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Associations between Soil Variables and Vegetation Structure and Composition of Caribbean Dry Forests

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Abstract - Soil–vegetation associations have been understudied in tropical dry forests when compared to the amount of extant research on this issue in tropical wet forests. Recent studies assert that vegetation in tropical dry forests is highly heterogeneous and that soil variability may be a contributing factor. In this study, we evaluated the relationship between soil variables and vegetation structure and composition between 2 dry-forest types, plateau and depression forests, considered distinct by prior vegetation studies performed on Mona Island. Depression-forest sites are of particular interest because they are critical habitats for the endangered *Cyclura cornuta stejnegeri* (Mona Island Iguana) on the island. These stands establish at sinkholes within the island's limestone platform where there are deeper soils. Plateau forest is the dominant vegetation association on the island and has been characterized as a low-productivity forest type with an open canopy. We asked 2 main questions in this study: (1) Are depression and plateau forests distinct types that can be distinguished in terms of plant-species structure, diversity, and soil features? and (2) Can we identify associations between soil and vegetation features? We performed vegetation and soil analyses at 6 different depression- and plateau-forest sites on Mona Island. Contrary to the suggestions of previous studies, we did not detect any significant differences between depression and plateau forests in any measured vegetation or soil variables. We discuss several hypotheses to explain our results.

Introduction

A central paradigm in ecology is that plants vary in their tolerance to different environmental conditions and in their ecological requirements, resulting in spatial variation in distribution and abundance of plant species across environmental gradients as plants colonize habitats (Hall et al. 2004, Swaine

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1996). Among environmental conditions, soil features and topography can play important roles in shaping plant communities, mainly through their effects on soil-water content and nutrient availability (Miyamoto et al. 2003, Sollins 1988). However, studies on the association of plant-species distribution and abundance with soil features in tropical sites are still dominated by studies that focus on wet forests; there is less data available from dry-forest sites (but see Peña-Claros et al. 2011 and references therein). Worldwide, tropical dry forests comprise 42% by area of all tropical ecosystems (Murphy and Lugo 1986). Nevertheless, at present, dry forests are considered the most endangered tropical biome (Janzen 1988), mostly due to their widespread transformation to agricultural systems (Miles et al. 2006, Quesada and Stoner 2004). Increasing our understanding of how plant and soil features interact in dry forests is therefore critical to understanding how these forests function and to evaluate their potential for restoration in relation to factors that may negatively influence these systems in the future (e.g., climate change and habitat transformation; Collevati 2013, Kirschbaum et al. 1995, Magrin et al. 2007).

Mona Island is located in the Caribbean Sea between Puerto Rico and Hispaniola (Cintrón and Rogers 1991). The island is an elevated limestone platform with limited beach formations that support a variety of vegetation associations of high conservation value (Cintrón and Rogers 1991, Martinuzzi et al. 2008, Perotto-Baldivieso et al. 2009). The limestone bedrock of the island's platform has led to subtle topographic variability that may influence soil features indirectly. For example, large sinkholes in which deeper soils tend to form have led to the establishment of a forest type known as depression forest (Cintrón and Rogers 1991, Martinuzzi et al. 2008, Perotto-Baldivieso et al. 2009). Depression forests are characterized by taller canopies (~12 m in height), cooler understories, and greater litter accumulation relative to plateau forests, which constitute the dominant forest type on the island. In contrast to depression forests, plateau forests are described as having shallower soils, open and shorter canopies (~5 m in height), and soil formation occurring among a matrix of unevenly exposed limestone bedrock (Cintrón and Rogers 1991). Previous studies have shown that differences in topography and vegetation structure between these 2 forest types (as they were described originally) were consistent with differences in dominant plant composition (Cintrón and Rogers 1991). Furthermore, differences in topography and vegetation structure and composition should lead to differences in the processes of soil formation, and may reflect differences in their soil features (i.e., soil depth, water-holding capacity, and nutrient availability). On Mona Island, depression forests are designated as critical habitat for the conservation of the endangered rock iguana *Cyclura cornuta stejnegeri* Barbour & Noble (Mona Island Iguana) because it nests in the deeper soil deposits within this forest type (Haneke 1995).

In this study, we evaluated the relationship between soil features and vegetation structure and composition to address 2 main questions: (1) Are depression and plateau forests distinct types that can be distinguished in terms of plant-species structure, diversity, and soil features? and (2) Can we identify associations between soil and vegetation features? Studies evaluating the association between soil-nutrient availability and plant-species richness in wet forests have found a positive association between these 2 variables (i.e., Clinebell et al. 1995, Swaine 1996). However, other studies have shown that this relationship is not necessarily universal (Peña-Claros et al. 2011). We hypothesized that Mona Island depression forests would have deeper and wetter soils and higher nutrient availability than plateau forests.

We also assessed whether there were differences in plant-species diversity between depression and plateau forests. *Capra hircus* Erxleben (Feral Goat), introduced on Mona Island by Europeans in the 1500s, has been a concern for managers due to their impact on vegetation structure and composition (García et al. 2000). In addition, a previous study suggested that Feral Goats had a tendency to occupy depression forests more than less-productive plateau forests (Meléndez-Ackerman et al. 2008). Therefore, another goal of our study was to assess the potential differential influence of Feral Goat browsing on the vegetation composition of these 2 forest types.

Field-site Description

Mona Island is located in the Caribbean Sea between Puerto Rico and the Dominican Republic (18°05'N, 67°54'W). The island is a limestone-dolomite platform covering an area of 55 km^2 (Cintrón and Rogers 1991). Mean annual temperature and precipitation estimated over 54 years is 26.5 °C (range = 22.7–29.1°C; the highest temperatures occur July–September) and 887 mm (range = 285–1518 mm), respectively (Rojas-Sandoval 2010). On this island, the dry season extends from December to April, and the rainy season lasts from May to November, coinciding with the Atlantic hurricane season (Rojas-Sandoval and Meléndez-Ackerman 2011). Vegetation is classified as subtropical dry forest, with a large portion of the species showing xeromorphic adaptations (Woodbury et al. 1977). Calcareous systems within Caribbean dry forests, like those on Mona Island, are characterized by exposed limestone bedrock with poor water-holding capacity (Lugo et al. 2001). The vegetation of Mona Island is comprised of at least 16 associations mostly influenced by changes in macro- and micro-relief and by an east–west ocean salt-spray effect (which correlates with the east–west gradients in canopy closure that occur on this island and most likely also with vegetation productivity; Cintrón and Rogers 1991, Martinuzzi et al. 2008, Rojas-Sandoval and Meléndez-Ackerman 2013). The plateau forest as described by Cintrón and Rogers (1991), occupies approximately 80% of the island's area and is characterized by open canopies, exposed limestone on the ground, and a semi-deciduous shrubby association of columnar cacti, xerophytic shrubs, and small trees (1–3 m in height; Fig. 1a). Depression forests grow in patchily distributed sinkholes or relief depressions within the island's platform. Depression forests are characterized by having taller canopies (10–12 m in height), shady floors, and sparse understories (Fig. 1a). Across the island, lowlands and shallow sinkholes are covered by red residual soils, while the limestone-dolomite platform is overlain by thin, calcareous soils (González et al. 1997, Rivera 1973).

