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LAND USE HISTORY, ENVIRONMENT, AND TREE COMPOSITION IN A TROPICAL FOREST

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Abstract. The effects of historical land use on tropical forest must be examined to understand present forest characteristics and to plan conservation strategies. We compared the effects of past land use, topography, soil type, and other environmental variables on tree species composition in a subtropical wet forest in the Luquillo Mountains, Puerto Rico. The study involved stems $\geq$10 cm diameter measured at 130 cm above the ground, within the 16-ha Luquillo Forest Dynamics Plot (LFDP), and represents the forest at the time Hurricane Hugo struck in 1989. Topography in the plot is rugged, and soils are variable. Historical documents and local residents described past land uses such as clear-felling and selective logging followed by farming, fruit and coffee production, and timber stand improvement in the forest area that now includes the LFDP. These uses ceased 40–60 yr before the study, but their impacts could be differentiated by percent canopy cover seen in aerial photographs from 1936. Using these photographs, we defined four historic cover classes within the LFDP. These ranged from cover class 1, the least tree-covered area in 1936, to cover class 4, with the least intensive historic land use (selective logging and timber stand improvement). In 1989, cover class 1 had the lowest stem density and proportion of large stems, whereas cover class 4 had the highest basal area, species richness, and number of rare and endemic species. Ordination of tree species composition (89 species, 13 167 stems) produced arrays that primarily corresponded to the four cover classes (i.e., historic land uses). The ordination arrays corresponded secondarily to soil characteristics and topography. Natural disturbances (hurricanes, landslides, and local treefalls) affected tree composition, but these effects did not correlate with the major patterns of species distributions on the plot. Thus, it appears that forest development and natural disturbance have not masked the effects of historical land use in this tropical forest, and that past land use was the major influence on the patterns of tree composition in the plot in 1989. The least disturbed stand harbors more rare and endemic species, and such stands should be protected.

Key words: biodiversity; conservation; disturbance; land use history; Luquillo Experimental Forest; Puerto Rico; soil; species diversity; topography; tree community; tropical forest.

Introduction

"An ecosystem is a historical construction, so complex that any actual state has a negligible a priori prob,-ability" (Margalef 1968:30). Nonetheless, if one knows the details of an ecosystem's history, and how environmental factors such as soil and topography influence structure and composition, much of that ecosystem's present state can be understood. This approach has successfully explained characteristics of temperate and boreal forests where there are adequate data on both historical land use and environment (Glitzenstein et al. 1990, Foster 1992, Hörnberg et al. 1999, Motzkin et al. 1999). For tropical forests, also, there is information on past land use (Gordon 1982, Bush and Colinvaux 1994, Burslem et al. 1998) and detailed descriptions of present stand characteristics and environments (e.g., Dallmeier and Comiskey 1998). Few tropical studies, however. have synthesized land use and environment to explain present stand characteristics (Clark et al. 1995, Zimmerman et al. 1995). and history has often

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been ignored in tropical forest research (Clark 1996. Whitmore and Burslem 1998).

In this paper, we evaluate the relative influence of past land use vs. environment on the present tree composition of a tropical forest in Puerto Rico, and we assess the implications of our results for conservation of biodiversity. At issue are such questions as: How long do the effects of land use persist after those uses end? Do environmental features such as topography and soil override past land use in determining tree composition? How do different past land uses affect present species diversity? The answers to these questions may help us to understand the present species composition and assess its stability, in order to predict and manage future forest composition in the face of disturbance and change (Lugo 1995).

Environmental factors such as soil and topography are well known to affect individual tree species, community composition, forest structure, and dynamics (Ashton 1969, Newbery et al. 1986, Baillie et al. 1987, Duivenvoorden 1996). In Puerto Rico, for example, the tree *Dacryodes excelsa* (see Table 1 for botanical authorities) is often found on ridges and *Inga* spp. often occur along streams (Crow and Grigal 1979, Basnet 1992, Scatena and Lugo 1995). Tropical forest height and canopy dynamics also reflect soil and topography (Hartshorn 1978, Jans et al. 1993, Poorter et al. 1994). In Puerto Rico, for instance, streamside forest has more treefall gaps than does forest in other topographic settings (Scatena and Lugo 1995).

The effects of land use are less well studied than environmental factors. Prehistoric land uses are inferred from the presence of soil charcoal and archaeological artifacts (Sanford et al. 1985, Piperno 1990, Horn and Sanford 1992, Taylor et al. 1999). These land uses still affect general forest composition (e.g., Gómez-Pompa and Kaus 1990, Peters 2000), but precise effects are obscure (Lambert and Arnason 1982). The disturbance from human impacts that ended a few centuries ago is implied from the present abundance of long-lived secondary tree species (Hartshorn 1980, Bush and Colinvaux 1994, Burslem et al. 1998, Proctor and Miller 1998). Human activity in the past century, however, readily explains details of forest structure and composition (Foster and Brokaw 1982, Saldarriaga et al. 1988, Clark et al. 1995). In Puerto Rico, the effects of past land use on present forests have been demonstrated at the landscape scale (Thomlinson et al. 1996, Foster et al. 1999), in recently abandoned agricultural areas (Zimmerman et al. 1995. Aide et al. 1996). and within forest stands (García-Montiel and Scatena 1994). However, the relative effects of past land uses vs. the effects of environmental factors such as topography and soil on tree species composition and diversity are not well known, in Puerto Rico or elsewhere in the tropics.

