

Landscape assessment of tree communities in the northern karst region of Puerto Rico

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Abstract The northern karst of Puerto Rico is a unique formation that contains one of the island's largest remaining forested tracts. The region is under ever-increasing human pressure, but large portions of it are being considered for conservation. Forest classification of the region is at a coarse scale, such that it is considered one vegetation type. We asked whether there were distinct tree assemblages which would necessitate targeted

conservation strategies to ensure their protection. We examined tree species and communities across the region at three different major topographic positions along *mogotes*, or haystack-shaped hills. We found distinct tree communities on hilltops and valleys, with significantly more non-native species in valleys and significantly more endemic species on hilltops and hillsides. At a landscape level, we identified at least four different communities within each topographic position. Two *mogote* top communities were separated geographically (west and south) within the region, while two others co-occurred in the east-central part of the region. *Mogote* side and valley communities were less distinct geographically. Temperature, elevation, and precipitation were important variables in separating some communities, suggesting that abiotic stress may play an important role in the distribution of some species. In contrast, the lack of geographic separations of other communities suggested that variables such as soil conditions, land use and biotic interactions such as dispersal limitation may also be important. Conservation planning strategies should target the south, west, and east-central areas that harbor distinct *mogote* top plant communities to ensure protection of the widest range of tree species and communities in the karst region.

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Introduction

Understanding patterns and processes of biological diversity in space is a fundamental problem in ecology and conservation (Rosenzweig 1995; Barnosky et al. 2001; Moritz 2002). Biophysical variables, such as climate, have long been recognized for large scale correlations with species distributions and patterns of diversity (Cracraft 1985; Wiens 1989; Whittaker et al. 2001) but local scale variation in moisture, soils, and exposure also influence the distribution of species and communities (Gentry 1992; Clark et al. 1998).

An important component of biological diversity, particularly for conservation applications, is distinctiveness of sites (Dinerstein et al. 1995; Sarkar and Margules 2002). Conservation planning critically depends on information about the spatial distribution of biodiversity, but especially in tropical areas, this information is often lacking (Groves et al. 2000; Ferrier 2002). One of the greatest challenges faced by conservation biologists, then, is to obtain detailed information on the geographic distribution of species and communities and their relationship to human activities.

Puerto Rico is part of the Caribbean hotspot of biodiversity, one of the top five conservation hot spots based on numbers of endemic species and habitat loss (Meyers et al. 2000). Like most islands in the Caribbean, Puerto Rico has been heavily deforested and subject to the introduction of many non-native species (Franco et al. 1997; Lugo and Brown 1999; Rivera et al. 2000). Forest cover increased from an estimated 6%, by the late 1940s, to about 42% by 1991 as the society transitioned from an agricultural to industrial-based economy (Birdsey and Weaver 1987; Helmer et al. 2002; Grau et al. 2003). Thus, most Puerto Rican forests are secondary forests in various stages of regeneration. Past land use can influence plant species diversity and composition for decades following abandonment (Foster et al. 1999; Aide et al. 2000; Rivera et al. 2000; Marcano-Vega et al. 2002) and in many areas, the forest is dominated by non-native species (Franco et al. 1997; China 2002; Lugo and Helmer 2004).

One of the largest forested areas in Puerto Rico occurs on its limestone belt (Lugo et al. 2001). This area is distinguished by karst topography including haystack-shaped hills (hereafter *mogotes*), sinkholes, caves, and underground rivers (Monroe 1976). Prior to abandonment, the sinkholes and valleys in the region were heavily disturbed for agriculture and homesteads, while the *mogote* sides and tops were deforested or selectively logged (Rivera et al. 2000). This region probably holds the greatest plant diversity on the island, with approximately 23% of Puerto Rico's endemic tree species found there (Lugo et al. 2001; Little et al. 1988). The numerous aquifers and underground rivers are also an important component of the island's water supply. However, the northern karst is under increasing pressure from human development and is the object of recent local conservation efforts by NGOs, State, and Federal agencies.

The northern karst of Puerto Rico has been classified as one or two land cover units or vegetation types (i.e., moist or wet limestone forest) in conservation planning (e.g., The Nature Conservancy, S. Keel unpubl.) and mapping (Helmer et al. 2002). In the absence of finer-scale information on plant communities, this coarse classification suggests an equivalency across the northern karst that may be unwarranted and could compromise conservation efforts if species and communities are actually confined to geographically distinct areas (Brooks et al. 2004).

Previous studies of karst vegetation, both in Puerto Rico (Dansereau 1966; China 1980; Trejo-Torres and Ackerman 2002) and in other parts of the Caribbean (Asprey and Robbins 1953; Proctor 1986; Brewer et al. 2003), have identified distinct communities along topographic gradients. Intensive studies in Puerto Rico have focused on describing one local forest within the karst (Alvarez-Ruiz et al. 1997; Acevedo-Rodriguez and Axelrod 1999). The few landscape level assessments of karst vegetation have used Forest Inventory Analysis data (China and Helmer 2003, Brandeis unpubl.). These methods involve systematic sampling, and because of the large amount of disturbance that took place in the karst, ecotones and very disturbed forest are over represented in the database.

In this study, we sampled vegetation only in closed canopy secondary forests. Sampling was conducted at a landscape level along a toposequence. This scheme increased the likelihood of sampling plant assemblages typifying native karst vegetation and of detecting unique assemblages among them. Specifically we asked: What are the tree and shrub communities in the karst and how are they distributed across the area? and how is plant species richness (particularly endemics and non-natives) distributed in the landscape? Finally, we discuss the conservation implications of our findings and provide a basis to frame a more targeted conservation strategy.

