzen 1967), and the difference in the mean plot altitude (663 and 347 m in the northern and southern plots, respectively). Plots on the northern side are similar to those on the Cunha Cunha Pass area, as both areas receive high rainfall, the mountains are not a barrier to dispersal, and the mean plot altitudes are similar (663 and 659 m in the northern and Cunha Cunha Pass plots, respectively).

DISCUSSION

In an analysis of 50-km-wide buffer zones outside of 198 PAs (IUCN categories I and II), DeFries *et al.* (2005) concluded that there was an 'increasing isolation of PAs in tropical forests', due to

deforestation outside PAs, which effectively turns PAs into islands in a sea of deforested land. Especially in Southeast Asian and Caribbean PAs that contain mountains, we believe that this isolation due to deforestation does not end at the PA boundary, but it extends all the way up to high-altitude areas where protection is *de facto*, and forests remain due to a rugged inaccessible terrain. This phenomenon causes further isolation of intact forest, and further decreases the capacity of PAs to conserve species, especially along an elevation gradient. In cases like Jamaica, where the relict lowland forest fragments show high beta diversity, it becomes increasingly important to conserve each fragment, which is different from the rest in its tree species composition and which houses a large number of endemic species.

DIFFERENTIAL FOREST CLEARANCE BETWEEN HIGH- AND LOW-ALTITUDE AREAS IN NATIONAL PARKS.—National Parks in Southeast Asia and the Caribbean have shown a higher deforestation rate at lower altitudes. In several PAs of Kalimantan, upland areas were reported as having 'much less deforestation' due to lower accessibility than lowlands areas, and montane forest (> 500 m elevation) were excluded from the analysis presumably because they did not undergo significant deforestation (Fuller *et al.* 2004). In the Gunung Palung National Park in Kalimantan, lowland forest loss amounted to 56 percent of lowlands (< 500 m elevation), with seemingly little deforestation in montane areas (although this was not assessed) (Curran *et al.* 2004). In the Bukit Barisan Selatan National Park in southwest Sumatra, Gaveau *et al.* (2007) found that 84 percent of the total forest area lost was in lowland and hill forest (< 1000 m elevation). The deforestation rate was 1.7 percent/yr in lowlands (0–500 m) compared with 0.2 percent/yr in upper montane forest

(1500–2200 m). In the Celaque National Park in Honduras, forest loss was 93 percent greater in the 1000–1800 m altitudinal range, than it was above 1800 m (Southworth *et al.* 2004): 13 km^2 of forest was lost between 1000 and 1800 m, but < 1 km^2 was lost above 1800 m. In Mexico, lowland forest (< 1000 m) in conventional PAs stands a 21 percent probability of being cut down, while montane forest (> 1000 m) has only a 3 percent probability of being cut (Deininger & Minten 2002).

COMPARISON OF BLUE MOUNTAIN FORESTS WITH OTHER FORESTS IN THE CARIBBEAN.—Like Jamaica, Puerto Rican lowland moist forests are described by Gould *et al.* (2006) as being located in a matrix of urban, agricultural, and forest cover, yet surprisingly they have maintained a 90 percent native species composition, similar to our 84 percent native species composition for the Blue Mountain lowland plots. Our pH values were higher than the pH values recorded in lowland moist forest plots in Puerto Rico (4.4 and 4.8 in the two forest types described, Gould *et al.* 2006). The mean slope angles in Puerto Rican forests (10° and 30° in the two forest types described by Gould *et al.* 2006) were also generally lower than those in our lowland plots. In the Dominican Republic, lowland moist forests of Los Haitises, a center of floristic richness and endemism (Brothers 1997), had 20 percent endemism according to the published flora vs. 30 percent endemism in the Blue Mountains according to the Jamaican flora. The continuous variation in tree elevation ranges observed in our tree species was also observed in the tree species growing below a 2200 m pine-cloud forest ecotone in the Dominican Republic (Martin *et al.* 2007). In the Dominican Republic, the mean range of 38 species in a montane forest in the Cordillera Central spanned *ca* 724 m (1284–2008 m) elevation, similar to our mean elevation range of 913 m.