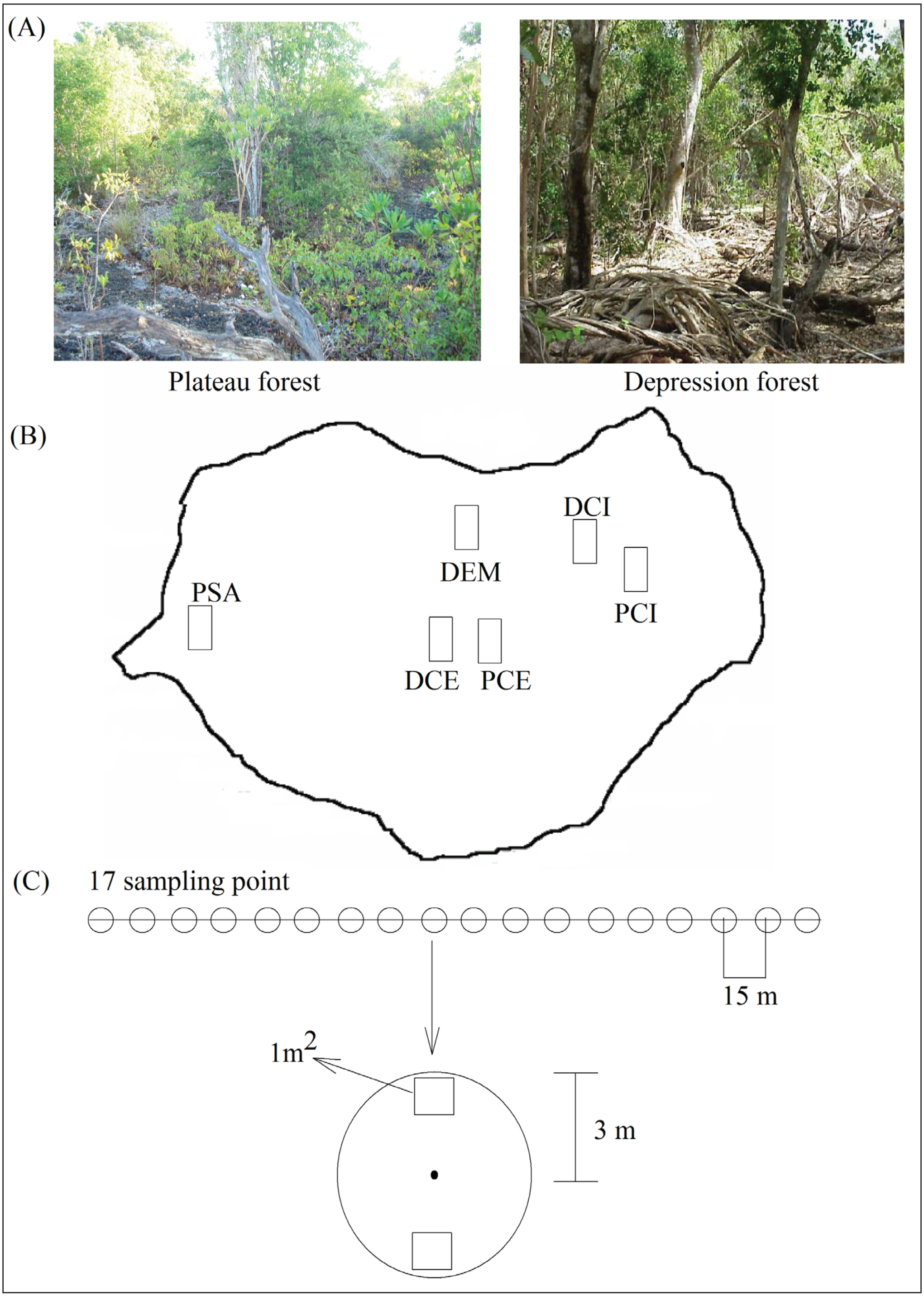

Figure 1. Experimental design on Mona Island. (A) Typical landscape in plateau forests and depression forests. (B) Location of forest sites across Mona Island included in this study. (C) Sampling design: 17 focal points; each included a 3-m-radius circular plot and two 1m^2 quadrats. See text for site-name abbreviations.

Methods

Sampling design

We gathered vegetation data at 3 depression-forest sites (Indio = DCI, Cerezo = DCE, Empalme = DEM; Fig. 1b) and 3 plateau-forest sites (Sardinera = PSA, Camino Centro = PCE, Camino Indio = PCI; Fig. 1b). Among forest sites, the minimum separation distance is 1.9 km between DCE and PCE and the maximum distance is 7.8 km between DCI and PSA (Fig. 1b). At each site, we set-up a 240-m-long permanent transect with17 georeferenced sample points separated by 15 m. Each sample point corresponded to the center of a 3-m-radius circular plot. Within each circular plot, we established two 1-m^2 quadrats located 2 m from the center of the circular plot and oriented perpendicular to the transect (Fig. 1c). We tagged and identified all established vegetation >1 m in height within circular plots, and tagged and identified all established vegetation <1 m in height within quadrats. For the analyses, we referred to plants recorded within circular plots as canopy plants and plants recorded within quadrats as understory plants. We classified all tagged plants as trees, shrubs, lianas, herbs, grasses, cacti, or vines. For each species, we calculated the importance-value index (IVI) using its relative density and frequency (Brower et al. 1997) as follows:

$$\mathrm{IVI} = (f_i / \sum f) + (d_i / \sum d)$$

where f_i is the relative frequency of the species i across sampling units relative to the sum of relative frequencies for all species, and d_i is the relative density of the species i for a given sampling area relative to the sum of densities for all species. We sampled a total area of 1441.26 m^2 at each forest site.

In October 2003, we collected soil samples within circular plots for chemical (Al, C, Ca, Mg, Mn, Na, K, P, S, N, C/N ratio, and loss-on-ignition [LOI]) and physical (pH, depth, gravimetric soil-water content, and soil hardness) analyses. Within each circular plot, we collected three 100–150-g core samples at 3 randomly selected areas at depths ≤10 cm because most soils were very shallow (see Results). We also collected 17 samples within each transect for a total of 102 samples over the 6 transects. For each sample collected, we placed a 40–60-g subsample in a cloth bag for soil chemical analyses and sealed the remaining sample in a plastic bag for gravimetric soil-water content and pH analyses. Chemical analyses were performed in the soil biology laboratory at the International Institute for Tropical Forestry (Rio Piedras, PR). All soil samples were oven dried at 65 °C and ground to pass through an 18-mesh sieve. We determined total C and N for samples using the macro dry-combustion method by means of the LECO CNS-2000 Analyzer (Leco Corp. 2003) wherein, a small weighted sample encapsulated in tin foil, is combusted by heating to a high temperature (950 °C) and flushed in a stream of purified oxygen. The combustion gases are collected in a vessel known as the ballast. Total C is measured as CO_2 by the infrared detector, and total N is determined as N_2 by a thermal conductivity cell. Total C and N values are reported as a percentage. Blanks and reference materials of known concentration and of similar matrix to the unknown samples were run with each batch to assure the quality of the analysis.

The ground soil samples were digested using a digestion block with automatic temperature control, a modification of the wet-oxidation method recommended by Huang and Schulte (1985) that employs concentrated HNO_3, 30% H_2O_2, and concentrated HCl. The digested samples were analyzed in a Spectro Ciros ICP emission spectrometer (Spectro Corporation, Mahwah, NJ, USA) for total content of Ca, K, P, Mg, Fe, Al, Mn, and Na. The results are reported as mg/g on a dry basis at 105 °C. Blank and NIST-certified reference samples were analyzed in each batch to ensure the completeness of elemental recovery. We oven-dried a representative subsample of the soils at 105 °C for a period of 24 h and determined the moisture-factor correction gravimetrically. The same soil subsamples were ignited in a muffle furnace at 490 °C to obtain ash content. To determine gravimetric soil-water content, we sieved soil samples through a 2-mm mesh and weighed 15 g of wet soil for each sample, after which they were dried in an oven at 105 °C for 48 h, cooled for 30 min, and reweighed. We then estimated soil-water content (WC) as the ratio of the difference between the wet soil weight (SW_w) and the dry soil weight (SW_d) divided by the wet soil weight ($WC = (SW_w - SW_d) / SW_w$).