Besides our forest study plot in Puerto Rico. there are a number of other large tropical forest plots in which environment and species composition are well understood (Condit 1995). Unlike our plot. however. these others have been little affected by humans. In order to weigh the relative impacts of land use vs. environment on tree composition, our study exploits an unusual combination of detailed information on land use history, environment, natural disturbance, and species distributions in a tropical forest stand. Although unusual in detail, the features of this stand have broad relevance because the land uses and environmental factors that influence this forest are widespread (Beard 1944, Perfecto et al. 1996, Grieser Johns 1997, Kellman and Tackaberry 1997, Lugo et al. 1999).

Methods

Study area and site

This study was conducted in the University of Puerto Rico's El Verde Research Area (18°20' N, 65°49' W) in the Luquillo Experimental Forest, Luquillo Mountains, Puerto Rico (Waide and Reagan 1996). In vegetation and topography, the Research Area is typical of the tabonuco forest zone (below 600 m elevation) in the Luquillo Mountains (Brown et al. 1983, Lugo and Scatena 1995) and is in an area of forest that has suffered from human disturbance (Foster et al. 1999). The forest is classified as *subtropical* wet in the Holdridge life zone system (Ewel and Whitmore 1973) and *tropical montane* in Walsh's (1 996) tropical climate system. The forest type is locally named "tabonuco forest," after a dominant tree, *Dacryodes* excelsa. Rainfall at the field station averages 3500 mm/yr. March and April tend to have less rainfall than other months, but there is usually no month with <200 mm (Brown et al. 1983).

The study site was the 16-ha (320 × 500 m) Luquillo Forest Dynamics Plot (LFDP; southwest corner at 18°20' N, 65°49' W) which is part of the Luquillo Experimental Forest Long-Term Ecological Research (LTER) program and the Center for Tropical Forest Science network of forest plots. Establishment of the LFDP began in June 1990, when it was professionally surveyed and PVC posts were sited to divide the plot into 400 20 × 20 m quadrats. Each quadrat was then divided into 16 5 × 5 m subquadrats. The south edge of the LFDP was located 35 m from the "radiation center" used in the Rain Forest Project (Odum and Pigeon 1970), and the radiation in 1963 may have damaged a few small trees at the edge of the plot. The LFDP was previously known as the "Hurricane Recovery Plot" (HRP; Zimmerman et al. 1994).

In this paper, we analyze the LFDP tree community as it was at the time Hurricane Hugo struck the forest in 1989. Hurricanes have severely damaged forest in the Luquillo Mountains every 50–60 yr, on average, in the past few centuries (Scatena and Larsen 1991). This includes hurricanes in 1928 and then in 1932, 57 yr before the present study. Other natural disturbances