Methods

Sampling

Study site locations across the landscape were selected non-randomly to achieve a representation throughout the forested northern karst region. Once a general location was selected, sampling sites were randomly selected based on

the presence of forest vegetation with a closed canopy (i.e., newly regenerating pastures and actively cultivated orchards were not sampled) and accessibility. In each study site, we placed between two and four vegetation plots depending on accessibility. We placed plots along a topographic gradient from *mogote* top to side to valley (i.e., sinkholes). We stratified sampling and analysis by topographic position because previous studies identified different communities at different positions (Asprey and Robbins 1953; China 1980; Proctor 1986; Trejo-Torres and Ackerman 2002; Brewer et al. 2003). In some of the coastal sites where the karst topography is less distinct and only small remnants remain forested, samples were taken along a transect within forested ravines. We had a total of 65 study sites and 198 vegetation plots. Of these vegetation plots, 60 were tops, 73 sides, and 65 valleys (Table 1).

Vegetation plots were 425 m² circles, following the protocol of Martin et al. (1996), in which we identified and measured the diameter at breast height (dbh) of each stem of tree and shrub species with dbh ≥ 2.5 cm. For individuals with more

Table 1 Species richness and physical structure of each topographic position and clustering-derived tree communities for each topographic position

Community	N Plots	Endemic species per plot	Native species per plot	Non-native spp.	Individuals (#/ha)	Basal area (m ² /ha)
Tops	60	2.6 (0.2)	21.8 (0.6)	0.2 (0.1)	4834.9 (249.7)	21.2 (1.1)
A	11	2.0 (0.5)	21.5 (1.5)	0.9 (0.2)	4746.5 (571.4)	23.6 (2.1)
B	17	3.6 (0.3)	22.7 (1.3)	0	3443.6 (357.1)	16.1 (1.6)
C	12	2.0 (0.3)	20.5 (0.9)	0	6637.3 (431.8)	22.2 (2.1)
D	20	2.4 (0.4)	22 (1.2)	0.2 (0.2)	4984.7 (373.5)	23.6 (2.0)
Sides	73	2.4 (0.2)	23.9 (0.8)	0.7 (0.1)	3171.3 (174.8)	23.0 (0.9)
E	7	1.0 (0.4)	20.4 (1.2)	0.7 (0.2)	5079.0 (605.7)	29.2 (3.1)
F	17	2.1 (0.4)	23.4 (1.6)	0.7 (0.2)	3515.6 (298.2)	21.7 (1.5)
G	26	2.2 (0.3)	22.0 (1.2)	1.0 (0.2)	1924.9 (122.8)	24.1 (1.5)
H	23	3.3(0.3)	27.4 (1.3)	0.2 (0.1)	3745.3 (266.0)	21.0 (1.4)
Valleys	65	1.0 (0.1)	17.3 (0.7)	2.3 (0.2)	2120.2 (110.1)	29.2 (2.2)
J	10	1.5 (0.4)	23.6 (1.9)	1.9 (0.5)	2774.1 (240.2)	21.6 (2.6)
K	28	0.8 (0.2)	14.4 (0.9)	2.3 (0.2)	1605.0 (116.0)	27.3 (1.8)
L	13	1.3 (0.3)	17.7 (1.3)	1.9 (0.4)	2564.7 (262.5)	36.0 (8.2)
M	14	0.7 (0.2)	18.0 (1.2)	3.1 (0.3)	2270.6 (231.2)	32.3 (5.2)

A = *Lonchocarpus glaucifolius* tops (west), B = *Sideroxylon cubensis* tops (south), C = *Gymnanthes lucida* tops (east-central), D = *Bursera simaruba* tops (east-central), E = *Lonchocarpus glaucifolius* sides, F = *Coccoloba diversifolia* sides, G = *Dendropanax arboreus* sides, H = *Neolaugeria resinosa* sides, J = *Eugenia monticola*-*Casearia guianensis* valleys, K = *Guarea guidonia* valleys, L = *Casearia sylvestris* valleys, M = *Syzygium jambos* valleys

Cells contain means with standard errors in parentheses of all plots within each community type. Number of individuals and basal area are calculated per hectare, all other means are per plot. Native species per plot includes endemic species

than one stem, we measured each stem with dbh ≥ 2.5 cm. At each plot we also recorded topographic position (i.e., top, side, or valley), slope (degrees), aspect (percent), and an estimate of bare rock, debris, and herbaceous vegetation cover. Vegetation plots on *Mogote* sides were placed at all aspects (even distribution, mean 180°), and slopes ranged from 27% to 150% with a normal distribution with a mean of 75.7% (S.D. 24.1).

Analysis

For each plot we summarized the number of individuals of each species and used this in community analyses. We chose number of individuals rather than basal area, because we believe it was a better measure of processes of community assemblage, such as dispersal and establishment, whereas basal area was likely to reflect growth rates and order of establishment and thus was prone to outlier effects of very large trees. Recorded species were classified as native, endemic to Puerto Rico, or non-native (Liogier and Martorell 2000). We calculated Shannon's diversity index and species richness for different classes of plants (i.e., endemic species richness = total number of endemic species only).

We used classification, ordination, and indicator species (PC-ORD 4.0, McCune and Mefford 1999) to identify distinct communities; and regression, analysis of variance (JMP 5.0, SAS Institute 2002), and GIS mapping (Arcview 3.2, ESRI 1999) to identify correlates with environmental factors (i.e., topographic position, climate, elevation, location). Using ANOVA, we compared species diversity among topographic positions and clustering-derived plant community groups.

First, we performed non-metric multidimensional scaling (NMS) ordination, with Sørensen distances, on the entire dataset, then on each topographic position (*mogote* tops, *mogote* sides, valleys) separately. We used random starting configurations for 40 runs with real data and 50 runs with randomized data. The instability criterion for accepting a solution was 0.00001 or 400 iterations. Using a flexible beta linkage with Sørensen distances and $\beta = -0.25$ we classified communities within each topographic position

and for the entire dataset (Legendre and Legendre 1998; McCune and Grace 2002).

