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PHYTOGEOGRAPHICAL TRENDS, CENTERS OF HIGH SPECIES RICHNESS AND ENDEMISM, AND THE QUESTION OF EXTINCTIONS IN THE NATIVE FLORA OF PUERTO RICO

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AS LIVING INTEGRAL components of the landscape, native plants are subject to all of the natural forces that shape, influence, and characterize any given geographical area. Particularities of each taxon's autecology will determine the extent of its geographic distribution and impose limits as to the diversity of ecosystems within which it may occur. These factors will also determine the relative density, frequency, and "importance" each species can achieve within its range of distribution. Significant and prolonged shifts in the prevailing climatic conditions[1] or catastrophic events[2,3] can impose lasting effects on an area and its floristic identity, but the natural vegetation cover will simply evolve in structure and composition to accommodate these. However, anthropogenic modifications to the landscape can radically affect factors that determine the permanence of natural vegetation cover, and in some cases can extirpate a local flora altogether.

The physical geography and native flora of Puerto Rico and the U.S. Virgin Islands are among the most thoroughly explored and studied in the Caribbean Region. This statement, while frequently made and widely accepted, necessarily requires two fundamental caveats. The first is that while it is true that the island's native wildlife and plants have been extensively studied, the bulk of this work, particularly for plants, is confined to the past eighty years.[4] The second caveat concerns the fact that by the time the island became the object of sustained and systematic scientific exploration and research, forest cover had been reduced to less than 10% of the total land area and mature natural vegetation covered less than 1%.[5,6]

This paper examines the current state of the native flora of Puerto Rico vis-à-vis changes encountered in systematic floras published 60 years apart.[7,8] Specifically, what species characterize the native flora of Puerto Rico?, where are the island's centers of high plant species richness and en-

demism located?, which native species are presently most rare and endangered?, and have any extinctions occurred in the native flora?

METHODS

An attempt was made to assess changes in the island's flora between the publishing of Britton and Wilson's flora[7] and Liogier and Martorell's reassessment.[8] In order to compare both inventories, a working list of all of the species documented in Liogier and Martorell[8] was prepared. After eliminating all species that did not include Puerto Rico within their natural range of distribution, a new list of just native species resulted. This list of 2410 native species was then checked against the native species reported earlier by Britton and Wilson.[7]

Within the particular constraints that the history of the study of the flora of Puerto Rico presents (see below) an attempt was made to assess the extinction of species on the island. Careful examination was made of the descriptions presented by Britton and Wilson[7] in order to identify those species that at that time were of very limited range. Britton and Wilson[7] reported a number of native plant species as described for the island by Urban[9] but that were not seen by them during their explorations. When Liogier and Martorell[8] reassessed the flora, they reported 15 of these species as still unseen. In order to ascertain the present status of these species local herbariums were visited (DNRA, UPR-Botanical Garden) as well as collections at the National Herbarium in Washington, D.C. and the New York Botanical Garden. Local experts were interviewed and fieldtrips made to areas mentioned in the herbarium vouchers for these species.

The voluminous and detailed unpublished fieldnotes compiled by taxonomist Roy O. Woodbury on the forests of Puerto Rico between 1955–1983 were used to identify centers of high plant diversity and endemism on the island. In addition to Woodbury's data, other local plant experts were consulted and their data utilized.

Because of their determining influence on the structure and composition of forested ecosystems, it was decided that only trees would be used in the analysis of chorological affinities between prominent centers of high species richness. The distribution of tree species endemic to Puerto Rico was determined and similarity between regions assessed with the use of Sorensen's Similarity Index.[10]

RESULTS

The Native Flora of Puerto Rico

Though he never physically visited Puerto Rico, remaining instead in Hispaniola, the first to make mention of the flora of the island was Fernandez de Oviedo in his book ***Historia general y natural de las Indias, Islas y Tierra Firme del Mar Oceano.*** Initially published in abridged form in 1535 (finally edited and printed in its entirety between 1851 and 1855) this wide ranging work was made up of fifty parts, five of which were dedicated to the description of native trees and medicinal plants from the islands (Liogier, this volume). Puerto Rico received visits from many prominent foreign botanists