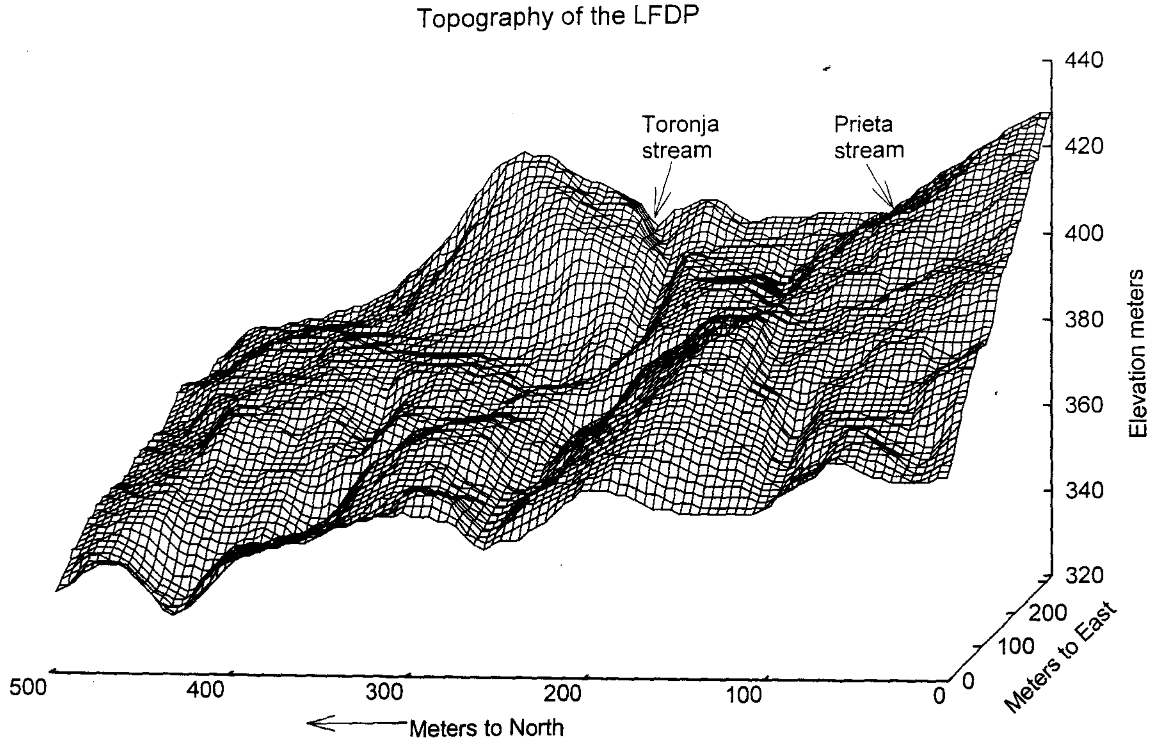

FIG. 1. Topographic map of the 16-ha Luquillo Forest Dynamics Plot (LFDP) at El Verde, Puerto Rico. The grid shows the altitude of the 20 X 20 m quadrats with interpolations of the 5 × 5 m subquadrats. (Modified from Willig et al. [1996], copyrighted 1996 by the Association for Tropical Biology, PO. Box 1897, Lawrence, Kansas 66044-8897. Reprinted by permission.)

in Luquillo forests include small-scale treefalls unrelated to hurricanes, landslides, and flood damage along streams (Guariguata 1990, Scatena and Lugo 1995).

Elevation, topography, and soils

Topography on the LFDP includes northwest-running drainages that form steep northeast- and southwest-facing slopes (Fig. 1). Elevation ranges from 333 m a.s.l. at the northern end of the LFDP to 428 m at the south. The elevation for each 20 × 20 m quadrat on the plot was calculated as the mean of the surveyed elevations for the four quadrat corners. The percentage slope of each quadrat was also derived from corner elevations. Slopes are steeper at the higher, southern end of the LFDP. Each quadrat was assigned to one of four topographic classes (valley, slope, bench, or ridge) based on the predominant class in each quadrat as determined from the topographic map. Slopes were designated when > 15%, whereas benches were defined as relatively flat areas not associated with valleys or ridge tops.

The Soil Survey Staff of the U.S. Department of Agriculture surveyed LFDP soils using qualitative observations, surface sampling along transects, randomly selected plots. and I m deep randomly located soil pits (Soil Survey Staff 1995). Results from that survey were interpolated to form a picture of the soils across the LFDP. Using the soil map, we assigned a soil type (Fig. 2) and a code for percent rock cover to each 20 × 20 m quadrat, based on the predominant soil in each quadrat. All the soils are formed from volcaniclastic sandstone. Zarzal, Cristal, and Prieto clays on the LFDP are deep. Coloso and Fluvaquents are formed from alluvium in the stream channels. Zarzal covers 67% of the LFDP, Cristal 22%, Prieto 6%, Fluvaquents 4%, and Coloso 1 %. Zarzal clay covers most of the northern and southern parts of the LFDP, with Cristal in the middle and east. Zarzal has low fertility, Cristal and Coloso low to moderate, Prieto moderate, and Fluvaquents moderate to high (Soil Survey Staff 1995). Soil pH values are: Zarzal 4.8, Cristal 5.0, Coloso 5.1, Prieto 5.4, and Fluvaquents 6.1. The sequence Zarzal, Cristal, Prieto, Coloso, and Fluvaquents represents a gradient of increasing wetness and poor drainage (Soil Survey Staff 1995).

Land use history

Information on the history of land use in and around the LFDP came from several sources, including interviews, public documents, forest surveys, and aerial photographs. In the early 1990s, we interviewed local residents to determine the land use history of El Verde forest and, in particular, El Verde Tract 11 in which the LFDP is now located (García-Montiel 2002). First