We identified indicator species for each group classified from the clustering procedure using the IndVal method (Dufrêne and Legendre 1997). The IndVal method combines a species' relative abundance and relative frequency of occurrence among groups to identify characteristic species of each group (those found mostly in a single group and occurring in most of the samples within that group), with indicator values ranging from 0 to 100 (perfect indication of a particular group) (Dufrêne and Legendre 1997; Legendre and Legendre 1998). The statistical significance of the maximum indicator value for each species was evaluated using a Monte Carlo randomization method with 5000 permutations and $\alpha = 0.05$, and we used a threshold of 25 for indicator values.

We calculated importance values for each species, in each cluster-derived group, as the average of relative density, relative basal area, and relative frequency (Curtis and McIntosh 1951). The sum of importance values of all species equals 100. We named each community by its maximum indicator species. When the maximum indicator species did not have one of the five highest importance values, we included in the name a second species with the highest frequency among the species with the top five importance values.

The distinction between indicator values and importance values is an important one. Indicator values allow a comparison of the frequency and abundance of species *among* two or more *a priori* groups of sample units (McCune and Grace 2002). They assess the fidelity of a species to a particular community type and the pervasiveness of the species within a group; we use them to identify indicator species for each of our cluster-derived community types. Importance values measure the relative dominance of species *within* a group of sample units, in terms of area occupied, frequency of occurrence, and abundance, and do not imply that a species is an indicator. For example, a particular species may have a high importance value in several community types, making it a poor indicator species, but a good descriptor of the community. We use importance values to describe forest structures of each com-

munity and to facilitate comparisons with other studies.

We used Daly et al. (2003) climate model for Puerto Rico to derive average precipitation and temperature of each sample point for use as predictor variables. Their model was based on elevation and weather data from 45 stations throughout the island (of which 25 were in the study area). Within the sampled region, elevation increased from north to south and was positively correlated with precipitation and negatively correlated with temperature.

Results

Species diversity and forest structure

We found a total of 242 species of shrubs and trees with dbh ≥ 2.5 cm. Of these species, 26 were endemic, 31 were non-native, and 43 species were found in only one sample plot. We found between 7 and 41 (mean = 22.2) species per vegetation plot. Ten species, including three endemics and one non-native species, were found only on *mogote* tops, occurring in 2–3 plots each. Thirty species, including five endemic and four non-native species, were found exclusively on sides, occurring in 1–4 plots each. Finally, 29 species, including 12 non-natives, were only found in valleys and occurred in 2–9 plots each.

Shannon's diversity index was highest on the *mogote* sides (Shannon's index $F_{2,195} = 4.8$, $P = 0.009$). Both endemic and native species richness were significantly greater on *mogote* sides and tops than valleys, whereas non-native species richness decreased along the topographic gradient from valleys to tops (Table 1). Within the *mogote* sides, species richness and Shannon's index were greater on north (315° – 45° , $N = 10$) and west (225 – 315° , $N = 11$) facing hills than south (135 – 225° , $N = 11$) or east (45 – 135° , $N = 14$) facing slopes (quadratic fits, species richness: $r^2 = 0.40$, $P < 0.0001$, $N = 46$; Shannon's index: $r^2 = 0.33$, $P = 0.0002$, $N = 46$), and endemic species richness increased with steepness of slopes ($r^2 = 0.19$, $P = 0.0019$, $N = 49$).

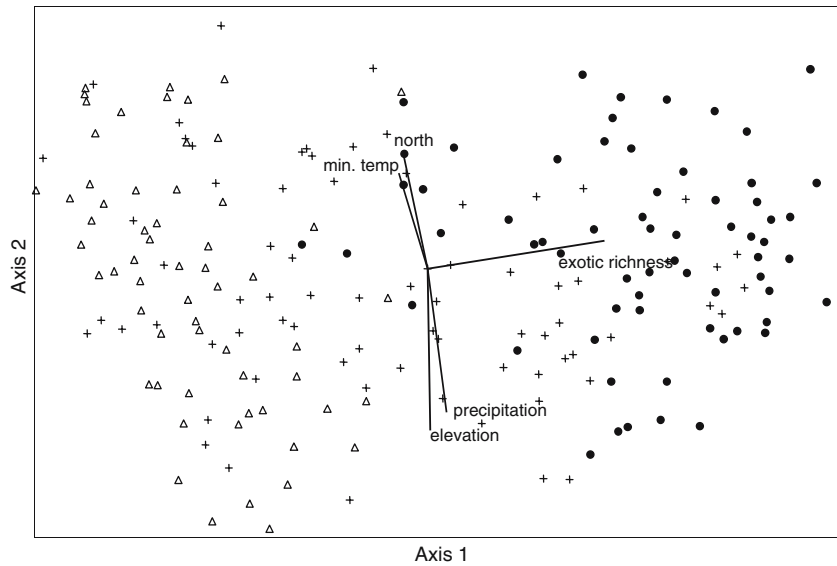
Numbers of tree or shrub individuals per hectare ranged from 682 to 9,812. We found a

large range in basal area from 2.0 m²/ha to 123.5 m²/ha (median 23.0 m²/ha). The upper end of the range was strongly affected by five large trees with a dbh greater than 100 cm. Each of these trees was found in a valley plot and they were from different species (*Spathodea campanulata* [192 cm dbh], *Ficus trigonata* [185 cm], *Ceiba pentandra* [130 cm], *Spondias mombin* [125 cm], *Cedrela odorata* [100 cm]). *Ardisia obovata* was the most frequently encountered tree, occurring in 58% of all of the plots. It was followed by *Thouinia striata* (54%), *Comocladia glabra* (52%), and *Guettarda scabra* (47%). The forest structure differed along the topographic gradient. The average total number of individuals per plot increased from valley to hilltop ($F_{2,198} = 52.6$, $P < 0.0001$), while the average basal area was significantly higher in valleys than hilltops or hillsides ($F_{2,198} = 8.1$, $P = 0.0004$, Table 1). However, this last result must be interpreted with caution because values were not normally distributed.