over the next three centuries who made collections that remain in herbaria throughout Europe.[4,11] However, it wasn't until Agustin Stahl, a Puerto Rican doctor born in Aguadilla, started publishing his *Estudios sobre la Flora de Puerto Rico* in 1883, that the plants of the island were studied in earnest.[12] Stahl's seminal work notwithstanding, *Flora Portoricensis* published from 1903 to 1911 by the German botanist Ignatius Urban remains the first systematic accounting of the native flora of Puerto Rico. Shortly thereafter Britton and Wilson's *Botany of Porto Rico and the Virgin Islands*, drawing heavily on Urban's work but adding years of intensive fieldwork, came to crystalize what was known concerning the flora of the islands. An additional fifty years later Liogier and Martorell[8] produced a checklist that reviewed nomenclature, included new additions, and updated distributions for Britton and Wilson's flora. Recent updates have also been produced on specific groups of plants.[13–15]

A comparison of these two works produced some 60 years apart was performed. In spite of the considerable differences in infrastructure and logistics, not to mention the intensive fieldwork carried out by numerous botanists on the island since the 1950s, particularly the work of E. Little (USDA-FS) and R. O. Woodbury (UPR), the thoroughness of Britton and Wilson's work[7] is remarkable. Sixty years of specialized prospecting and increased accessibility to the most remote recesses of the vegetation of the island had added only 297 native species to their flora by 1982.

In light of the above, the basis of what is known on the composition and distribution of the native flora of Puerto Rico,[7] was produced at a time when the vegetation of the islands had undergone some 400 years of modification. Unlike the other islands in the Greater Antilles which received early concentrated studies of their floras (*Hispaniola*: Plumier 1680; *Jamaica*: Sloane 1696, 1707, 1725; *Cuba*: Grisebach 1860; in Liogier[11]), the vegetation of Puerto Rico was described in detail at a time when forests covered less than 10% of the island, and its mature, natural vegetation had been reduced to less than 1%.[5,6] Presently secondary forests of differing ages and composition cover more than 30% of the island's total land area[16] as testimony to the value of these isolated pockets of natural vegetation as sources of propagation.

TABLE 1 summarizes characteristics of the Greater Antilles and their native floras. The floras of the larger islands of Cuba and Hispaniola are remarkably rich and diverse when compared to the smaller Jamaica and Puerto Rico. Yet,

TABLE 1 Relationships between Native Floras of Islands that Make up the Greater Antilles

Island	Area (km^2 x 1000)	Species	% Endemic	Source
Cuba	114.9	6375	49.9	Borhidi 1991[24]
Hispaniola	76.2	5000	36.0	Toledo 1985[26]
Jamaica	10.9	3003	26.1	Toledo 1985[26]
Puerto Rico	8.9	2410	9.9	Liogier and Martorell 1982[8]

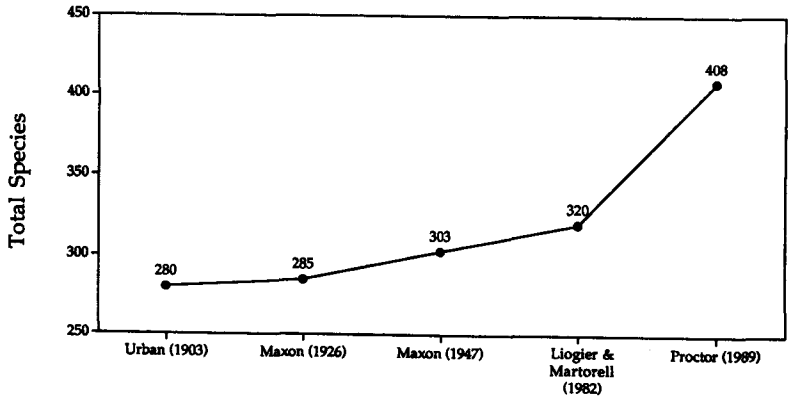

FIGURE 1 Totals for pteridophytic flora of Puerto Rico and the U.S. Virgin Islands.