Statistical analyses

Vegetation variables. We performed tests for differences in average species density (species/m^2) and plant density (individuals/m^2) across forest types using MANOVA tests with forest type and location as main effects and then with an independent 2-way ANOVA test for each variable separately. These analyses were performed using JMP 7.0 (SAS Institute, Cary, NC, USA).

Species-area curves. For each forest site, we constructed species-accumulation curves and diversity statistics using the accumulation-cover estimator (ACE) from Estimate S (V. 8; Colwell 2006) to evaluate differences in species richness among sites and to assess whether our sampling areas were representative of the standing vegetation composition.

Soil Variables. We tested for differences in all soil variables between depression and plateau forests using MANOVA tests (Wilks λ test: $F_{1,75} = 12.19$, $P < 0.001$). Because this analysis showed significant differences between the 2 forest types, we performed individual 2-way ANOVA tests for each soil variable using forest type (depression forests vs. plateau forest) and forest site as main effects.

Ordination analysis. To test for differences in vegetation composition among forest sites and the contribution of soil variables to these differences, we conducted a redundancy ordination analysis (RDA) using Canoco 4.5 (Ter Braak and Šmilauer 2002). RDA is the canonical form of principal component analysis and detects relationships between vegetation composition and environmental variables (Jongman et al. 1995). For the RDA analysis, we only included soil variables that showed significant differences across forest types in the MANOVA analyses (see Results). Prior to the RDA analysis, we performed pairwise correlations to evaluate the likelihood of strong variable-associations before inclusion. Most associations we evaluated were ranked as weak–moderate, thus, we included all soil variables with significant forest-type effects in the analysis. For the RDA analysis, we log-transformed data for species abundance to fit normal distribution assumptions and used site as a co-variable. To test the significance of the ordination model, we used a Monte-Carlo permutation test with 500 restricted permutations using the species-centering and standardizing option to obtain a species–soil correlation matrix. To identify the soil variables best correlated with species composition, we performed a stepwise regression with backward selection. We undertook separate analyses for circular plots and quadrats. For the RDA analysis, we pooled the quadrat pairs from each sample point and used this information to select the species and the soil variables that contributed most to the final ordination model.

Results

Vegetation variables

MANOVA tests showed significant effects of forest type, site, and their interaction to the variation in the average plant-species density (Wilk's λ: $F = 7.4$, $P < 0.0001$; effect tests: $F > 11.3$, $P < 0.0001$ in all cases). Forest type had a significant effect on species density for both canopy and understory strata (2-way ANOVA forest type: $F_{1,2} > 4.6$, $P < 0.03$ in all cases), but so did the forest type × site interactions ($F_{2,96} > 9.8$, $P < 0.0001$ in all cases; Fig. 2a, c) indicating a high heterogeneity in species density within forest types. This analysis also showed that site effect

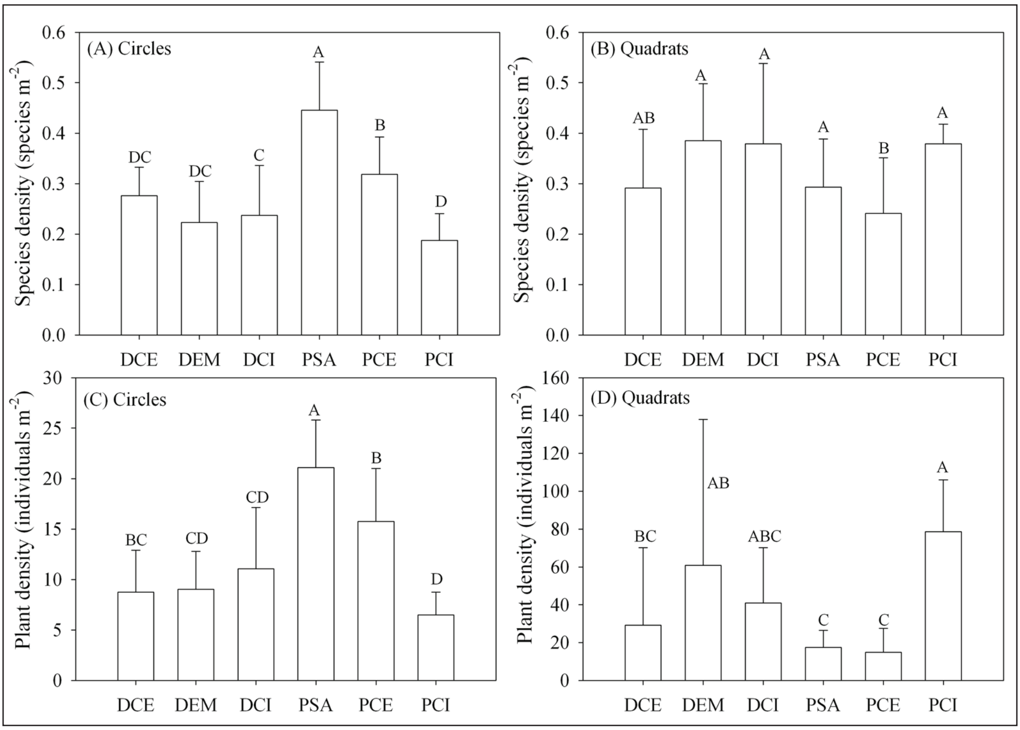

Figure 2. Species density and plant density estimated from vegetation surveys performed in circular plots (canopy species graphs: A and C) and quadrats (understory species graphs: B and D). Bars with different letters are statistically different from each other. See text for site-name abbreviations.

was significantly different for the species density at the canopy layer ($F_{2, 100}$ = 14.3, $P < 0.0001$) but not for the species density at the understory layer ($F_{2,96}$,= 2.7; P = 0.50; Fig. 2b, d). On average, plateau forest sites had greater species density in the canopy layer, but this pattern was not consistent across replicates. Similarly, species density in the understory layer was higher at depression forests than plateau forests, but replicates within forest types were significantly different from each other. On average, plots at PCI had lower species density relative to other plateau forest sites and a slightly lower average relative to depression forest sites.

For plant density, results of univariate 2-way ANOVAs also indicated significant effects for forest type, site, and their interaction for the canopy layer ($F_{1,2} > 21.4$, $P < 0.0001$ in all cases; Fig. 2c). On average, plateau forests had more plants per unit area than depression forests, but plots at PCI were an exception and had the lowest average plant density of all sites. Differences in plant density in the understory layer were not significant between the 2 forest types ($F_{1,2}$ = 0.83, P = 0.36), but they were significant among the different replicates ($F_{2,2}$ = 3.4, P = 0.04). Plant density was visibly lower at the plateau sites PSA and PCE relative to the other plateau sites. For plant density, a highly significant forest type × site interaction effect was also detected for the understory layer ($F_{2,96}$ = 12.7, $P < 0.001$; Fig. 2d), indicating significant heterogeneity within forest types.