Tree communities

Ordination of the full data set showed a separation of *mogote* tops from valleys, with sides intermediate and overlapping both. The best NMS solution was a two-dimensional solution (stress = 19.53, instability = 0.00443). *Mogote* tops and valleys separated along ordination axis 1 which was most closely correlated with non-native species richness ($r^2 = 0.45$), suggesting that it represented a disturbance axis (Fig. 1). The second axis was correlated with elevation ($r^2 = 0.41$), climate (precipitation $r^2 = 0.39$, minimum temperature $r^2 = 0.24$) and latitude ($r^2 = 0.29$, Fig. 1). Indicator species analysis identified species representative of *mogote* top communities and valley communities. *Mogote* top indicators included *Clusia rosea* (IndVal = 60.7), *Sideroxylon salicifolia* (IndVal = 53.5), *Bursera simaruba* (IndVal = 52.5), and *Exothea paniculata* (IndVal = 52.4). Valley community indicators included *Casearia sylvestris* (IndVal = 63), *Guarea guidonia* (IndVal = 60.2), and *Spathodea campanulata* (IndVal = 44.7). *Mogote* side communities were less distinct with only three significant indicator species with an indicator value

Fig. 1 Non-metric multidimensional scaling ordination separated *mogote* tops (open triangles) from valleys (filled circles), with sides (plus signs) overlapping both. Overlaid are variables correlated with ordination axes with $r^2 \geq 0.25$, showing direction and relative strength (length of line) of correlation



greater than 25: *Thouinia striata* (IndVal = 37.5), *Comocladia glabra* (IndVal = 36.9), and *Ocotea coriacea* (IndVal = 27.9). Excluding the sides from the indicator species analysis did not qualitatively change the indicator species for tops and valleys. Indicator values generally increased slightly and in a few cases the order of indicator species was altered.

Because sampling was stratified by topography, we conducted cluster analysis and ordination separately for each of the three topographic positions. For all three topographic positions, we selected a two-dimensional NMS solution.

Mogote tops

The best two-dimensional NMS solution for the tops had a stress of 20.68 and instability of 0.00377. The first axis was correlated with maximum temperature ($r^2 = 0.38$), elevation ($r^2 = 0.25$), and precipitation ($r^2 = 0.22$). The second axis was most strongly correlated with latitude ($r^2 = 0.73$), as well as with minimum temperature ($r^2 = 0.61$), elevation ($r^2 = 0.52$), precipitation ($r^2 = 0.45$), and endemic species richness ($r^2 = 0.32$). Flexible beta clustering had a percent chaining of 1.22. The best clustering based on dendrogram examination and separation in ordination space was three and four groups. When the community types were plotted in physical space, the three *mogote* clusters

separated in the west, south, and east-central portions of the study area. When we plotted four *mogote* clusters, the east-central cluster separated into two groups, but they were not distinct in physical space (Fig. 2). Points in the southern cluster had, on average, the highest precipitation but were not significantly different from average precipitation of the western cluster (Tukey–Kramer means comparison test $\alpha < 0.05$). However, the western cluster had the narrowest (highest minimum and lowest maximum) and the southern cluster the greatest (lowest minimum) range in temperatures among the *mogote* tops (Tukey–Kramer means comparison test $\alpha < 0.05$).

The western group, hereafter the “*Lonchocarpus glaucifolius* top”, was characterized by seven significant indicator species with an indicator value greater than 25. The dominant indicator species for this group, was *L. glaucifolius* with an indicator value of 88.1. The next highest indicator value for this group was *Ocotea coriacea* (Table 2). *Lonchocarpus glaucifolius* also had a much higher importance value than any other species. This was the only *mogote* top community for which an exotic species, *Adenanthera pavonina* (IndVal = 36.4), was an indicator. In the southern group, “*Sideroxylon cubensis* top”, we found 13 indicator species. The species with the highest indicator value was *S. cubensis* (Table 2), followed by *Psidium amplexicaule*. The east-central groups divided into two groups, the