though close in total land area, Jamaica and Puerto Rico show almost threefold differences in total endemism. While Jamaica contains topographical and climatological extremes (mainly in the way of higher, wetter summits) not present in Puerto Rico,[17] these alone would not seem to account for such a wide difference in endemism. Is this seemingly incongruent disparity in endemism related to a differential loss of species due to extinction or simply a measure of thoroughness in what is known of the islands' respective floras? For example, 47 endemic plant species had been added to the total flora for Jamaica in the ten years following Adams'[17] assessment.[18] Comparatively, considering only the pteridophytes of Puerto Rico, 88 new native species were added in the seven years that followed Liogier and Martorell (FIG. 1). In fact, 13 endemic pteridophytes have been described since 1984.[13]

Centers of High Species Richness and Endemism

Considering that the young secondary forests that presently cover over a third of the island of Puerto Rico[16] have depended in great part on propagules from the few isolated pockets of mature natural vegetation that survived the wide deforestation suffered on the island, then these 'refuges' must be areas of comparably higher species richness and endemism. TABLE 2 (see FIG. 2) summarizes a review of localized species counts that identify those areas on the island that have uncommonly high total numbers of plant species and endemics.

The distribution of these areas (FIG. 2) shows a major region of high plant diversity which coincides with the montane areas of the volcanic interior of the island. High plant species richness centers are also associated with nonmontane sites within the limestone regions of the north and south coasts. Ultramafic substrates under different climatic regimes (TABLE 2) as well as 'white sand' areas along the north coast also harbor distinctive plant assemblages.

The distribution of endemics in Puerto Rico shows additional relevance when one specifically studies the distribution of endemic tree species on the

TABLE 2 Centers of High Species Richness and/or Endemism in Puerto Rico

Site	Community Type	Maximum Elevation (m)	Mean Annual Precipitation (mm)	Substrate	Species Richness
1 Luquillo Mts.	Lower and upper montane forests	1074	3500	Volcanic	830 spp/ >250 tree spp
2 Cayey Mts.	Lower and upper montane forests	900	2800	Volcanic	—
3 Las Tetas	Upper montane thicket	860	2000	Volcanic	314 spp in top 50 m
4 Torrecilla	Upper montane forest	950	2200	Volcanic	—
5 Toro Negro	Lower and upper montane forests	1340	2800	Volcanic	381 spp/ 100 trees
6 Guilarte-Membrillo	Lower and upper montane forests	1200	2200	Volcanic	—
7 Maricao	Lower and upper montane forests	900	2600	Ultramafic	845 spp/ 278 trees
8 Susua	Moist and dry forests	470	1400	Ultramafic	200 + spp
9 Sierra Bermeja	Dry forest	330	500	Ultramafic	167 spp
10 Guanica	Dry forest	230	600	Calcareous	657 spp
11 Guajataca	Moist forest	200	1500	Calcareous	488 spp/ 207 trees
12 Sabana Hoyos	Moist forest	300	1800	Calcareous	495 spp/ 188 trees
13 Ciales	Moist forest	400	2000	Calcareous	—

Figures for species richness are from unpublished data provided by R. Woodbury and G. Proctor. Site numbers correspond to those used in FIGURE 2 of this paper.

island. Trees make up 61% of the total 232 plant species endemic to Puerto Rico. Using distributional information provided in Little and Wadsworth[19] and Little et al.[20] the occurrence of these species was studied and summarized in TABLE 3. The distribution of endemic tree species in Puerto Rico shows a distinct predominance in montane sites. Better than two thirds (67%) of all endemic tree species for the island occur in montane habitats.

The chorology of endemic tree species shows trends and affinities that further accentuate the role of montane habitats. FIGURE 3 is a graphic representation of the regional distribution of endemic tree species for Puerto Rico. The highest numbers of endemic tree species occur in the montane habitats of the Luquillo Mountains in the northeast, and in the Central Mountains. Montane areas of the Cayey Mountains in the southeast and Maricao in the west,

FIGURE 2 Distribution of centers of high species richness and/or endemism in Puerto Rico. Shaded area represents forest lands (Little et al. 1974,[19] p. 25). Bold outline within map represents continuous mountainous areas. Chorological centers are represented by spheroids (volcanic substrate), and triangles (non-volcanic substrates). Arrows show gradients of decreasing species richness. **Key to locale numbers**: (1) Luquillo Mountains, (2) Cayey Mountains, (3) Las Tetas, (4) Cerro Torrecilla, (5) Toro Negro, (6) Guilarte/Membrillo, (7) Maricao Mountains, (8) Susua, (9) Sierra Bermeja, (10) Guanica, (11) Guajataca, (12) Sabana Hoyos, (13) Ciales.