Species-accumulation curves

Species-accumulation curves were not uniform across sites (replicates) within a forest type regardless of forest stratum (i.e., canopy or understory) except for plateau forests sampled at the understory, which had similar curves across sites (Fig. 3). Understory censuses yielded on average a higher number of species per site than canopy censuses. Nevertheless, species-accumulation curves failed to show accumulation patterns that were consistent for all sites within a forest type or all sites within each of the forest strata. The maximum number of species observed at a given site was higher for understory censuses (60–25 species: DCI > DEM > DCE = PCE > PSA = PCI; Fig. 3a) than for the canopy censuses (50–10 species: DCE = PCE > PSA > DEM > DCI > PCI; Fig. 3b). Canopy censuses yielded 3 sites (2 depressions and 1 plateau) with well-defined asymptotes that indicated very robust estimates of the canopy diversity. Well-defined asymptotes were absent in all of the understory censuses, and all of them yielded accelerated curves (i.e., observed values underestimated diversity) and generated the 2 steepest curves, both of which were from depression sites (Fig. 3b).

Combined, depression (98 species) and plateau forests (58 species) comprised 105 plant species. The IVI analysis showed that shrubs rather than trees were the dominant growth form at the canopy level based on their relative frequency and density (Table 1). Shrubs within the Euphorbiaceae (spurge family) were dominant in the understory layer in both forest types. None of the canopy species evaluated reached IVI values higher than 49%, which suggested that there were no signs of extreme dominance in this forest layer. Among understory plants, herbs and grasses were the dominant growth forms in depression forests, while non-woody growth forms including herbs, grasses, and vines were dominant in plateau forests (Table 1). In fact, young trees were never among the 10 most common understory plants regardless of forest type (Table 1). Signs of extreme dominance by any species were also lacking in the understory layer among plateau forests, which had a significant representation of species that were either legumes or euphorbs. In contrast, the understory of 2 out of 3 sites in depression forests were highly dominated by the herb species *Synedrella nodiflora* (L.) Gaertn. (Nodeweed) (IVI > 50%). For both canopy and understory strata, 9 species had IVI values higher than 20% (Table 1).

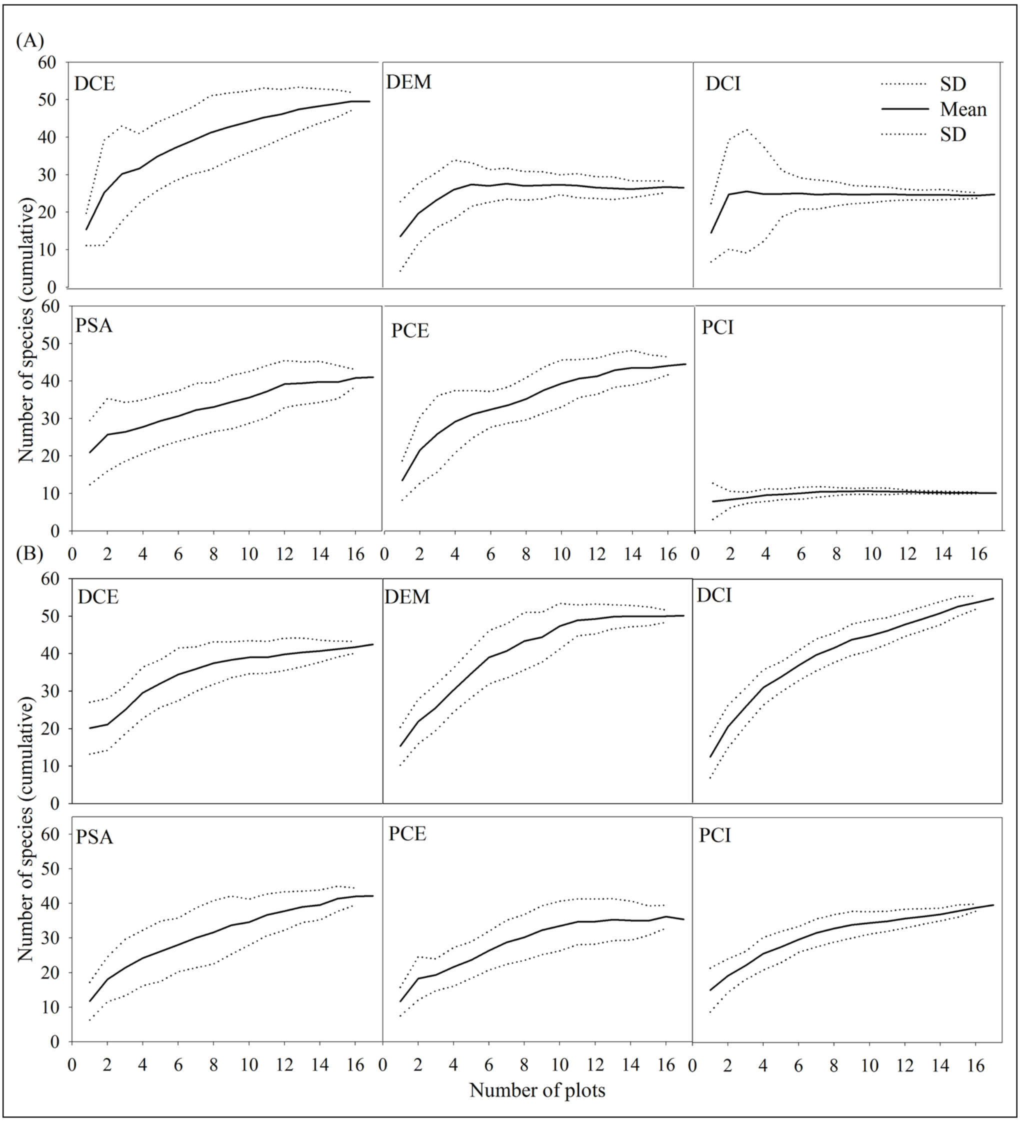

Figure 3. Cumulative species curves for (A) canopy layer and (B) understory layer. See text for site-name abbreviations.

Table 1. Importance-value index (IVI) for species at depression and plateau sites in 2 different forest strata: (A) canopy and (B) understory. Species included were those highly correlated with 8 soil traits and with the highest IVI values. Classification was based on the PLANTS database (USDA–NRCS 2015). GLM linear regression between axis 1 and individual species $^{*}P < 0.05$, $^{**}P < 0.001$.