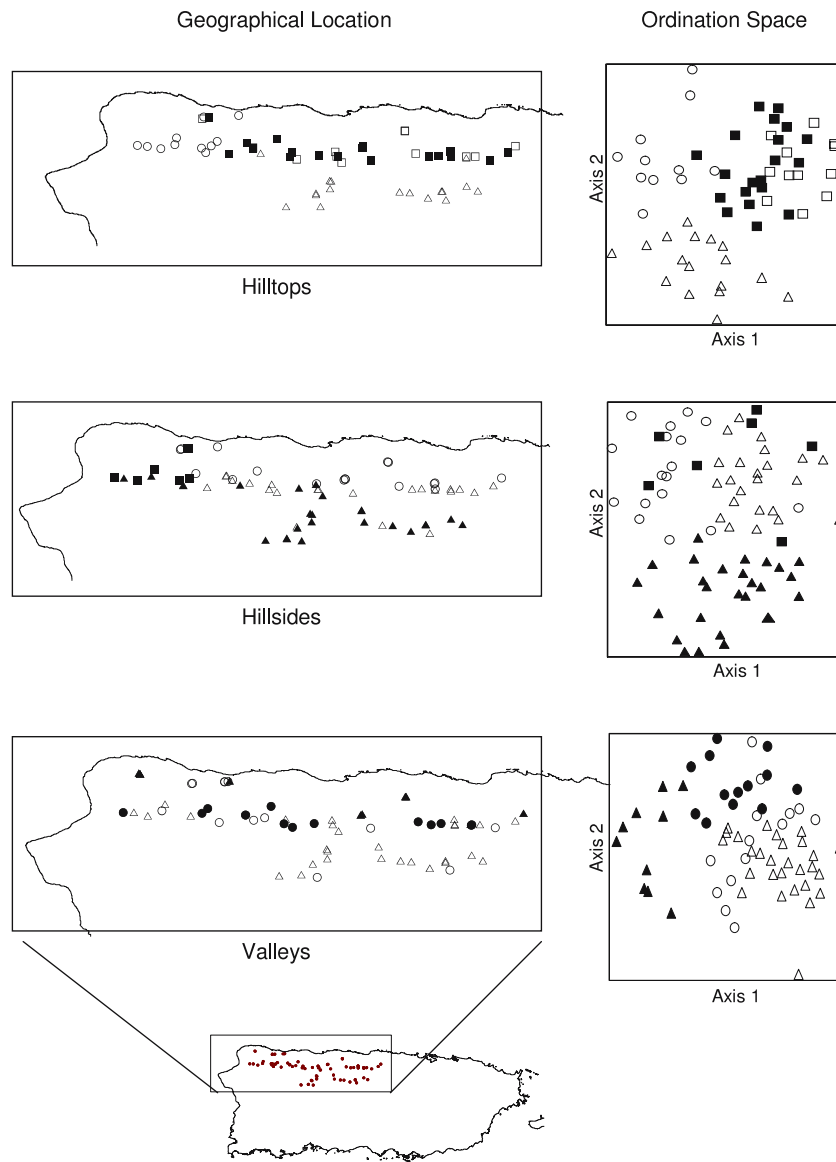


Fig. 2 Distribution of *mogote* top (top), side (middle), and valley (bottom) tree communities of the Puerto Rican northern karst zone in geographical (left) and non-metric multidimensional scaling ordination (right) space. Each topographic position is based on four groups derived from flexible beta clustering. For tops, open circles = *Lonchocarpus glaucifolius* tops, open triangles = *Sideroxylon cubensis* tops, filled squares = *Bursera simaruba* tops, open squares = *Gymnanthes lucida* tops. Maximum temperature was positively, and elevation and precipitation negatively correlated with axis 1, latitude and minimum temperature were positively and elevation, precipitation, and endemic species richness negatively correlated with axis 2 (see text for regression coefficients). For sides, open circles =

Coccoloba diversifolia sides, open triangles = *Neolaugeria resinosa* sides, filled triangles = *Dendropanax arboreus* sides, filled squares = *Lonchocarpus glaucifolius* sides. Elevation, precipitation, and endemic species were weakly positively correlated with axis 1, while latitude and minimum temperature were weakly positively, and non-native species richness and elevation weakly negatively correlated with axis 2. For valleys, filled circles = *Casearia sylvestris* valleys, open circles = *Syzygium jambos* valleys, filled triangles = *Eugenia monticola*-*Casearia guianensis* valleys, open triangles = *Guarea guidonia* valleys. Elevation and precipitation were positively, and native species richness, minimum temperature, latitude, and endemic species richness were negatively correlated with axis 1

Table 2 Indicator tree species of communities in the northern karst of Puerto Rico

Species	Indicator value	Importance value	Occurrence (# plots)
<i>Mogote tops</i>			
Community A: <i>Lonchocarpus glaucifolius</i> tops			
<i>Lonchocarpus glaucifolius</i>	88.1	15.6	10
<i>Ocotea coriacea</i>	47	2.1	7
<i>Guapira fragrans</i>	46.9	2.8	6
<i>Bourreria domingensis</i>	45.7	3.6	9
<i>Licaria salicifolia</i>	42.3	2.6	8
<i>Guettarda scabra</i>		5.6	9
<i>Bursera simaruba</i>		4.7	10
<i>Neolaugeria resinosa</i>		3.7	6
Community B: <i>Sideroxylon cubensis</i> tops			
<i>Sideroxylon cubensis</i>	79.9	7.5	14
<i>Psidium amplexicaule</i>	51.2	3.6	11
<i>Neolaugeria resinosa</i>	46	6.9	15
<i>Pimenta racemosa</i>	43.1	3.2	13
<i>Tabebuia haemantha</i>	41.4	4.4	15
<i>Myrsine guianensis</i>	33.4	5	6
<i>Clusia rosea</i>		6.5	14
<i>Ardisia obovata</i>		4.9	14
Community C: <i>Gymnanthes lucida</i> tops			
<i>Gymnanthes lucida</i>	94.4	21	12
<i>Coccoloba diversifolia</i>	50.6	18.5	12
<i>Krugiodendron ferreum</i>	33.1	2.6	8
<i>Xylosma buxifolium</i>	29.3	1.4	5
<i>Bursera simaruba</i>		6.7	12
<i>Sideroxylon salicifolia</i>		5.2	11
<i>Exothea paniculata</i>		3.8	10
Community D: <i>Bursera simaruba</i> tops			
<i>Bursera simaruba</i>	45.7	8.6	20
<i>Sideroxylon salicifolia</i>	41.2	6.4	19
<i>Gyminda latifolia</i>	40.4	2.6	13
<i>Coccoloba diversifolia</i>		16.3	19
<i>Eugenia monticola</i>		6	16
<i>Guettarda scabra</i>		5.7	16
<i>Mogote sides</i>			
Community E: <i>Lonchocarpus glaucifolius</i> sides			
<i>Lonchocarpus glaucifolius</i>	96.7	21.6	7
<i>Guettarda scabra</i>	45.3	8.5	5
<i>Bursera simaruba</i>	45.2	10.6	6
<i>Bourreria domingensis</i>	39.1	3.1	4
<i>Licaria salicifolia</i>	29.4	3.1	5
<i>Neolaugeria resinosa</i>		3.5	5
Community F: <i>Coccoloba diversifolia</i> sides			
<i>Coccoloba diversifolia</i>	65.9	13	16
<i>Krugiodendron ferreum</i>	59.8	4.2	13
<i>Casearia guianensis</i>	51.5	4	12
<i>Sideroxylon salicifolia</i>	43.6	6.4	10
<i>Picramnia pentandra</i>	30.6	1	6
<i>Bursera simaruba</i>		6.3	14
<i>Eugenia monticola</i>		4.7	11