TABLE 3 Geographical Distribution of Endemic Tree Species of Puerto Rico

	Geographical Region										
	1	2	3	4	5	6	7	8	9	10	11
Total species	67	52	40	44	22	32	19	10	18	14	2
(percent)	(48)	(37)	(28)	(31)	(16)	(23)	(13)	(7)	(13)	(10)	(–)

Geographical regions are: (1) Luquillo Mountains, (2) Central Mountains, (3) Cayey Mountains, (4) Wet Ultramafic–Maricao, (5) Wet Limestone–Rio Abajo, (6) Northern Moist Limestone Hills, (7) Moist Ultramafic–Susua, (8) Moist Volcanic, (9) Dry Limestone–Guanica, (10) Dry Volcanic, (11) Dry Ultramafic–Sierra Bermeja.

however, harbor total endemic tree species numbers more in accordance with the northern moist limestone hills. The interior lowlands exhibit comparatively lower totals of regional endemic tree species. The lowest values for the island are unsurprisingly associated with younger coastal alluvial deposits.

TABLE 4 presents a tabulation of the chorological distribution of the endemic tree species of Puerto Rico and affinities between them. The highest totals for endemic tree species are found in the Luquillo and Central Mountains. The Luquillo Mountains alone contain close (48%) to half of all endemic tree species known on the island. In spite of a general trend of species richness that increases along a humidity gradient within substrates, moist limestone had a higher total than wet limestone. This inconsistency with the general trend may be a reflection of the limited area of wet limestone vis-à-vis moist limestone, as well as a higher affinity for 'dry' species within the moist limestone. When compared by substrate, means for total endemic tree species are: volcanic(36) > limestone(26) > ultramafic(22). The mean for the 4 montane regions (51) is three times the mean (17) of the 7 non-montane regions.

The highest similarity values are all within the 'wet' montane habitats. Though the Luquillo Mountains and the Central Mountains contain the highest number of endemic tree species, both show higher similarity indices with the Cayey Mountains than with each other perhaps due to its geographical location between the two. The limestone regions show a greater affinity of endemic tree species with the ultramafic sites than with the volcanic sites, possibly reflective of the similarity in the physical characteristics of these soil types. In general, there is a clear trend of similarity that follows the humidity gradient: wet > moist > dry.

Extinctions in the Flora of Puerto Rico

Various factors assist in identifying species lost from a regional flora due to extinction. Some of these would include: taxonomical certainty; documented evidence that the species occurred in the region; and, recent, or at least successive surveys of the region. In the particular case of Puerto Rico all three considerations mentioned above are restricted to data from the past ninety years. Therefore, any evaluation of the island's loss of plant species to extinction must be tempered by the very plausible concern that estimates