Family	Species	Acronym	Growth habit	Coefficient value	Depression forest			Plateau forest		
					DCE	DCI	DEM	PCE	PCI	PSA
Canopy										
Apocynaceae	*Pentalinon luteum* (L.) B.F. Hansen & Wunderlin	Penlut	Vine	0.02^{*}	2.5	–	–	–	–	–
	Plumeria obtusa L.	Pluobt	Tree	0.62^{**}	4.3	1.3	2.5	10.1	19.9	8.4
Burseraceae	*Bursera simaruba* (L.) Sarg.	Bursim	Tree	0.38^{*}	6.6	5.8	5.4	1.9	–	7.7
Cactaceae	*Pilosocereus royenii* (L.) Byles & G.D. Rowley	Pilroy	Cactus	0.42^{**}	–	–	–	1.7	15.0	9.1
Celastraceae	*Crossopetalum rhacoma* Cranz	Crorha	Tree	0.49^{**}	–	–	–	0.8	–	2.4
Erythroxilaceae	*Erythroxylum areolatum* L.	Eryaer	Tree	0.049	3.8	2.6	–	–	–	–
Euphorbiaceae	*Croton betulinus* Vahl	Crobet	Shrub	1.13^{**}	–	–	–	–	–	23.7
	Croton discolor Willd.	Crodis	Shrub	2.59	–	23.2	22.1	13.2	37.5	15.7
	Croton lucidus L.	Croluc	Shrub	5.27^{**}	15.6	14.8	23.8	39.1	–	42.7
	Euphorbia petiolasris Sims	Euppet	Shrub	2.44^{**}	5.7	42.3	37.6	1.6	14.1	7.3
	Jatropha multifida L.	Jatmul	Shrub	0.049	–	4.1	1.1	–	–	–
	Phyllanthus epiphyllanthus L.	Phyepi	Shrub	2.01	29.2	–	–	36.5	–	–
Myrtaceae	*Eugenia foetida* Pers.	Eugfoe	Tree	0.42	–	1.3	11.1	6.7	–	2.1
	Myrcianthes fragrans (Sw.) McVaugh	Myrfra	Tree	0.38	6.0	5.6	11.9	6.5	–	–
Nyctaginaceae	*Pisonia albida* (Heimerl) Britton ex Standl.	Pisalb	Tree	0.13	–	–	8.3	2.9	–	–
Polygonaceae	*Coccoloba microstachya* Willd.	Cocmic	Tree	0.99^{*}	9.9	8.9	5.3	18.3	–	9.9
Rhamnaceae	*Krugiodendron ferreum* (Vahl) Urb.	Krufer	Tree	0.15	1.3	7.5	3.6	0.9	–	–
	Reynosia uncinata Urb.	Reyunc	Tree	1.42^{**}	18.9	14.6	10.7	10.6	28.1	12.7
Rubiaceae	*Antirhea acutata* (DC.) Urb.	Antacu	Shrub	0.46^{*}	–	3.8	2.5	8.1	21.3	3.3
	Exostema caribaeum (Jacq.) Roem. & Schult.	Exocar	Tree	0.22^{**}	–	–	–	0.8	–	8.2
	Psychotria nutans Sw.	Psynut	Tree	0.25^{*}	–	–	13.74	1.2	–	–
Solanaceae	*Solanum persicifolium* Dunal	Solper	Herb	0.12^{*}	10.4	–	–	–	–	–
Sterculiaceae	*Melochia tomentosa* L.	Meltom	Shrub	0.49	2.5	5.7	13.3	2.5	3.1	7.2
Tiliaceae	*Corchorus hirsutus* L.	Corhir	Shrub	1.32	5.7	12.7	18.6	1.7	48.3	7.3
Verbenaceae	*Lantana involucrata* L.	Laninv	Shrub	0.09	–	–	–	–	–	5.1

Table 1, continued.

Family	Species	Acronym	Growth habit	Coefficient value	Depression forest DCE	Depression forest DCI	Depression forest DEM	Plateau forest PCE	Plateau forest PCI	Plateau forest PSA
Understory										
Asclepediaceae	*Metastelma lineare* Bello	Metlin	Vine	0.36^{*}	–	–	–	2.1	4.1	9.4
Asteraceae	*Synedrella nodiflora* (L.) Gaertn.	Synnod	Herb	16.1^{*}	50.6	10.5	62.8	–	–	–
Bignoniaceae	*Tabebuia heterophylla* (DC.) Britton	Tabhet	Tree	0.009^{**}	–	0.6	–	–	–	–
Bromeliaceae	*Tillandsia utriculata* L.	Tilutri	Herb	0.19	1.6	–	–	–	–	–
Cactaceae	*Melocactus intortus* (Mill.) Urb.	Melint	Cactus	0.08^{*}	–	–	–	1.0	3.2	–
	Opuntia repens Bello	Opurep	Cactus	0.46^{*}	5.9	4.2	3.2	3.1	0.7	2.9
Capparaceae	*Capparis cynophallophora* L.	Capcyn	Shrub	0.05	3.5	–	–	–	–	–
Commelinaceae	*Callisia repens* (Jacq.) L.	Calrep	Herb	2.06^{**}	14.1	–	14.9	–	–	–
	Commelina elegans Kunth	Comele	Herb	1.72^{**}	12.9	9.4	10.6	–	0.7	4.9
Cyperaceae	*Cyperus filiformis* Sw.	Cypfil	Herb	0.29^{*}	–	1.3	–	–	–	–
	Cyperus nanus Willd.	Cypnan	Herb	1.05^{**}	4.3	7.3	5.8	–	–	–
Fabaceae	*Centrosema virginianum* (L.) Benth.	Cenvir	Vine	4.04^{*}	4.1	9.2	5.2	12.6	12.9	30.6
	Chamaecrista nictitans (L.) Moench	Chanic	Herb	1.89^{*}	7.2	3.1	0.6	16.9	3.9	7.3
	Galactia dubia DC.	Galdub	Vine	8.01^{*}	3.8	12.4	5.5	14.8	35.1	6.3
Erythroxilaceae	*Erythroxylum aerolatum* L.	Eryaer	Tree	0.49^{*}	0.8	1.9	0.6			
Euphorbiaceae	*Croton betulinus* Vahl	Crobet	Shrub	2.77^{**}	–	2.4	–	–	17.6	22.8
	Croton lucidus L.	Croluc	Shrub	2.78^{*}	5.0	5.3	4.8	29.6	–	24.6
	Euphorbia petiolaris Sims	Euppet	Shrub	0.46	2.4	3.5	5.7	–	1.9	3.7
Lamiaceae	*Salvia serotina* L.	Salabu	Herb	0.73^{*}	1.0	–	9.0	–	–	–
Malvaceae	*Sida abutifolia* Mill.	Sidabu	Herb	1.03^{*}	–	10.4	0.0	–	–	–
	Sida glabra Mill.	Sidgla	Herb	2.47^{**}	2.8	11.4	8.2	–	–	–
	Sidastrum multiflorum (Jacq.) Fryxell	Sidmul	Shrub	2.55	2.0	24.7	1.3	–	–	1.1
Myrtaceae	*Myrcianthes fragrans* (Sw.) McVaugh	Myrfra	Tree	0.14	3.6	0.6	3.7	–	–	–
Poaceae	*Eragrostis ciliaris* (l.) R. Br.	Eracil	Grass	0.76	3.5	2.3	0.9	–	2.8	–
	Paspalum blodgettii Chapm.	Pasblo	Grass	1.12	6.1	1.6	4.4	15.8	2.4	7.3
	Setaria utowanaea (Scribn.) Pilg. in Engler & Prantl	Setuto	Grass	4.36^{**}	25.2	14.7	10.7	21.5	5.7	10.1
Rhamnaceae	*Krugiodendron ferreum* (Vahl) Urb.	Krufer	Tree	0.02	–	0.6	1.2	–	–	–
Rubiaceae	*Exostema caribaeum* (Jacq.) Roem. & Schult.	Exocar	Tree	0.02	–	–	–	2.1	–	0.9
	Psychotria nutans Sw.	Psynut	Tree	0.02	1.6	–	–	1.0	–	–
Solanaceae	*Solanum persicifolium* Dunal	Solper	Herb	0.01	–	–	1.2	–	–	–
Sterculiaceae	*Ayenia insulicola* Cristóbal	Ayeins	Herb	9.64	10.4	7.8	11.7	–	29.6	39.3

Soil variables

MANOVA tests showed significant differences among forest types ($F_{1,96} = 23.82$, $P < 0.001$), sites ($F_{2,96} = 11.90$, $P < 0.001$) as well as significant forest type × site interaction effects ($F_{2,96} = 11.12$, $P < 0.001$) for both chemical and physical variables. High heterogeneity within forest types was pervasive for 14 of 17 variables showing significant site effects (Table 2). Even when more than half of the variables generated a significant effect for forest type, significant interaction effects limited our interpretation of the results. Exceptions were the variables K, soil depth, and soil pH for which interaction effects were absent. Our results showed that soils at depression forests had more K, were more basic, and were deeper than soils in plateau forests (Table 3). However, it should be noted that even for these variables, there was always an overlap between 1 depression and 1 plateau site. Specifically for K and soil depth, the depression site DCI overlapped with the plateau site PSA, and for soil pH we observed an overlap between the depression site DCE and the plateau site PCE (Table 3). Results also showed a gradient-like variation across plateau sites in 9 of 17 soil variables with significant site effects, although not always in the same direction. Soil contents of Al, Fe, K, and Mn increased from the southwestern to the eastern side of the island (PSA < PCE < PCI; Table 3, Fig. 1), and soil contents of C, Ca, N, S, and LOI decreased along the same trajectory (PSA > PCE > PCI; Table 3, Fig. 1). For the remaining variables showing significant site effects, variation across space showed that PCE (a plateau site located in the middle of the island) had higher soil contents of Na and Mg, deeper and softer soils, and more basic elements compared to the other 2 plateau sites (PSA and PCI) located in the eastern and western ends of the island portions of the island, respectively (Table 3, Fig. 1).