Table 2 continued

Species	Indicator value	Importance value	Occurrence (# plots)
Community G: <i>Dendropanax arboreus</i> sides			
<i>Dendropanax arboreus</i>	72.3	5	23
<i>Guarea guidonia</i>	67.1	8.6	18
<i>Thouinia striata</i>	51.4	10.5	24
<i>Casearia sylvestris</i>	48.2	3.1	20
<i>Andira inermis</i>	44.9	2.8	22
<i>Zanthoxylum martinicense</i>		3.1	13
Community H: <i>Neolaugeria resinosa</i> sides			
<i>Neolaugeria resinosa</i>	70.3	9	22
<i>Ardisia obovata</i>	66.1	4.6	23
<i>Psidium amplexicaule</i>	55.3	2.3	13
<i>Tabebuia haemantha</i>	49.9	2.5	13
<i>Tabebuia heterophylla</i>	48	4.6	16
<i>Guettarda scabra</i>		6.5	23
<i>Bursera simaruba</i>		4.1	17
Valleys			
Community J: <i>Eugenia monticola</i> - <i>Casearia guianensis</i> valleys			
<i>Eugenia monticola</i>	76.6	3.1	8
<i>Coccoloba diversifolia</i>	71.1	2.3	8
<i>Ardisia obovata</i>	71	4.3	9
<i>Bourreria domingensis</i>	70	1.6	7
<i>Casearia decandra</i>	66.7	3.6	8
<i>Casearia guianensis</i>	65	7.5	9
* <i>Terminalia catappa</i>	27.3	4.2	3
<i>Calophyllum calaba</i>		3.3	4
Community K: <i>Guarea guidonia</i> valleys			
<i>Guarea guidonia</i>	48.6	17	28
<i>Urera baccifera</i>	33.7	2	12
<i>Inga vera</i>	30.8	3.8	14
<i>Guarea ramiflora</i>	25	0.9	7
* <i>Spathodea campanulata</i>		6.1	15
<i>Dendropanax arboreus</i>		4.4	22
<i>Casearia sylvestris</i>		4.2	21
<i>Quararibea turbinata</i>		4.1	16
Community L: <i>Casearia sylvestris</i> valleys			
<i>Casearia sylvestris</i>	53.5	7.6	13
<i>Inga fagifolia</i>	43.1	1.9	8
<i>Roystonea borinquena</i>	38.1	4.6	8
<i>Myrcia splendens</i>	30.4	2.1	5
* <i>Spathodea campanulata</i>		24.1	6
<i>Zanthoxylum martinicense</i>		5.4	9
<i>Ocotea floribunda</i>		3.6	10
Community M: <i>Syzygium jambos</i> valleys			
* <i>Syzygium jambos</i>	84.8	13.5	14
<i>Piper amalago</i>	30.4	1.3	7
<i>Casearia aculeata</i>	28.6	1.2	4
<i>Guarea guidonia</i>		11.6	12
<i>Ficus trigonata</i>		6.1	4
<i>Casearia sylvestris</i>		3.7	13
<i>Ocotea leucoxylon</i>		3.4	6

Both indicator values and importance values are shown for the five highest values. Numbers in bold stand for the top five values of each category. Occurrence is the number of plots of each community in which the species appear (see Table 1 for total plots of each community). Endemic tree species names are shown in bold while asterisks indicate non-native species

“*Gymnanthes lucida* top”, dominated by *G. lucida* (Table 2) with *Coccoloba diversifolia*, and another group, the “*Bursera simaruba* top”, with three nearly equivalent indicator species: *Bursera simaruba*, *Sideroxylon salicifolia* and *Gyminda latifolia*. The *G. lucida* tops were significantly less diverse than the *B. simaruba* tops based on Shannon’s diversity index, while the *S. cubensis* tops were most diverse and had significantly higher endemic species richness than the other groups ($F_{3,60} = 4.1$, $P = 0.01$). The *G. lucida* tops had significantly more individuals than any of the other *mogote* top groups and the southern *S. cubensis* tops had significantly fewer individuals than either of the eastern groups ($F_{3,60} = 9.1$, $P < 0.0001$, Table 1). The *S. cubensis* tops also had significantly lower basal area than did the *B. simaruba* tops ($F_{3,60} = 3.6$, $P = 0.02$).

Mogote sides

The best NMS solution for the sides had a stress of 19.74 and instability of 0.00048. Axis one was weakly correlated with elevation ($r^2 = 0.26$), precipitation ($r^2 = 0.14$), and endemic species richness ($r^2 = 0.13$), while axis 2 was weakly correlated with latitude ($r^2 = 0.22$), minimum temperature ($r^2 = 0.18$), non-native species richness ($r^2 = 0.18$), and elevation ($r^2 = 0.13$). Clustering had a percent chaining of 1.92 and, based on the cluster dendrogram and the ordination, we selected four divisions for further analysis.

Mogote side groups were less distinct in physical space than tops (Fig. 2). However one group, made up of seven samples, was found only in the west, the “*Lonchocarpus glaucifolius* side” group. The dominant indicator species for this group was *L. glaucifolius*, followed by *Guettarda scabra* and *Bursera simaruba* (Table 2). A second group, the “*Coccoloba diversifolia* side” group, was found only in the north and its indicator species included *C. diversifolia* and *Krugiodendron ferreum*, as well as *Casearia guianensis* and *Sideroxylon salicifolia* (Table 2). The other two groups, the “*Dendropanax arboreus* side” group and the “*Neolaugeria resinosa* side” group, were widespread. The *D. arboreus* side indicator species included *Dendropanax arboreus*, *Guarea guidonia*, *Thouinia striata*, and *Casearia sylvestris*

(Table 2). *Thouinia striata* had the greatest importance value. The *N. resinosa* side indicator species included *Neolaugeria resinosa*, *Ardisia obovata*, *Psidium amplexicaule*, *Tabebuia haemantha*, and *Tabebuia heterophylla*. The *L. glaucifolius* side group had significantly lower diversity (Shannon’s index) than the other *mogote* side groups (Tukey–Kramer means comparison test $\alpha < 0.05$). There was no difference in *mogote* side aspect or slope among the groups, with the exception of the *L. glaucifolius* sides which were found only on east to southeast facing slopes. *Lonchocarpus glaucifolius* sides had significantly more, and *D. arboreus* sides significantly fewer individuals ($F_{3,73} = 20.3$, $P < 0.0001$, Table 1) than the other groups, and *L. glaucifolius* sides had slightly higher basal area than *N. resinosa* sides ($F_{3,73} = 2.8$, $P = 0.048$, Table 1).