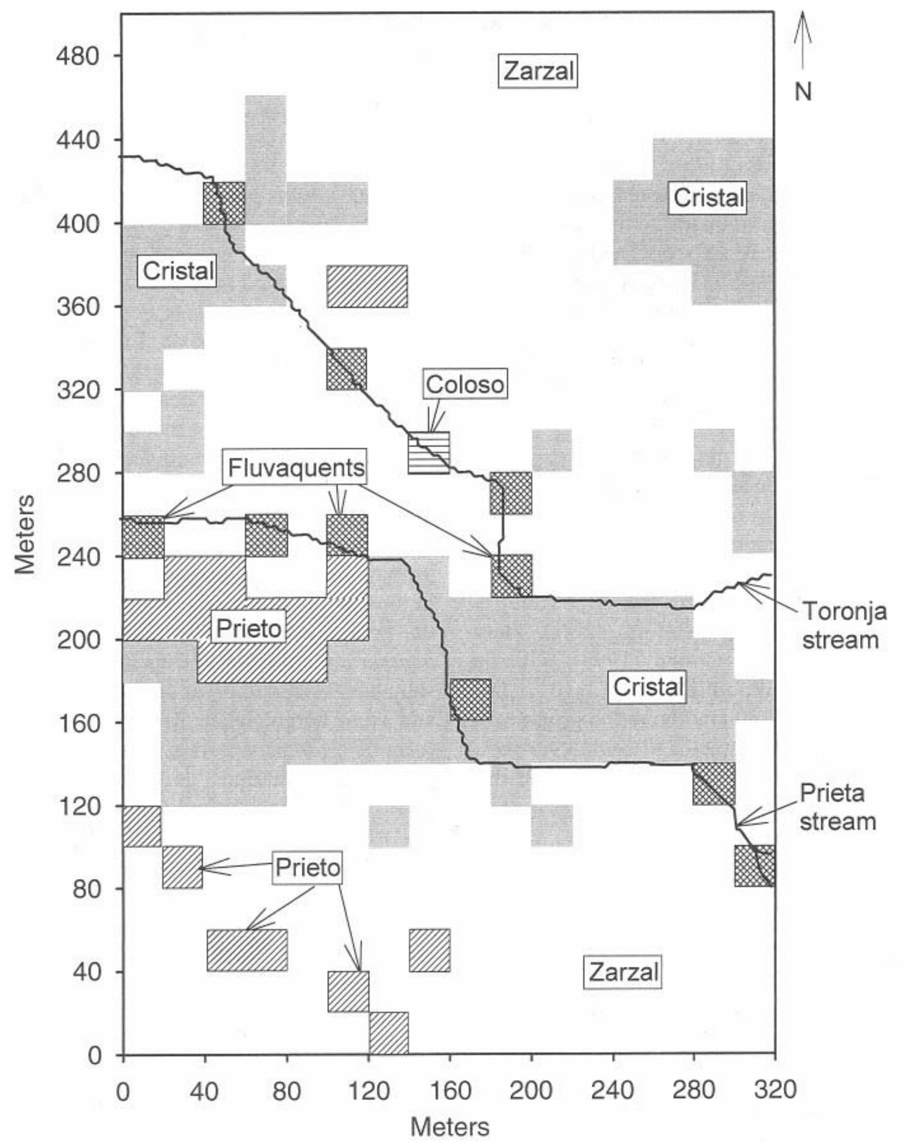

FIG. 2. Distribution of soil types and perennial streams in the 16-ha Luquillo Forest Dynamics Plot at El Verde, Puerto Rico.

we spoke with Alejo Pinto Estrada, who had lived in the area all his life and was manager of El Verde Field Station. He introduced us to other lifelong residents of the area whom we questioned generally about past land use. We corroborated their information using the Archives Generales de Puerto Rico (1854, 1865, 1866, 1885, 1905), follow-up interviews with the original informants, and interviews with other residents.

Gerhart (1934) conducted a cruise survey in 1934 and collected information on El Verde Tract 1 1 (in which the LFDP is located) while the USDA Forest Service was considering it for purchase. The surveyors walked magnetic east–west transects ~ 100 in apart and 20 m wide. assessing the timber value and describing the condition of the vegetation in qualitative terms such as "cutover," "culled," or "virgin." These descriptions were standard forestry survey terms that essentially mean substantial tree removal (cutover), selective logging (culled), or minor human disturbance (virgin: not recorded where the LFDP is now located). Other observations recorded by Gerhart (1934) included the presence of coffee and qualitative state of tree regeneration. Odum (1970) described the activities of the Forest Service after El Verde's purchase in 1934.

Assessment of' historical canopy cover from aerial photographs

To look for evidence of past land use, we analyzed aerial photographs of the Luquillo Experimental Forest area taken in 1936 (Foster et al. 1999). Using the photographs. we divided the LFDP into four sections according to apparent percent canopy cover in 1936. Canopy cover classes were defined as: cover class 1 (<20%), cover class 2 (20–50%), cover class 3 (50–80%), and cover class 4 (>80%). We designated each 20 × 20 in quadrat according to its cover class. Quadrats straddling the boundaries between cover classes were assigned to the predominant cover class in that quadrat. Cover classes were also assigned on a 5 × 5 m subquadrat scale for use in species accumulation curves. When designating the canopy cover class. we did not distinguish between cover of planted trees vs. natural forest.

Inventory of stems

We identified, tagged. and mapped to the nearest 0.5 m (within 5 × 5 m subquadrats) all self-supporting woody stems $\geq$ 10 cm D_{130} (diameter at 130 cm above ground; D_{130} avoids the ambiguity of "breast height" [Brokaw and Thompson 2000]) in the LFDP. The diameters of leaning or prone stems were measured at 130 cm along the trunk from the rooting point. These methods generally followed Condit (1998), with the exception that if a tree had multiple stems 210 cm D_{130} originating at a height <130 cm above the ground, we tagged and measured the diameter of each stem separately. In this paper, we used either the number of separate stems $\geq$ 10 cm D130 or individual trees (which might have more than one stem $\geq$ 10 cm D_{130}), as required for the different analyses that we will describe. Trees were identified by sight in the field or from voucher specimens (see Table 1 and the Appendix for species names). Botanists at the University of Puerto Rico, Missouri Botanical Garden, and New York Botanical Garden identified vouchers, which are deposited at El Verde Field Station and New York Botanical Garden. Nomenclature follows Liogier (1985, 1988, 1994, 1995, 1997), except that we used Henderson et al. (1995) for palms.