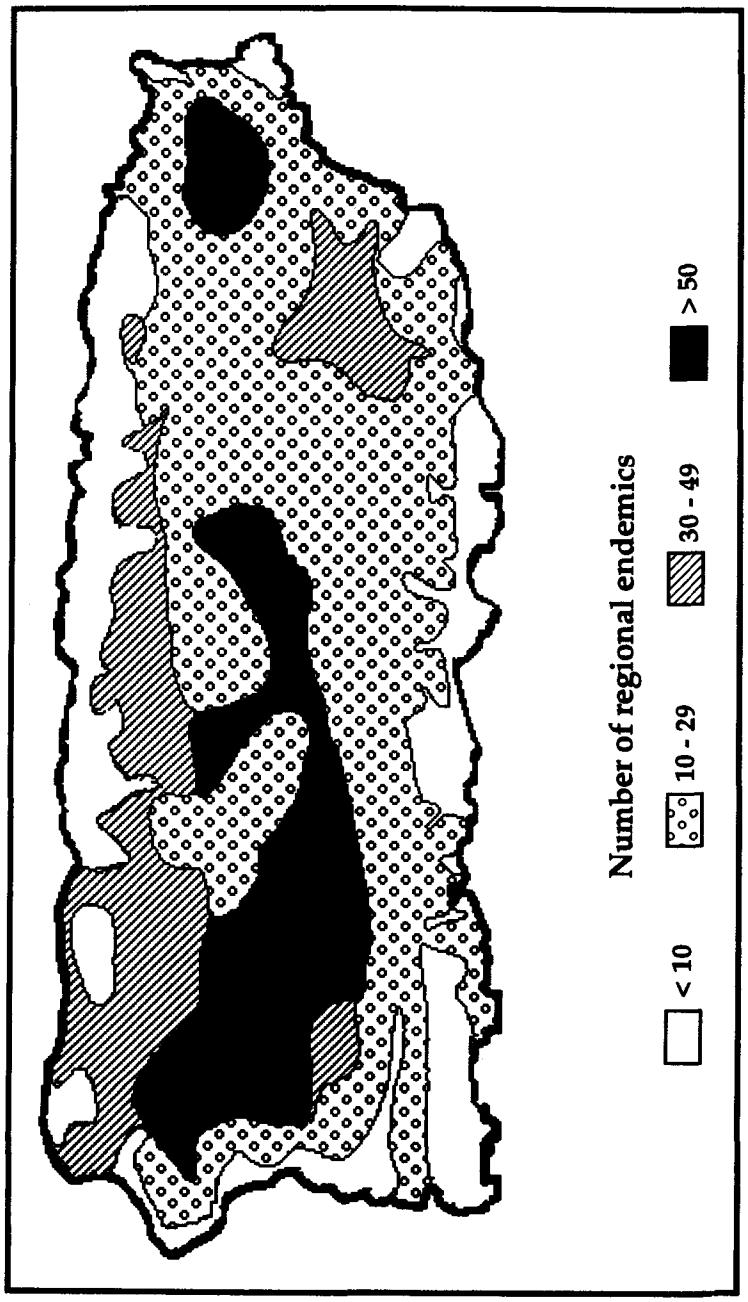

FIGURE 3 Geographical distribution of endemic tree species in Puerto Rico.

TABLE 4 Tabulation of Chorological Relationships within the Distribution of the 141 Tree Species Endemic to Puerto Rico

Geographical Regions	1	2	3	4	5	6	7	8	9	10	11
1	67	38	37	24	8	2	2	–	–	–	–
2	64	52	32	29	8	1	2	1	–	–	–
3	69	70	40	20	7	1	1	–	–	–	–
4	43	60	48	44	10	6	12	2	2	–	–
5	18	22	23	30	22	10	3	3	1	–	–
6	4	2	3	16	37	32	7	4	6	2	–
7	5	6	3	38	15	27	19	2	5	2	–
8	–	3	–	7	19	19	14	10	1	3	–
9	–	–	–	6	5	24	27	7	18	6	1
10	–	–	–	–	–	9	12	25	38	14	1
11	–	–	–	–	–	–	–	–	10	13	2

Column and row numbers refer to geographical regions: (1) Luquillo Mountains, (2) Central Mountains, (3) Cayey Mountains, (4) Wet Ultramafic–Maricao, (5) Wet Limestone–Rio Abajo, (6) Northern Moist Limestone Hills, (7) Moist Ultramafic–Susua, (8) Moist Volcanic, (9) Dry Limestone–Guanica, (10) Dry Volcanic, (11) Dry Ultramafic–Sierra Bermeja. Diagonal of underlined numbers represents totals for each region. Numbers within the matrix half to the right of the diagonal of regional totals represent total species in common between any two regions (w). Numbers within the matrix half to the left of the diagonal of species totals represent similarities indices (in percent), as per the equation: <s.i. = $(2w/a+b) \times 100$; where 'w' represents species in common between any two regions, and 'a' and 'b' represent total species for each of the regions.

based on available documentation are very likely underestimates of some degree.