Like the Blue Mountains, Cuba's lowland seasonal rain forests, which were once the most extensive areas on the island, have been reduced to 'semicultivated fragments' due to their high suitability for agriculture (Borhidi 1991). About 16.5 percent of flowering plants (not just trees) of Cuba are endangered (Borhidi 1991), which is similar to the 19 percent of threatened flowering plants of the Blue Mountains (IUCN 2009). Along an elevation gradient in Cuba, the number of endemic flowering plant species increased with altitude up to about 1600 m, after which the number of endemics decreased due to a gradual decrease in lowland endemics and due to no further increase in montane endemics (Borhidi 1991). In the Blue Mountains, the number of endemic trees rises up to about 750 m, after which it falls abruptly due to the absence of lowland endemics, and then there is another peak at about 1750 m, caused by an increase in montane endemics (Fig. S2). This shows that forests between 500 and 750 m in Jamaica are a more important habitat for endemic tree species than the corresponding lowland areas in Cuba (for endemic flowering plant species).

SPECIES DISSIMILARITY AND ITS RELATION TO THE ENVIRONMENT.— Beta diversity of forest trees in the neotropics is influenced by an interplay of environmental factors and geographic distance (Potts *et al.* 2002). Certain habitat conditions favor the growth of a particular guild of species, while geographic distance influences dispersal. Like the Blue Mountains, Panama's high species dissimilarity is thought to be partly due to habitat variation, especially rainfall (Pyke *et al.* 2001). It does, however, appear in our study that environmental factors may play a more important role in driving beta diversity than geographic distance, as plots on the northern side of the Blue Mountains are more similar to the distant Cunha Cunha Pass plots in the east, which receive high rainfall, than to the closer drier plots on the southern side of the mountain. This greater influence of environment, rather than geographic distance, on beta diversity in tree species was also found in a study of lowland plots ranging from 30 to 880 m elevation in northwest Borneo (Potts *et al.* 2002).

THE PROTECTED AREA HOTSPOT ZONE.—The Caribbean is the third most important biodiversity hotspot for the conservation of global biodiversity (Myers *et al.* 2000). The region has about 7000 endemic plant species (Mittermeier *et al.* 1998). According to the FAO (2006), of all regions assessed worldwide, the Caribbean has the highest percentage of threatened tree species (18%, as a percentage of the number of native tree species in individual countries). In our case, notwithstanding over 200 yr of deforestation and forest degradation in the BJCMNP, the lowlands are still relevant for conservation because of their high endemism and variation in tree species composition. To further focus conservation efforts in the right place, and place a 'premium on priorities', it is necessary to focus within PAs to find the zones that are priorities for conservation action. The higher deforestation rate and higher incidence of threatened species in the lowland compared with the montane areas in PAs can be applied to the zonation system for national parks and strict nature reserves. Here, we propose the term 'protected area hotspot zone' for lowland areas between the PA boundary and the core high-altitude forest. High-altitude forests begin from about 500 to 1500 m according to specific site conditions and the size of the mountain mass—the Massenerhebung effect (Grubb 1974). Within the PA hotspot zone, PA management effectiveness can be judged more accurately as this zone is not protected *de facto*, unlike the montane areas. The measurement of PA effectiveness within this zone will allow legal protection to be truly assessed, and prevent PAs from gaining credibility due to large remaining inaccessible, high-altitude areas. Management regimes in the PA hotspot zone should focus on enforcement of forest legislation (Gaveau *et al.* 2009) and forest rehabilitation activities. The institution of the zone may increase the success rate of many 'paper parks', especially in the Caribbean and Southeast Asia, where parks have not demonstrated their effectiveness in preventing deforestation.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

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

TABLE S1. *Environmental variables and NMS axes scores for Blue Mountain lowland plots.*

FIGURE S1. Blue Mountains study area within the wider Caribbean and the elevation distribution of land in the BJCMNP.

FIGURE S2. The number of endemic tree species along an elevation gradient in the Blue Mountains and the number of endemic flowering plant species along an elevation gradient in Cuba.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

ADAMS, C. D. 1972. Flowering plants of Jamaica. University of the West Indies, Mona, Jamaica.

ASPREY, G. F., AND R. G. ROBBINS. 1953. The vegetation of Jamaica. Ecol. Monogr. 23: 359–412.

BELLINGHAM, P. J., E. V. J. TANNER, AND J. R. HEALEY. 2005. Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. J. Veg. Sci. 16: 675–684.