The plot census started in 1990, the year after Hurricane Hugo (September 1989). In order to reduce the loss of information through tree mortality and decomposition after the hurricane, we made a rapid inventory between September 1990 and February 1991 of steins ($\geq$ 10 cm D_{130}) that had been damaged and/or apparently killed by Hurricane Hugo. An inventory of all live stems ($\geq$ 10 cm D_{130}) on the LFDP started in June 1990 and continued until February 1992. Together, these inventories constitute the first census of the LFDP for stems $\geq$ 10 cm D_{130}, and we believe that these data represent the tree community as it would have been at the time of Hurricane Hugo. In later inventories (after February 1992). we found some large ($\geq$ 10 cm D_{130}) unrecorded stems that we suspect, because of their size, may have been overlooked in the tangle of hurricane damage during the first census. Using the individual growth rate of these stems (if they had been measured more than once), or the species-specific median growth rate (for stems 10–30 cm D_{130}), we calculated the probable size of these unrecorded stems at the time of the first census. If a stem would have been $\geq$ 10 cm D_{130} at the time of the first census, we included the stem in the first census data (the estimated diameters were also used to calculate basal area. Although adding "missed" sterns produced large percentage changes for a few uncommon species, the overall effect was relatively small. The "missed" stems assigned to the first census represented only 2.2% of the total stem numbers and 1.4% of the total basal area. and are unlikely to affect the overall analysis. Large *Cecropia schreberiana* and *Trema micrantha* (L.) Blume found after the first census were not allocated to it, as our observations and growth data suggest that these fast-growing pioneer species most likely established after Hurricane Hugo. Several large *Prestoea acuminata* (a palm, syn. *P. montana* [Henderson et al. 1995]) were also found in inventories after the first census. The lack of secondary growth in *P. acuminata* precludes diameter extrapolations to determine the stem diameter at the time of the first census. The allocation of "missed" *Prestoea acuminata* to the first census was made on an individual stem basis, depending upon the diameter ($\geq$ 10 cm D_{130}) and stem height when first encountered. The growth form of *Cyathea arborea* (tree fern) also precludes diameter extrapolations, and its "stems" were generally $\geq$ 10 cm diameter before they reached a height of 130 cm from the ground. *Cyathea arborea* stems found after the first census were, therefore, not allocated to it irrespective of their diameter when first measured. The inclusion of additional stems and corrections to the data and species identifications account for the differences in species and stem numbers between this paper and Zimmerman et al. (1994).

As previously mentioned, we inventoried dead stems (between September 1990 and February 1991) that we believed had been killed by Hurricane Hugo. Of these 1259 dead stems (9.6% of the total in the first census), 1101 were identified to species from bark and tree form. and 12 were identified as *Inga* sp. Of the dead stems, 146 (1.1% of the total in the first census; "Dead" in the Appendix) were impossible to identify. These unidentified stems were included in the total stem number, basal area. and size class distributions calculated for this census.

Analyses

We plotted species–area and species–individual accumulation curves following the method in Condit et al. (1996). The whole LFDP was divided into several sets of non-overlapping squares of different sizes: 6400 squares measuring 5 × 5 m, 1600 of 10 × 10 m, 400 of 20 × 20 m, 96 of 40 × 40 m, 40 of 60 × 60 m, 24 of 80 × 80 m, and 15 of 100 × 100 m. In cases in which the rectangular LFDP could not be divided into the required squares, a strip along the east or north edge of the plot was omitted. For each set of squares

TABLE 1. Density (stems ≥ 10 cm D_{130}, diameter at 130 cm above ground) and basal area (m^2) ha^{-1} of all tree species in the entire 16-ha Luquillo Forest Dynamics Plot (LFDP) at El Verde, Puerto Rico, at the time of Hurricane Hugo.