Valleys

The best two-dimensional NMS solution for the valleys had a stress of 23.41 and instability of 0.00049. Axis 1 was correlated with native species richness ($r^2 = 0.48$), elevation ($r^2 = 0.35$), minimum temperature ($r^2 = 0.30$), precipitation ($r^2 = 0.29$), latitude ($r^2 = 0.28$), and endemic species richness ($r^2 = 0.18$), but axis 2 was not correlated with any of the variables for which we had measurements. The flexible beta clustering had a percent chaining of 2.54.

The valley groups were not distinct in physical space (Fig. 2). All of the groups were widespread although two groups were not found in the south. The first cluster division separated a northern group, “*Eugenia monticola*-*Casearia guianensis* valleys”, that was characterized by high native species diversity and relatively few cultivated species. Indicator species for this group included *Eugenia monticola*, *Coccoloba diversifolia*, *Ardisia obovata*, and *Bourreria domingensis*; and *C. guianensis* had the highest importance value (Table 2). The second division separated a widespread group, “*Guarea guidonia* valley”, whose indicator species included *Guarea guidonia*, *Urera baccifera* and *Inga vera*. The third division separated a group that we did not find in the south, “*Casearia sylvestris* valley” group, characterized by *Casearia sylvestris*, *Inga fagifolia*, and

Roystonea borinquena; *Spathodea campanulata* had a much higher importance value than any other species in this group, though it occurred in few plots, and it had a high, but non-significant indicator value (IndVal = 39.5). The final, widespread group, “*Syzygium jambos* valley” group, was characterized most strongly by *S. jambos* and also included *Piper amalago* and *Casearia aculeata* as indicators. The *E. monticola*-*C. guianensis* valley group had the highest total native diversity ($F_{3,65} = 8.8$, $P < 0.0001$) and the *G. guidonia* valleys had lower density of trees than the other types of valleys ($F_{3,65} = 8.3$, $P < 0.0001$, Table 1).

Comparison with cluster analysis for all points

We performed a cluster analysis on the entire dataset (percent chaining = 0.51) to evaluate the robustness of the groups we found within topographic positions. The first division separated virtually all valley plots from virtually all of the *mogote* top plots, with sides split between the two groups. The four *mogote* top groups separated out quite consistently. The *L. glaucifolius* top and side groups (both in the west) formed a single group. Most of the *N. resinosa* side group joined with most of the *S. cubensis* top. The *G. lucida* top group formed its own group, and the *B. simaruba* tops formed a group with the *C. diversifolia* sides. The *D. arboreus* sides formed their own group with a few sites from tops, valleys and other side groups. The valley groups were less consistently divided, although each group was mostly represented by one cluster, except for the *C. sylvestris* valleys that were divided into two separate groups (one dominated by *S. campanulata*).

Discussion

In Puerto Rico, vegetation mapping has usually been done at a coarse scale (Dansereau 1966; Helmer 2002), while finer scale vegetation assessments have not usually been spatially explicit (Dansereau 1966; Trejo-Torres and Ackerman 2002). Here we have identified different plant communities within a region typically considered one forest type. Consistent with previous studies, we found distinct plant communities across a topographic gradient in the northern

karst (Dansereau 1966; Chinaea 1980; Trejo-Torres and Ackerman 2002), but we also found distinct plant communities within topographic positions, some of which were discretely distributed in geographic space. The processes promoting the existence of distinct species assemblages in the northern karst of Puerto Rico are probably a blend of abiotic, biotic, and historical-anthropogenic forces and this study provides a foundation for more detailed future studies.

Ordination and cluster analysis separated *mogote* top and valley communities while side communities were intermediate and overlapped both. Within topographic positions, tops showed the most distinct plant communities and the clearest separation in geographic space. *Mogote* sides were the most variable topographic position we sampled, with differences in aspect, slope, and degree of disturbance (related in part to relief and slope). This toposequence reflects both an environmental gradient and a gradient in land use intensity. *Mogote* tops and sides have shallower soils with greater drainage and are more exposed to wind than the more protected and deeper soils of valleys (Chinaea 1980; Brewer et al. 2003). At the same time, disturbance has been greater in karstic valleys and sinkholes and lowest on the tops (Rivera et al. 2000). Valleys were heavily deforested and continuously disturbed for agriculture, whereas tops and slopes were often deforested, but less frequently used for plantations or homesteads. However, differences in plant communities between *mogote* tops and valleys have been found throughout the Caribbean (Asprey and Robbins 1953; Chinaea 1980; Brewer et al. 2003), including relatively undisturbed areas, which suggests that the difference in species assemblages largely reflects the response of plant species to environmental conditions.

The higher native species richness and lower non-native species richness on tops and sides compared to valleys probably reflects land use history. It is also likely that valleys are more prone to invasions due to better environmental conditions (Stohlgren et al. 1999). North and west facing slopes had greater species diversity. Chinaea (1980) suggested that northwest slopes were less exposed to the drying effects of wind and sun

which may contribute to this pattern. The increase in endemic species richness with slope steepness could be due to adaptation of plants to well drained, unstable limestone, or could represent refugia where the steepest slopes were less likely to be disturbed by selective logging, charcoal production, or agriculture (Lugo et al. 1981). These patterns suggest that when *mogotes* are leveled, more native species are lost than when a similar surface area in a valley is altered.