Table 2. Results for 2-way ANOVA testing for differences in soil variables between depression and plateau sites with forest type and site as main effects. NS = not significant.

	Forest type		Site		Forest type × Site	
Variables	*F*	*P*	*F*	*P*	*F*	*P*
Depth	22.48	0.0001	5.88	0.0030	1.01	NS
Hard	81.19	0.0001	5.92	0.0030	27.74	0.0001
Water content	8.59	0.0040	2.97	NS	16.94	0.0001
pH	13.03	0.0005	15.11	0.0001	1.92	NS
C	0.64	NS	9.76	0.0001	1.91	NS
N	3.78	NS	5.90	0.0030	2.07	NS
C/N	4.81	NS	1.23	NS	3.37	NS
P	47.01	0.0001	2.44	NS	5.48	0.0050
Ca	1.58	NS	5.73	0.0040	2.59	NS
Mg	46.49	0.0001	60.64	0.0001	32.83	0.0001
K	11.70	0.0009	20.01	0.0001	0.46	NS
Na	33.17	0.0001	3.22	0.0400	25.19	0.0001
Mn	4.54	0.0300	14.34	0.0001	4.64	0.0001
Al	0.62	NS	8.53	0.0004	4.36	0.0100
Fe	0.03	NS	8.64	0.0004	5.51	0.0050
S	0.15	NS	3.50	0.0300	2.43	NS
LOI	0.41	NS	9.52	0.0002	1.97	NS

Table 3. Soil variables at different sites within depression and plateau forests. Values are mean ± SE. Soil variables that distinguished forest types are indicated by * (see forest-type values in Table 2).

	Depression forests			Plateau forests		
Variable	DCE	DCI	DEM	PCE	PCI	PSA
Soil depth (cm)*	10.31 ± 2.42	11.64 ± 7.35	8.40 ± 1.82	8.60 ± 3.20	4.55 ± 4.08	5.05 ± 4.63
Soil hard (kgf/cm2)*	73.23 ± 15.58	178.67 ± 42.02	93.08 ± 33.22	165.44 ± 46.54	197.65 ± 38.73	216.91 ± 69.16
Water content (%)*	0.68 ± 0.04	0.59 ± 0.07	0.63 ± 0.04	0.67 ± 0.04	0.63 ± 0.03	0.67 ± 0.04
pH*	7. 61 ± 0.14	7.80 ± 0.14	7.50 ± 0.22	7.66 ± 0.16	7.33 ± 0.29	7.44 ± 0.34
C (%)	14.96 ± 4.10	20.34 ± 9.53	19.09 ± 9.49	20.40 ± 6.69	13.27 ± 2.99	24.31 ± 9.58
N (%)	1.23 ± 0.35	1.53 ± 0.58	1.38 ± 0.58	1.60 ± 0.49	1.26 ± 0.25	1.82 ± 0.45
C/N	12.22 ± 0.18	12.95 ± 0.39	13.35 ± 0.42	12.73 ± 0.29	10.53 ± 0.24	13.03 ± 0.57
P (mg/g)*	3.20 ± 1.32	4.25 ± 1.77	5.48 ± 3.68	1.45 ± 0.37	2.34 ± 0.75	1.81 ± 0.51
Ca (mg/g)	26.12 ± 17.24	49.53 ± 36.14	31.09 ± 18.59	32.61 ± 12.19	23.09 ± 14.72	36.07 ± 10.23
Mg (mg/g)*	6.94 ± 0.87	5.11 ± 0.71	4.32 ± 0.51	5.23 ± 0.80	4.65 ± 0.34	3.88 ± 0.42
K (mg/g)*	31.70 ± 6.23	27.72 ± 12.77	21.70 ± 8.26	23.68 ± 5.61	27.46 ± 4.29	14.52 ± 5.14
Na (mg/g)*	0.45 ± 0.04	0.45 ± 0.09	0.53 ± 0.11	0.47 ± 0.07	0.40 ± 0.06	0.30 ± 0.05
Mn (mg/g)	1.88 ± 0.25	1.78 ± 0.67	1.60 ± 0.84	1.47 ± 0.32	2.09 ± 0.23	1.08 ± 0.33
Al (mg/g)	58.39 ± 7.99	46.98 ± 19.92	57.04 ± 17.27	48.50 ± 12.05	64.03 ± 7.32	43.16 ± 16.70
Fe (mg/g)	52.13 ± 8.21	38.32 ± 19.72	52.57 ± 18.14	44.24 ± 11.20	58.30 ± 6.53	38.93 ± 15.55
S (%)	0.18 ± 0.04	0.22 ± 0.06	0.18 ± 0.06	0.18 ± 0.06	0.17 ± 0.03	0.21 ± 0.04
LOI (%)	38.77 ± 5.90	47.29 ± 13.17	44.17 ± 13.48	46.38 ± 9.33	36.54 ± 4.70	51.32 ± 12.96

Multiple regression analyses for plant abundance as a function of soil variables were statistically significant for the canopy and understory strata and explained 31.9% ($F_{4,97}$ = 11.3, P = 0.0001) and 24.9% ($F_{2,99}$ = 16.4, P = 0.0001) of the variation in this parameter, respectively. Plant abundance in the canopy layer was best explained by K, P, soil hardness, and soil-water content; at the understory layer, it was best explained by K and Mg (Table 4). Multiple regression analyses for species richness in the canopy and understory strata as a function of soil variables were statistically significant and explained 37.2% and 20.9% of the variation in this parameter, respectively (Table 4). Species richness in the canopy layer was best explained by K, Na, soil-water content, hardness, and pH, while in the understory it was best explained by variation in K and Mg (Table 4).

The Monte Carlo permutation test following the RDA analysis on vegetation–soil variables shows that the first 2 axes of the ordination were significant for both canopy (both axes P = 0.001; Fig. 4a) and understory strata (both axes P = 0.002; Fig. 4b). Nevertheless, the RDA ordination also indicated a large overlap between forest types in species composition as well as great heterogeneity for this parameter within a given site. The magnitude of this overlap was reduced in the ordination for the canopy layer (Fig. 4a) compared to the ordination for the understory layer (Fig. 4b). Species composition explained very little of the difference among forest sites as indicated by the small amount of variation explained by the species data from both forest strata (cumulative variance in canopy: axis 1 = 4.4%, axis 2 = 7.4%; cumulative variance in understory: axis 1 = 5.4%, axis 2 = 9.3%). In contrast, variation among forest sites was better explained by soil variables (i.e., the species–environment correlations). For the canopy layer, the cumulative variance in the species–soil variables correlation was 33.8% in axis 1 and 57.4% in axis 2. For

Table 4. Regression analysis for vegetation (plant abundance and species richness) and soil variables separating by forest strata.