Family and species	Typical mature height†	LFDP, 16 ha No. stems per ha	LFDP, 16 ha Basal area (m^2)
Anacardiaceae			
Mangifera indica L. ‡	m—l	0.3	0.062
Annonaceae			
Guatteria caribaea Urb.	m	2.9	0.075
Oxandra laurifolia (Sw.) A. Rich.	sm	0.3	0.010
Araliaceae			
Dendropanax arboreus (L.) Decne. & Planch.	m	2.9	0.093
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	m	12.8	0.726
Arecaceae			
Prestoea acuminata (Willd.) H. E. Moore	sm–m	266.6	4.892
Roystonea borinquena O.F Cook§	m	3.1	0.368
Bignoniaceae			
Tabebuia heterophylla (DC.) Britton	sm–m	21.1	1.031
Boraginaceae			
Cordia borinquensis Urb.§	sm	0.7	0.009
Cordia sulcata DC.	m	9.3	0.230
Burseraceae			
Dacryodes excelsa Vahl	1	64.8	4.587
Tetragastris balsamifera (Sw.) Kuntze	1	7.8	0.275
Cecropiaceae			
Cecropia schreberiana Miq.	m	8.3	0.553
Celastraceae			
Maytenus elongata (Urb.) Britton	sm	0.1	0.001
Chrysobalanaceae			
Hirtella rugosa Pers.§	sm	0.8	0.009
Clusiaceae			
Calophyllum calaba L. ‡	m	3.8	0.186
Clusia clusiodes (Griseb.) D' Arcy	m	0.2	0.006
Clusia rosea Jacq.	m	0.5	0.050
Combretaceae			
Buchenavia tetraphylla (Aubl.)	1	11.8	2.931
Cyatheaceae			
Cyathea arborea (L.) J. E. Sm.	sm	0.3	0.003
Cyrillaceae			
Cyrilla racemiflora L.	m–1	1.5	0.102
Elaeocarpaceae			
Sloanea herteriana Choisy	1	33.2	1.257
Euphorbiaceae			
Alchornea latifolia Sw.	m	13.0	0.773
Aclorneopsis floribunda (Benth.) Muell. Arg.	sm–m	5.7	0.384
Croton poecilanthus Urb.‖	sm–m	8.2	0.246
Drypetes glauca Vahl	sm	10.5	0.234

TABLE 1. Continued.

Family and species	Typical mature height?	LFDP, 16 ha No. stem per ha	LFDP, 16 ha Basal area (m^2)
Margaritaria nobilis L.	m	1.0	0.110
Sapium laurocerasus Desf.§	sm-m	9.9	0.545
Fabaceae, Mimosoideae			
Inga laurina (Sw.) Willd. Ex L.	1–m	35.3	2.459
Inga vera Willd. Ex L.	1–in	4.0	0.211
Inga sp. (*I. laurina* or *I. vera)*		0.8	0.086
Fabaceae, Papilionoideae			
Andira inermis (W. Wright) DC. (HBK)	m–1	4.5	0.150
Lonchocarpus latifolius (Willd.) DC.	sm–l	0.3	0.026
Ormosia krugii Urb.	m	7.6	0.390
Pterocarpus officinalis Jacq.	1	0.4	0.039
Flacourtiaceae			
Casearia arborea (Rich.) Urb.	sm–m	69.4	1.728
Casearia sylvestris Sw.	sm–m	14.4	0.192
Homalium racemosum Jacq.	1	11.6	1.078
Laetia procera (Poepp. & Endl.) Eichler	m	3.4	0.174
Lauraceae			
Beilschmiedia pendula (Sw.) Hemsl.	m–l	0.1	0.002
Nectandra antillana Meisn.	m	0.1	0.003
Nectandra turbacensis (Nees) Mez	m	4.1	0.322
Ocotea floribunda (Sw.) Mez	m	0.3	0.015
Ocotea leucoxylon (Sw.) Laness.	sm–m	10.9	0.333
Ocotea moschata (Meisn) Mez§	1	1.0	0.069
Ocotea portoricensis Mez§	m	0.1	0.001
Magnoliaceae			
Magnolia splendens Urb.‖	1	0.1	0.002
Malpighiaceae			
Byrsonima spicata (Cav.) HBK	sm–m	9.8	1.033
Byrsonima wadsworthii Little3	sm–m	0.8	0.021
Malvaceae			
Hibiscus pernambucensis Arruda‡	sm	0.3	0.004
Melastomataceae			
Calycogonium squamulosum Cogn.§	m	0.6	0.011
Henriettea fascicularis (Sw.) M. Gómez	sm–m	0.1	0.001
Miconia tetradra (Sw.) D. Don	sm–m	7.4	0.327
Meliaceae			
Guarea glabra Vahl	1	0.5	0.013
Guarea guidonia (L.) Sleumer	1	19.3	2.071
Swietenia macrophylla King‡	m–1	0.1	0.006
Trichilia pallida Sw.	sh–sm	2.7	0.047
Moraceae			
Artocarpus altilis (Parkinson) Fosberg‡	m	0.1	0.010
Ficus crassinervia Desf.	m–1	3.9	0.872
Ficus americana Aubl.	m–1	0.8	0.147
Pseudolmedia spuria (Sw.) Griseb.	m	0.8	0.032
Myrsinaceae			
Ardisia obovata Ham.	sm	0.1	0.001

TABLE 1 Continued.