Geographically, *L. glaucifolius* (a species found only in the karst, Little et al. 1988) dominated both *mogote* tops and sides in the west. In the south, the *S. cubensis* tops had high species diversity and endemic species richness. The southern region of the study area is typically at higher elevation and is wetter than the northern region. We also found two east-central groups that were geographically indistinguishable. *Gymnanthes lucida* tops and *B. simaruba* tops correspond well with Danseureau's (1966) mesoxerophytia (*G. lucida* group) and subxerophytia (*B. simaruba* tops) hill scrub communities and with China's (1980) dry woodland community type, and were found in areas with relatively less precipitation than the western or southern groups. Although the two groups shared species, the *B. simaruba* tops were significantly more diverse than the *G. lucida* tops. The *G. lucida* tops were characterized by many stems of *G. lucida* and a few other species. The distinction between these two groups is robust—it was evident even in the cluster analysis of all topographic positions. It is possible that edaphic conditions or biotic interactions contribute to the distinctiveness of these two communities.

The *mogote* sides had the highest species diversity because they contained both top and valley species and because they represent most of the karst's area. However, they were the least well-defined in ordination space, both in the full ordination (Fig. 1) and in the side ordination of cluster types (Fig. 2). The *D. arboreus* side community was the typical side community, with the wind-dispersed *T. striata* as an indicator species. This group was widespread except in the north-east section. Some of the sites from this group clustered with valley groups in the analysis of the entire dataset. In addition to the western *L. glaucifolius* group, the other two groups were

more closely allied to top communities than valleys. The *C. diversifolia* side group was most similar to the east-central *B. simaruba* top group in the full analysis, though the former was only found in the north. On the other hand the *N. resinosa* side was most similar to the southern *S. cubensis* top group, but it was found through the east-central band with just a few sites in the south.

In the valleys, the *E. monticola*-*C. guianensis* valley group had relatively high native species diversity and species compositions more similar to hilltops than other valley groups. This group was found towards the north and near the coast in areas that tend to be rockier, which may have made cultivation difficult and favored the persistence of native plants. The other groups tended to be more widespread, although the *C. sylvestris* valley group was only found along a central band. This group may have originated from abandoned pasture lands because many of the indicator species in this group (including *R. borinquena* and *S. campanulata*) are early successional species requiring considerable amounts of light to establish (Francis and Lowe 2000). In Rivera and Aide's (1998) study, most of their abandoned pasture sites fell at relatively low elevation, as does the *C. sylvestris* valley group, whereas their abandoned coffee sites typically were at higher elevations. The *S. jambos* and *G. guidonia* valleys were widespread and because coffee (*coffea* spp.) and *Inga vera* (commonly used as coffee shade) have their highest indicator values in these groups, it suggests that they developed from abandoned coffee plantations. The differences in the two groups may represent time since abandonment, type of coffee plantation, soil moisture, or pre-disturbance communities. Additional information on land use history could help disentangle these effects.

We found that topographic position and abiotic factors including precipitation, temperature, and exposure influenced the patterns of species diversity and plant communities, but did not fully explain them. We suspect that different climatic and edaphic conditions in the karst region are responsible for much of the geographic variation in *mogote* top communities. However, there are also likely to be differences in biotic processes, such as seed dispersal, seedling establishment and

herbivory. For example *L. glaucifolia* was the dominant species on tops and sides in the west. It is wind dispersed and we found a single individual in four plots in the east, approximately 35 km from the western points. This suggests that this species does get to other sites, but it has not established and become dominant in them.

Disturbance had a strong effect on species assemblages, especially in the valleys. Thus, whereas *mogote* top communities showed a strong relationship with environment and spatial location, valley and side communities appeared to reflect disturbance history more strongly than environment and were less geographically distinct. All of the valley communities included a non-native species with a high importance value (Table 2) and valleys had the lowest endemic species richness (Table 1). Land use legacies can favor certain species that perform better in the new environments that are created following abandonment (Foster et al. 2003). Thus when similar types of disturbance (e.g., coffee plantation or pasture) are distributed across an otherwise heterogeneous landscape, those sites with similar types of disturbance may appear similar to each other in spite of having different conditions that once supported distinct species assemblages. Endemic and rare native species frequently seem to be losers in the new forests because they tend to be dispersal limited, and thus more prone to losing establishment sites to dispersal-dominant and invasive species (Muller-Landau et al. 2002). A long history of disturbance in the karst valleys seems to have increased non-native species richness and dominance, while endemic species are rare in the valleys. Land use legacies may also have reduced community distinctiveness in space, but without pre-disturbance data we do not know whether valleys once showed spatially distinct plant communities as do the *mogote* tops today.

Our findings can be used to refine our understanding of plant community distributions within the northern karst life zone in Puerto Rico. We found individual species and community types in different parts of the study area. Environmental surrogates for biodiversity, usually based on features that can be derived from remote sensing or maps, are often used in conservation planning in the absence of information about species distri-

butions. The assumption is that a diversity of land units will encompass the majority of biological diversity (Groves et al. 2000, Ferrier 2002; Oliver et al. 2004). It is unlikely that mapped land units in the region we studied would have identified the different *mogote* top communities we found. Although they were important, even elevation and the climate model did not adequately explain the variation on the ordination axes. Spatial location was very important and serves as an important reminder that apparently similar land units that are separated in space may be different due to unknown abiotic variables, biotic interactions, dispersal limitation, or anthropogenic effects (Oliver et al. 2004; Brooks et al. 2004).

Conservation planning efforts for Puerto Rico's karst region should take into account the distributions of species and the different community types present, particularly the communities found on the *mogote* tops. Strategies that target the western, southern, and east-central portions of the karst will ensure the protection of the widest range of species and communities present in the region. The proposed conservation areas would encompass most of these sections (Lugo et al. 2001). However, if funding is not available for all of the land envisioned under the original proposal, our work can be used to develop criteria for prioritizing land acquisition.

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