Of those species Liogier and Martorell[8] reported as unknown, 8 have been collected in recent times (TABLE 5). Of the remaining 7 species, only 2 reach small tree size, and one of these (*Graffenrieda ottoschultzii* Urban and Ekman) is very doubtful as a bona fide species. Recent experience with other species also point to caution when writing off species to extinction. The West Indian walnut (*Juglans jamaicensis* C.DC.) was long considered lost from the island until relocated in the Central Mountains. Field work in the Luquillo Mountains in recent years has also changed the status of various species such as *Callicarpa ampla* Schauer, *Coccoloba rugosa* Desf., and *Styrax portoricensis* Krug and Urban to just name a few. In fact, *Styrax portoricensis* was long considered extinct and its 'rediscovery' won one fieldworker the American Horticultural Society's Wildlife Discovery Award for 1984. New, intensive surveys of natural areas will continue to turn up new distributional records for the island (e.g., *Samolus parviflorus* and *Nashia inaguensis*, both recent new records for Puerto Rico; J. Francis and G. Proctor, personal communication), and to a lesser degree, even some new species.

In spite of the above, all is not necessarily well with those species considered rare and endangered in Puerto Rico. TABLE 6 contains a list of those native species presently known to occur from only one locality on the island. Of the 30 species listed, 21 are endemic to the island and thus present a true risk of extinction. In fact, 47% of all species endemic to Puerto Rico are known to occur in three localities or less.[21]

TABLE 5 Rare and Endangered Species of Puerto Rico and the U.S. Virgin Islands Reported by Liogier and Martorell (1982) as Not Observed in Recent Times

Species	Family	Comments
Brachionidium ciliolatum	Orchidaceae	Epiphytic orchid; known only from type specimen collected in 1969
Caesalpinia portoricensis	Fabaceae	Woody vine; known only from type specimen collected in 1915
Catesbaea melanocarpa	Rubiaceae	Small tree; not reported in Puerto Rico since 1886; reported recently (1988) from St. Croix
Clidemia polystachya	Melastomataceae	Small tree; known only from type specimen collected by Plee (1822)
Cordia rupicola	Boraginaceae	Small tree; collections exist from Ensenada (1959), Guayanilla (1972), and recently Ponce (G. Breckon, personal communication)
Cordia wagnerorum	Boraginaceae	Shrub; collected in El Yunque (1966)
Cyperus urbanii	Cyperaceae	Sedge; collected in Coamo (1966) and Guanica (1979)
Dendropemon sintenisii	Loranthaceae	Epiphytic mistletoe; only known from the original collection in 1885
Graffenrieda ottoschulzii	Melastomataceae	Small tree; sterile specimen described from Inabon; doubtful sp, probably *Miconia pyrifolia* (J. Wurdack, personal communication)
Ipomoea krugii	Convolvulaceae	Herbaceous vine; not collected since 1882 near Mayagüez
Ossaea scabrosa	Melastomataceae	Shrub; collected in Maricao (1966) and Rio Abajo (1983)
Peperomia megalopoda	Piperaceae	Epiphytic herb; known only from type locality, not collected since 1929
Pilea leptophylla	Urticaceae	Herb; collected in Pandura (1975)
Sida eggersii	Malvaceae	Small tree; not collected since 1916 in Culebra
Solanum conocarpum	Solanaceae	Shrub; collected recently in St. John (P. Acevedo, personal communication)

DISCUSSION AND CONCLUSIONS

What components of the natural vegetation of the island may have been inexorably lost to the wide deforestation the island suffered may never be known. The West Indies have one of the highest concentrations of endemism of any phytogeographic region in the Neotropics.[22] Yet, Puerto Rico has an island plant endemism component that is three times less than that of Jamaica,

TABLE 6 Rare and Endangered Plant Species from Puerto Rico and the U.S. Virgin Islands Known from Only One Locality