Family and species	Typical mature height†	LFDP. 16 ha No. stems per ha	LFDP. 16 ha Basal area (m^2)
Myrtaceae			
Eugenia domingensis Berg	m	0.4	0.017
Eugenia stahlii (Kiaersk.) Krug & Urb.§	m	2.5	0.058
Myrcia deflexa (Poir.) DC.	m	0.8	0.012
Myrcia leptoclada DC.	sm	0.6	0.010
Myrcia splendens (Sw.) DC.	sh–sm	5.4	0.122
Syzygium jambos (L.) Alston‡	sm	1.3	0.043
Nyctaginaceae			
Pisonia subcordata Sw.	1	0.1	0.033
Oleaceae			
Chonanthus domingensis Lam.	m	11.8	0.659
Polygonaceae			
Coccoloba diversifolia Jacq.	sm	2.3	0.094
Coccoloba swartzii Meisn.	m	0.1	0.0001
Rhizophoraceae			
Cassipourea guianensis Aubl.	sh–sm	0.2	0.002
Rubiaceae			
Antirhea obtusifolia Urb.	sh–m	0.2	0.002
Chione venosa (Sw.) Urb.	sm–m	0.3	0.022
Faramea occidentalis (L.) A. Rich.	sh-sm	0.2	0.003
Genipa americana L. [natural and planted]	1	0.3	0.023
Guettarda valenzuelana A. Rich.	sm–m	7.2	0.219
Ixora ferrea (Jacq.) Benth.	sh–sm	0.4	0.004
Rondeletia portoricensis Krug & Urb.§	sm–m	0.2	0.005
Rutaceae			
Zanthoxylum martinicense (Lam.) DC.	m–1	1.7	0.170
Sabiaceae			
Meliosma herbertii Rolfe	m	0.4	0.008
Sapindaceae			
Cupania americana L.	1	0.1	0.001
Matayba domingensis (DC.) Radlk.	m	16.7	0.928
Sapotaceae			
Manilkara bidentata (A. DC.) A. Chev.	1	43.3	2.190
Micropholis guyanensis (A. DC.) Pierre	m	0.3	0.008
Micropholis garciniifolia Pierrell	m	0.8	0.025
Sterculiaceae			
Guazuma ulmifolia Lam.	sm–m	0.1	0.016
Symplocaceae			
Symplocos martinicensis Jacq.	sm–m	0.1	0.001
Theaceae			
Ternstroemia luquillensis Krug & Urb.‖	sm–m	0.1	0.001
Total dead		9.1	0.451
Total live and dead		822.0	36.700

† Mature height classes are 1, large (>21 m); m, medium (9–21m); sm, small (4.5–9m); sh, shrub (<4.5 m). See Little and Wildsworth (1964). Little et al. (1974). and Little and Woodbury (1976).

‡ Exotic in Luquillo Mountains (Little and Woodbury 1976).

§ Endemic to Puerto Rico (Little and Woodbury 1976).

‖ Endemic to Luquillo Mountains (Little and Woodbury 1976).

of the same size e.g., the 1600 10 × 10 m squares. we calculated the mean number of species per square. The mean number of species per square was then plotted against the size of that quare to produce a species–area curve. Species-individual curves were constructed in the same way but were plotted with the mean number of species per square against the mean number of individual trees (not separate stems) in the same size of square. These methods avoid unrealistic spatial configurations found in repeated-curve methods (Condit et al. 1996).

These analyses were repeated for each section of historical cover class in the LFDP, using non-overlapping square-shaped plots with the same sizes as those listed for the whole LFDP The number of squares fitted into each cover class varied with the size and shape of the cover class. The number and location of squares ≥ 10 × 10 m depended upon the cover class designation at the quadrat (20 × 20 m) scale, whereas the 5 × 5 m squares were based on cover class at the subquadrat scale. Using the finer resolution subquadrat scale slightly changed the total size of each cover class. When arranging squares ≥ 40 × 40 m, we omitted some marginal areas in each cover class that could not fit into squares. Cover class 1 had an irregular shape with a total area of only 1.16 ha. The closest possible approximation to a 100 × 100 m square was constructed within this class.

We searched for distinctive distributions of tree communities relative to historic canopy cover class and present environmental factors on the LFDP by using Nonmetric Multi-dimensional Scaling (NMS), incorporating PCORD (McCune and Mefford 1997). NMS is preferred over other ordination methods because it is based on ecologically relevant measures of community (dis)similarity. Analysis is conducted on the ranks of dissimilarity values ("distances") such that it is a nonparametric procedure (Clarke 1993). We present the ordination of species stem density in each of the 400 20 × 20 quadrats (rather than 5 × 5 m subquadrats), because the quadrat scale better matched the environmental variables and increased the sample size of stems within plots. A comparison of 5 × 5 m vs. 20 × 20 m distributions showed little difference. For each quadrat, we used stem density per species (analysis of relative density and relative basal area gave similar results). The ordination was performed by NMS using Sorenson's dissimilarity distance matrix (Jaccard's index produced nearly identical results). As suggested by

McCune and Mefford (1997). Principal Components Analysis (PCA) was carried out first and the axis scores were used as a starting point in NMS. This was done to increase the likelihood that NMS, which is an iterative procedure. would find the best solution (minimum stress), avoiding local minima (for additional explanation. see Clarke 1993. McCune and Mefford 1997). Three axes from NMS were interpreted by correlating them (Kendall's tau) with species stem density per quadrat and with a secondary matrix containing data on historical cover class, percentage slope, elevation, topographic type, soil type. and degree of rockiness in each quadrat. Elevation and percentage slope were continuous variables. whereas cover class, topography, soil type, and rockiness (ranked in increasing percent rock area per quadrat) were ordinal variables. Soil type and rockiness were coded from the soil map as previously described (Soil Survey Staff 1995). Soil types were also coded as increasing in soil "wetness" along the gradient: Zarzal, Cristal, Prieto, Coloso, and Fluvequent.