BORHIDI, A. 1991. Phytogeography and vegetation ecology of Cuba. Akademiai Kiado, Budapest, Hungary.

BROOKS, T., R. MITTERMEIER, C. MITTERMEIER, G. FONSECA, J. PILGRIM, S. OLDFIELD, G. MAGIN, AND C. HILTON-TAYLOR. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv. Biol. 16: 909–923.

BROOKS, T., S. PIMM, V. KAPOS, AND C. RAVILIOUS. 1999. Threat from deforestation to montane and lowland birds and mammals in insular south-east Asia. J. Anim. Ecol. 68: 1061–1078.

BROTHERS, T. S. 1997. Rapid destruction of a lowland tropical forest, Los Haitises, Dominican Republic. Ambio. 26: 551–552.

CHAI, S., E. TANNER, AND K. MCLAREN. 2009. High rates of forest clearance and fragmentation pre- and post-national park establishment: The case of a Jamaican montane rainforest. Biol. Conserv. 142: 2484–2492.

CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18: 117–143.

CURRAN, L. M., S. N. TRIGG, A. K. MCDONALD, D. ASTIANI, Y. M. HARDIONO, P. SIREGAR, I. CANIAGO, AND E. KASISCHKE. 2004. Lowland forest loss in protected areas of Indonesian Borneo. Science 303: 1000–1003.

DAVIS, S. D., V. H. HEYWOOD, O. HERRERA-MACBRYDE, J. VILLA-LOBOS, AND A. C. HAMILTON (Eds.). 1997. Centres of plant diversity: A guide and strategy for their conservation, pp. 376–380, Vol. 3. The Americas. IUCN Publications Unit, Gland, Switzerland.

DEFRIES, R., A. HANSEN, A. NEWTON, AND M. HANSEN. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. Ecol. Appl. 15: 19–26.

DEININGER, K., AND B. MINTEN. 2002. Determinants of deforestation and the economics of protection: An application to Mexico. Am. J. Agric. Econ. 84: 943–960.

DELLE, JAMES A. 1998. An archaeology of social space: Analyzing coffee plantations in Jamaica's Blue Mountains. Plenum Press, New York, New York.

EYRE, L. A. 1987. Jamaica: Test case for tropical deforestation? Ambio 16: 338–343.

FAO. 2006. Global forest resources assessment. Food and Agriculture Organisation, Rome, Italy.

FULLER, D. O., T. C. JESSUP, AND A. SALIM. 2004. Loss of forest cover in Kalimantan, Indonesia, since the 1997–1998 El Nino. Conserv. Biol. 18: 249–254.

GAVEAU, D., H. WANDONO, AND F. SETIABUDI. 2007. Three decades of deforestation in southwest Sumatra: Have protected areas halted forest loss and logging, and promoted re-growth? Biol. Conserv. 134: 495–504.

GAVEAU, D., L. LINKIE, SUYADI, P. LEVANG, AND N. LEADER-WILLIAMS. 2009. Three decades of deforestation in southwest Sumatra: Effects of coffee prices, law enforcement and rural poverty. Biol. Conserv. 142: 597–605.

GENTRY, A. 1992. Tropical forest biodiversity: Distributional patterns and their conservational significance. Oikos 63: 19–28.

GOULD, W. A., G. GONZALEZ, AND G. CARRERO RIVERA. 2006. Structure and composition of vegetation along an elevational gradient in Puerto Rico. J. Veg. Sci. 17: 563–574.

GREEN, G., AND R. W. SUSSMAN. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. Science 248: 212–215.

GRUBB, P. J. 1974. Factors controlling the distribution of forest-types on tropical mountains: New facts and a new perspective. *In* J. R. Flenley (Ed.). Altitudinal zonation in Malesia. Transactions of the 3rd Aberdeen-Hull Symposium on Malaysian Ecology, Miscellaneous Series 16, pp. 13–46. University of Hall, Department of Geography, Hull.

GRUBB, P. J., AND E. V. J. TANNER. 1976. The montane forests and soils of Jamaica: A reassessment. J. Arnold Arbor. 57: 313–368.

HALL, J., N. BURGESS, J. LOVLETT, B. MBILINYI, AND R. GEREAU. 2009. Conservation implications of deforestation across an elevational gradient in the Eastern Arc Mountains, Tanzania. Biol. Conserv. 142: 2510–2521.