Species	Family	Life Form	Habitat
Adiantum vivesii Proctor	Adiantaceae	Fern	Moist limestone
Aristida chaseae Hitchc.	Poaceae	Grass	Dry volcanic
Aristida portoricensis Pilger	Poaceae	Grass	Dry volcanic
Auerodendron pauciflorum Alain	Rhamnaceae	Small tree	Moist limestone
Brachionidium ciliolatum Garay	Orchidaceae	Epiphyte	Wet volcanic
Caesalpinia portoricensis Alain	Fabaceae	Woody vine	Dry limestone
Calyptranthes estremerae Alain	Myrtaceae	Small tree	Moist limestone
Catesbaea melanocarpa Krug and Urban	Rubiaceae	Small tree	Dry limestone
Chamaesyce orbifolia Alain	Euphorbiaceae	Herb	Dry limestone
Clidemia polystachya (Naud.) Cogn.	Melastomataceae	Small tree	—
Coccoloba pallida C.WR. in Griseb.	Polygonaceae	Small tree	Moist limestone
Coccoloba tenuifolia L.	Polygonaceae	Small tree	Moist limestone
Cordia bellonis Urban	Boraginaceae	Shrub	Wet ultramatic
Dendropemon sintenisii Krug and Urban	Loranthaceae	Epiphyte	Moist volcanic
Elaphoglossum serpens Maxon	Polypodiaceae	Fern	Wet volcanic
Eugenia bellonis Britton	Myrtaceae	Small tree	Dry volcanic
Eupatorium droserolepis Robinson	Compositae	Shrub	Wet volcanic
Forchhammeria polystachya Cogn.	Capparidaceae	Small tree	Moist limestone
Heliotropium guanicense Urban	Boraginaceae	Shrub	Dry limestone
Leptocereus gratianus Britton	Cactaceae	Small tree	Dry volcanic
Lyonia truncata var. *proctorii* J.	Ericaceae	Shrub	Dry volcanic
Mitracarpus maxwelliae Brit. and Wils.	Rubiaceae	Shrub	Dry limestone
Myrcia maricaoensis Alain	Myrtaceae	Small tree	Wet ultramatic
Opuntia borinquensis Brit. and Rose	Cactaceae	Cactus	Dry limestone
Panicum stevensianum Hitchc. and Rose	Poaceae	Grass	Moist volcanic
Pseudophoenix sargentii ssp. saona	Palmaceae	Small tree	Dry limestone
Scleria doradoensis Britton	Cyperaceae	Sedge	Moist volcanic
Tectaria estremerae Proctor and Evans	Aspleniaceae	Fern	Moist limestone
Thelypteris inabonensis Proctor	Thelypteridaceae	Fern	Wet volcanic
Vernonia proctori Urbatch	Compositae	Shrub	Dry volcanic

its closest counterpart in size (TABLE 1). Of the more than 3100 species documented in Liogier and Martorell's[8] checklist of the flora of Puerto Rico, only 2410 are actually native to the island. In the 52 years between the completed publishing of Britton and Wilson's flora[7] for the island and Liogier and Martorell reassessment[8] a total of 297 native species were added for the island. Yet, by the same token, the pterophytic flora native to the island increased by almost 100 species in a period of 7 years within the past decade (FIG. 1).

The island of Puerto Rico contains numerous centers of high species richness and endemism. Though some of these centers are associated with calcareous and ultramafic substrates, the majority of these sites occur within the montane volcanic interior of the island. In addition, when the distribution of endemic trees is examined it results that better than 67% of these are limited to montane habitats. The highest concentrations of endemic trees are found in the wetter montane habitats of the eastern and central mountain ranges. These montane habitats have provided stable environments long enough for the evolution of distinct paired species. Various pairs of closely related endemic species in the genera *Magnolia*, *Symplocos*, *Tabebuia*, and *Eugenia* occur with geographically disjunct distributions on eastern and western mountain ranges suggesting the long stability of these sites.[23] The role of these montane remnants as relicts of climatic extremes during the Pleistocene remains to be studied in detail on the island. Montane habitats characterized by less total rainfall in the southeast and western regions of the island have totals closer to those of the moist limestone hills of the north. The low concentrations of endemic species in the dry habitats of the island is not consistent with that of other islands in the West Indies.[23] While this could be a measure of disturbance of the dry coastal areas of the island, it could also very well point to the instability of these mainly calcareous areas during periods of sea level fluctuations.[25]

Because of a lack of long-term documentation on the native flora of Puerto Rico, the level of plant extinctions that may have occurred is difficult to assess. Inferences based on widespread and extreme modification of the natural landscape, relatively low numbers of dry habitat endemics, and disproportionate relative total endemism when compared to other Antillean islands, suggest that perhaps many species were lost (particularly endemics) before proper documentation occurred. On the other hand, examples of evolutionary disjunction in various species, and the rediscovery of numerous 'lost' species in recent times suggest additional complexity. Continued research in areas such as paleobotany, and the evolutionary taxonomy of 'paired' endemics are needed to provide much needed documentation towards the understanding of island plant population dynamics, particularly as these reflect resiliency to disturbance and forest fragmentation.

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