	Variables	Estimate (SE)	*T*	*P*
Canopy				
Plant abundance	P	-0.42 (0.12)	-3.43	0.0009
	Hard	0.05 (0.01)	2.86	0.0050
	Water content	-1.27 (0.54)	-2.35	0.0200
	K	64.35 (21.69)	2.97	0.0030
Species richness	K	-0.09 (0.03)	-2.93	0.0040
	Na	-5.87 (3.12)	-1.88	0.0640
	Hard	0.008 (0.004)	2.00	0.0480
	Water content	27.58 (4.91)	5.61	<0.0001
	pH	2.42 (0.98)	2.45	0.0160
Understory				
Plant abundance	K	5.89 (1.03)	5.71	<0.0001
	Mg	-29.36 (8.32)	-3.57	0.0006
Species richness	K	0.20 (0.04)	5.08	<0.0001
	Mg	-1.10 (0.32)	-3.41	0.0009

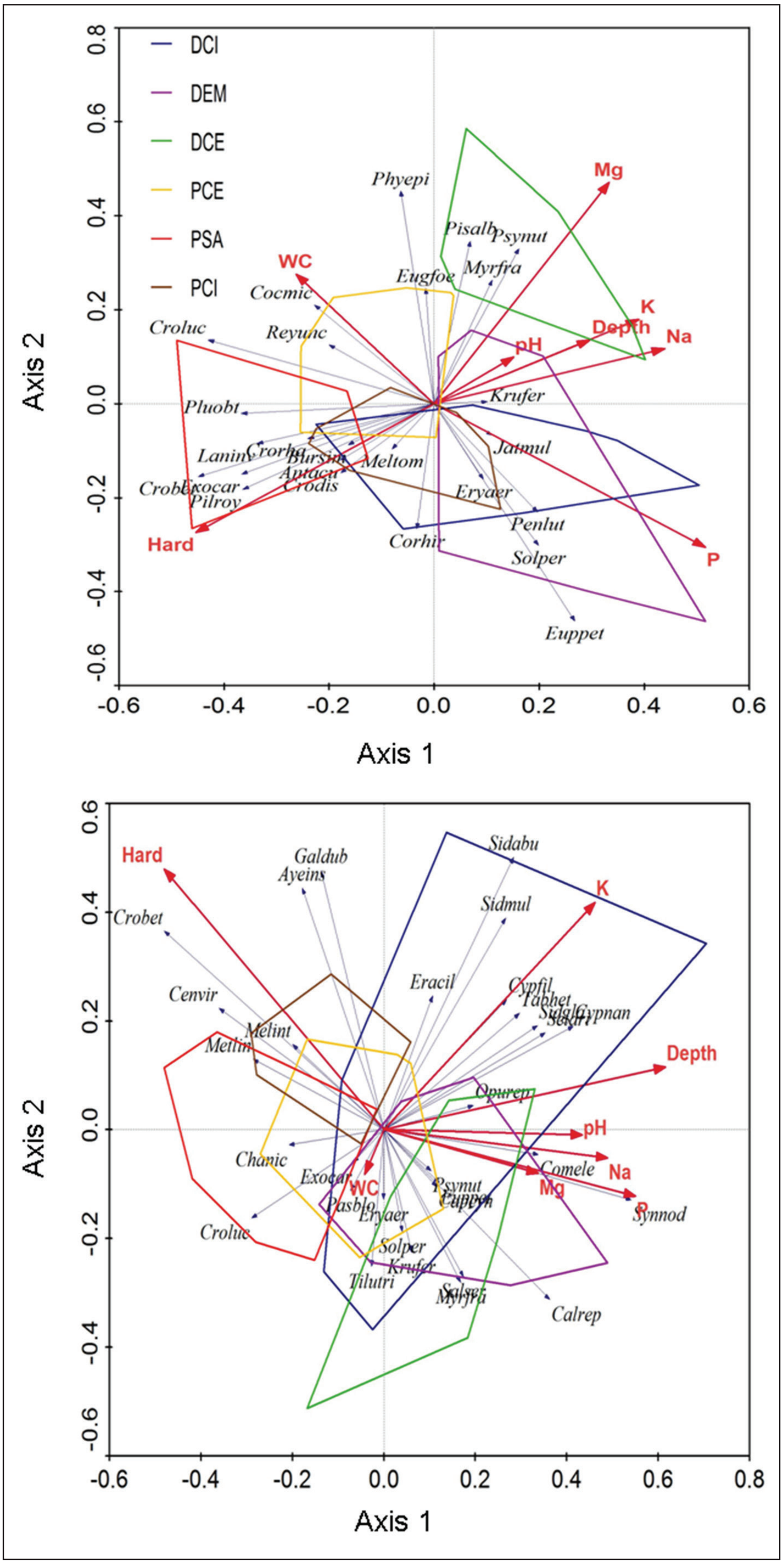

Figure 4. RCA ordination including vegetation data and soil variables. (A) Upper panel corresponds to canopy layer; (B) Lower panel corresponds to understory layer. Polygon shapes represent the boundaries of the clusters made by the arrangement of scores for vegetation–soil variables for the 6 different forest sites with respect to the first 2 ordination axes for the canopy and understory layers. Species and soil variables are indicated by arrows.

the understory layer, the cumulative variance in the species–soil variables explained by axis 1 and 2 was 30% and 50.2%, respectively. The canopy at the depression site DEM and the plateau site PSA showed little or no overlap with the remaining sites. In contrast, the understory layer at all sites showed some degree of overlap with each other. Linear regression tests of plant abundance for individual species as a function of variation in axis 1 (that resulted from the species–environment ordination) yielded significant results for 56% (14 of 25) and 61% (19 of 31) of the species from canopy and understory layers, respectively (Table 1). However, we did not detect response patterns that could be attributed to plant-growth form or taxonomic origin (Table1).

Discussion

Vegetation variables

Our results did not support the hypothesis that plateau and depression forests were distinct forest types on the basis of vegetation complexity (plant diversity, species density, and plant density) or composition (species composition and plant growth forms). For the 2 forest strata analyzed (canopy and understory), we found that most differences in vegetation complexity and composition were attributed to differences among sites rather than to differences among forest types as they were previously characterized by Mona Island's original surveys (Cintrón and Rogers 1991) and remote sensing approaches (Martinuzzi et al. 2008). The lack of distinct differences between these 2 forest types in species composition and diversity is particularly evident for the understory layer, where sites within each forest type showed high heterogeneity and, independent of their a priori classification, sites were considerably similar in vegetation complexity and composition.