IUCN. 2009. IUCN Red List of Threatened Species, version 2009.1. Available at http://iucnredlist.org (accessed 20 October 2009).

JAMAICA RAINFALL FOR THE YEAR. 1942, 1945. Duke Street Kingston. Available at http://docs.lib.noaa.gov/rescue/cd323_pdf/LSN2349.PDF (accessed 5 November 2009).

JANZEN, D. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101: 233–349.

JOPPA, L. N., AND A. PFAFF. 2009. High and far: Biases in the location of protected areas. PLoS ONE 4: e8273.

KELLY, D. 1988. The threatened flowering plants of Jamaica. Biol. Conserv. 46: 201–216.

KINNAIRD, M., E. SANDERSON, T. O'BRIEN, H. WIBISONO, T. HARIYO, AND G. WOOLMER. 2003. Deforestation trends in a tropical landscape and implications for endangered large mammals. Conserv. Biol. 17: 245–257.

LE QUÉRÉ, C., M. R. RAUPACH, J. G. CANADELL, G. MARLAND, L. BOPP, P. CIAIS, T. J. CONWAY, S. C. DONEY, R. FEELY, P. FOSTER, P. FRIEDLINGSTEIN, K. R. GURNEY, R. A. HOUGHTON, J. I. HOUSE, C. HUNTINGFORD, P. LEVY, M. R. LOMAS, J. MAJKUT, N. METZL, J. P. OMETTO, GLEN PETERS, I. C. PRENTICE, J. T. RANDERSON, C. ROEDENBECK, S. W. RUNNING, J. L. SARMIENTO, U. SCHUSTER, S. SITCH, T. TAKAHASHI, N. VIOVY, G. R. VAN DER WERF, AND F. I. WOODWARD. 2009. Trends in the sources and sinks of carbon dioxide. Nat. Geosci. 2: 831–836.

MARTIN, P., R. SHERMAN, AND T. FAHEY. 2007. Tropical montane forest ecotones: Climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. J. Biogeogr. 34: 1792–1806.

METEOROLOGICAL SERVICE OF JAMAICA. 2009. Available at http://www.metservice.gov.jm (accessed 5 July 2009).

MITTERMEIER, R., N. MYERS, J. THOMSEN, G. FONSECA, AND S. OLIVIERI. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conser. Biol. 12: 516–520.

MUCHONEY, D. M., S. IREMONGER, AND R. WRIGHT. 1994. Rapid ecological assessment: Blue and John Crow Mountains National Park, Jamaica. The Nature Conservancy, Arlington, Virginia.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

OKSANEN, J., R. KINDT, AND R. B. O'HARA. 2005. Vegan: Community ecology package, version 1.6-9. Available at http://cc.oulu.fi/~jarioksa/ (accessed 20 June 2009).

POTTS, M. D., P. S. ASHTON, L. S. KAUFMAN, AND J. B. PLOTKIN. 2002. Habitat patterns in tropical rain forests: A comparison of 105 plots in northwest Borneo. Ecology 83: 2782–2797.

PROCTOR, G. 1982. More additions to the flora of Jamaica. J. Arnold Arbor. 63: 199–315.

PYKE, C. R., R. CONDIT, S. AGUILAR, AND S. LAO. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. J. Veg. Sci. 12: 553–566.

RICHARDS, P. W. 1952. The tropical rainforest: An ecological study. Cambridge University Press, Cambridge, UK.

SHREVE, F. 1914. A montane rain-forest: A contribution to the physiological plant geography of Jamaica. Carnegie Institution of Washington, Washington, DC.

SOUTHWORTH, J., H. NAGENDRA, L. A. CARLSON, AND C. TUCKER. 2004. Assessing the impact of Celaque National Park on forest fragmentation in western Honduras. App. Geogr. 24: 303–322.

TANNER, E. V. J. 1977. Four montane rain forests of Jamaica: A quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. J. Ecol. 65: 883–918.

TANNER, E. V. J. 1986. Forests of the Blue Mountains and the Port Royal Mountains of Jamaica. In P. K. Bretting, D. A. Thompson, and M. Humphries (Eds.). Forests of Jamaica, pp. 15–30. The Jamaican Society of Scientists and Technologists, Kingston, Jamaica.

TURNER, I. M., AND R. CORLETT. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol. Evol. 11: 330–333.