The lack of vegetation differences between depression and plateau forests based on the parameters employed may be the result of several mechanistic hypotheses. For example, a number of researchers have suggested that feral ungulates (goats and pigs) are changing the vegetation on Mona Island (Cintrón 1991, García et al. 2000, Meléndez-Ackerman et al. 2008). Indeed, because of their impact on native biota manifested through changes in vegetation composition, biodiversity loss, and ecosystem degradation, feral ungulates are considered serious pests in many insular systems where they have been introduced (Cabin et al. 2000, Campbell and Donlan 2005, Coblentz 1978, Lowney et al. 2005). Thus, one hypothesis is that depression forests were considerably different in composition when they were first described (Cintrón and Rogers 1991), but herbivore-driven vegetation changes have occurred since which have homogenized different vegetation types. Our results regarding the dominant species across forest types indicate that tree species are not necessarily more numerous at depression sites relative to plateau sites as we expected; shrub species are equally diverse across forest sites. Alternative hypotheses (not mutually exclusive) may also explain the lack of current vegetation differences between depression and plateau forest sites. The Caribbean region where Mona Island occurs is frequently impacted by large tropical storms and hurricanes. In 1998, five years before this study, the Hurricane Georges, a category-3 storm, hit Mona Island with sustained winds of 185–193 km/h and gusts up to 240 km/h (Geerts et al. 2002). Hurricanes, as large-scale disturbances, are known to cause considerable short-term changes in vegetation structure within Caribbean forests (Lugo 2000), and some of these changes in vegetation structure and composition may be related to post-hurricane effects. Another hypothesis that may explain patterns of vegetation composition for depression and plateau forests on this island is that vegetation is intrinsically highly heterogeneous due to processes that manifest at different, potentially site-specific, spatial and temporal scales. For example, among depression forest sites, DCE was very different from the DEM and DCI in that it had the greatest number of plant species and the deepest soils. The DCE site is a sinkhole that presumably resulted from the wearing down of bedrock that is relatively thin at this site, while the DCI and DEM sites formed as a result of a lateral displacement of 2 bedrock plates along a major fault running across Mona Island (Frank et al. 1998). It is possible that the formation of DCE occurred more quickly and abruptly than the formation of the other 2 forest sites, leaving DCE relatively isolated from the remaining vegetation occurring in the rest of the limestone platform. In addition to the possibility of these geological processes playing a role in vegetation distribution, the occurrence of forested areas classified as depression forests may have been highly underestimated in previous studies (Cintrón and Rogers 1991, Martinuzzi et al. 2008) by excluding small-sized forested sinkholes across the island's platform. Perotto-Baldivieso and collaborators (2009) used high-resolution remote-sensing techniques to evaluate the distribution of forested sinkholes on Mona Island and showed, mainly through the inclusion of small-sized forested sinkholes (~5 m^2) that occur all over the island's platform, that depression-forest cover was larger than previously estimated. Under this scenario, areas classified as plateau-forest sites are likely to be a combinations of open- and closed-canopy vegetation influenced by the presence of small forested sinkholes. Significant site × forest-type interaction effects in soil hardness and a significant site effect in soil depth (both variables related to the presence and absence of sinkholes, see below) are consistent with this hypothesis.

Soil variables

In attempting to make cross-site comparisons regarding soil quality, one limitation is the different ways in which values for soil nutrients have been reported across studies. We were able to make some comparisons. Several soil parameters of Mona Island soils were consistent in many ways with soil parameters previously analyzed in subtropical dry forests associated with limestone bedrocks. For example, regardless of forest type, Mona Island soils were slightly basic and within the range of values previously reported for Guánica (pH = 7.8–7.9; Lugo and Murphy 1986, Wolfe and Van Bloem 2012), Yucatán (pH = 7.3–7.4; Solís and Campo 2004), and the Florida Keys (pH >7.0; Ross et al. 2003). As expected, Ca levels were also high and consistent with the variability exhibited in subtropical dry forest soils with reported limestone-based mineralogy (i.e., Ca values in Guánica = 4.7–85.26 mg/g; Murphy and Lugo 1986, Wolfe and Van Bloem 2012). Total P content of Mona Island soils tended to be higher than those reported in a number of subtropical dry forests regardless of their mineralogy. For example, P content of limestone-based soils was reported as 0.57–3.29 mg/g in Guánica (Lugo and Murphy 1986, Wolfe and Van Bloem 2012) and 1.7–2.9 mg/g in Yucatán (Solís and Campos 2004). In the volcanic soilsof St. Lucia, P content was 0.0002–0.00598 mg/g (González and Zak 1994). One possible explanation for these results is related to the potential effects of feral ungulates that return nutrients to the soil via their feces and are very common on Mona Island but not necessarily at other sites.

When we considered soil parameters, we found that there was not a clear separation between depression and plateau forests in terms of soil parameters except for P content, which consistently exhibited higher values at depression-forest sites. Even when depression-forest sites had deeper and less compacted soils, these variables as well as many others related to chemical composition showed highly significant site or site × forest-type interaction effects. The combined results suggest that Mona Island soils are highly heterogeneous and that it is difficult to separate these areas based on soil parameters alone except for soil P. In the past, it has been hypothesized that wildlife might be more attracted to depression forests which are commonly thought to be more productive and shadier than plateau forests (Cintrón 1991). Thus, the hypothesis that soils at these sites are nutrient-enriched via wildlife activities could be tested experimentally by comparing soil variables between ungulate-excluded and non-excluded areas within each of the forest sites.

Even when soil–vegetation associations did not manifest at the forest-type scale using current vegetation classification schemes, our data showed that on a finer scale, plant abundance and richness were related to a subset of soil variables but also that these associations had manifested differently in the canopy and understory vegetation layers. Variation in species richness and abundance in the canopy layer were both associated with a larger number of soil properties than in the understory layer where they were only associated with K and Mg. It should be noted that K, an important nutrient for plant production, was consistently associated with all vegetation variables regardless of forest stratum. The observed negative association between Mg concentrations with species richness and plant abundance is interesting in light of the fact that in calcareous alkaline soils Mg content is limited by the availability of competing ions such as Ca and K (Mayland and Wilkinson 1989). We discarded the possibility of Mg toxicity resulting from the dolomitic nature of Mona Island's limestone because Mg toxicity in plants is rare and only occurs when Ca/Mg ratios in soils fall below 1 (Bing et al. 2011), which was never the case at our study sites (Table 1). One possibility is that the negative association between Mg and vegetation variables merely relates to how Mg interacts in the presence of K. It is well known that factors that promote K uptake by roots also inhibit Mg translocation by plant roots (Mayland and Wilkinson 1989).

The fact that more soil variables exhibited associations with plant abundance and richness in the canopy layer suggests that any influence soil variables have on plant function are likely to be more relevant at later successional stages and not necessarily or perhaps less relevant at the colonization stage (or early successional stages). If so, plant dispersal on a per species basis would appear to be less limited by micro-sites on Mona Island than in other subtropical dry forests. The observed high degree of overlap in species composition among sites (regardless of forest type) at the understory layer certainly supports this hypothesis, but our results cannot rule out the possibility that the vegetation also influenced soil parameters as has been demonstrated in prior studies (Townsend et al. 2008, Wardel et al. 2004). Our results confirm the role of mineral nutrition, soil hardness, and soil-water content in the limitation of species distribution on Mona Island. In our study, variation in cations (mainly K and Mg), phosphorus, and soil hardness was more important than variation in water content regardless of forest layer. In water-limited environments, mature individuals of different species may exhibit various mechanisms of obtaining and storing soil water (Jackson et al. 1999), which may in turn weaken the association of plant-species distribution and soil-water content. We expected water-content relationships to be stronger in the understory layer where seedlings reside than in the canopy layer, but that was not the case. Our results suggest that P rather than N is a limiting factor in this forest. There were strong positive relationships between P variation and species distributions in both forest layers. We did not observe this pattern with N variation, but it is consistent with studies of tropical dry forests that have suggested a larger role of P over N limitation in these ecosystems (Ceccon et al. 2003, 2006; Gould et al. 2006).

Conclusion

Depression forests on Mona Island have been considered a critical habitat for the conservation of the endangered Mona Island Iguana; Haneke 1995). Therefore, the study of these habitats has become a priority to facilitate long-term monitoring and management. Although our study failed to find robust diagnostic traits in terms of soil and vegetation variables (i.e., those related to species composition and diversity), we cannot rule out that other parameters related to ecosystem function (i.e., productivity and canopy cover) may indeed be diagnostic for this forest type. Our data also show that depression forests on Mona Island are highly heterogeneous, highlighting the importance of determining if this heterogeneity represents the baseline-state for depression forests, or if this condition is the result of ongoing processes that may be altering them. In that regard, we suggest that long-term monitoring and experimental studies, as well as feral-ungulate exclusion experiments should be carried out to evaluate how dynamic these systems are and to clarify the underlying drivers of forest change at these sites.

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