RESULTS

Land use history of El Verde

Interviews with long-time residents, historical documents, Forest Service records, and aerial photographs from 1936 provide a history of land use at El Verde. Between 1924 and 1934, El Verde Tract 11 (including the present LFDP) was owned by the Bliss Plywood and Keystone Plywood Corporations, which operated a portable sawmill in the northern part of the tract (Archivos Generales de Puerto Rico and interviews). These Corporations felled parts of Tract 11 in the 1920s for plywood and timber. Cleared areas were then planted with coffee in the areas best suited for that purpose, or were farmed for rice, yams, sweet potatoes, sugarcane, and gandules (green pigeon peas; Gerhart 1934). Coffee was the major revenue source in Tract 11, but the plantations were abandoned after Hurricane San Felipe II struck in 1928 (Gerhart 1934). The Forest Service bought the tract in 1934, after conducting a timber cruise (Gerhart 1934) to assess forest structure, composition, and timber value. Aerial photos of El Verde taken in 1936 showed trails. houses near the present LFDP, and variations in canopy cover, including some straight, evidently human-made boundaries. Most land uses at El Verde ceased in the 1930s: however, the Forest Service selectively logged parts of what is now the LFDP and carried out "timber stand improvement" after 1934 (F. Wadsworth, cited by Odum 1970).

Canopy cover in1936 and land use history

As described in *Methods,* we used the aerial photographs from 1936 to divide the LFDP into four sections according to apparent percent canopy cover in 1936. Cover class 1 (<20% canopy cover) included 1.16 ha in the northeast of the LFDP. The aerial photographs showed that parts of this area were almost completely denuded of trees. The Forest Service recognized the extent of damage to this section. designated cover class 1, and planted *Calophyllum calaba* there after the tract was purchased (Fig. 3). The *C. calaba* were not apparent in the aerial photographs and. therefore, did not contribute to the canopy cover designation. *Caliphyllum calaba* was commonly used to reforest denuded areas of the Luquillo Mountains (Marrero 1947).

Cover class 2 (20–50% cover) included 3.96 ha in the east-central part of the present LFDP, and cover class 3 (50-80% cover) included 5.64 ha in the north and west. Low percentage canopy cover in cover classes 1, 2, and 3 of the LFDP was probably a result of the tree felling by Bliss Plywood Corporation. This assumption is supported by the Forest Service cruise survey in 1934 (Gerhart 1934), which indicated that parts of the forest north of the Prieta stream were "cutover," that is, heavily logged or cleared to remove the canopy (Fig. 4; Gerhart 1934).

Cover class 4 (>80% cover) included 5.24 ha in the south and west of the present LFDP (Fig. 3). The Forest Service cruise survey indicated that this area south of the Prieta had been "culled," that is, selectively logged (Fig. 4, Gerhart 1934). Thus in 1936, this area was presumably much less disturbed and so had more canopy cover than the "cutover" areas to the north. In 1937 and 1946, the Forest Service carried out "light thinning" in southern sections of what would be the LFDP (Odum 1970). Between 1944 and 1953, timber harvests in this area removed about half of the volume of tabonuco *(Dacryodes excelsa;* mostly trees 150 cm dbh), representing ~ 15% of the stand volume. During the Rain Forest Project (Odum and Pigeon 1970), an artificially made gap (the "Cut Center") of ~320 m^2 was created (Brown et al. 1983) in the southwest corner of what is now the LFDP.

In our census of the LFDP, we found evidence for plantations and farming in the areas of cover classes 1, 2, and 3. Remnants of coffee plantations persist in the understory of cover classes 2 and 3 (Fig. 3. shows 5 × 5 m subplots with stems of *Coffea arabica* $\geq$ 1 cm D_{130}). *Inga vera* and *I. laurina* (not shown). which were commonly planted to provide shade for coffee (described by local residents). are also found in these cover classes. In addition to coffee, large ($\geq$ 10 cm D_{130}) fruit trees. including mangos *(Mangifera indica)* and breadfruit *(Artocarpus Altilis)* were also found in cover class 2, whereas genipa *(Genipa americana)* was found in cover class 3. Genipa is native to the Luquillo Mountains (Little and Woodbury 1976), but is commonly planted in kitchen gardens for its fruit. With the exception of a few *C. calaba* and bananas *(Musa* sp.) on the border between cover class 3 and 4, little evidence of farming and no coffee plants were found in cover class 4.

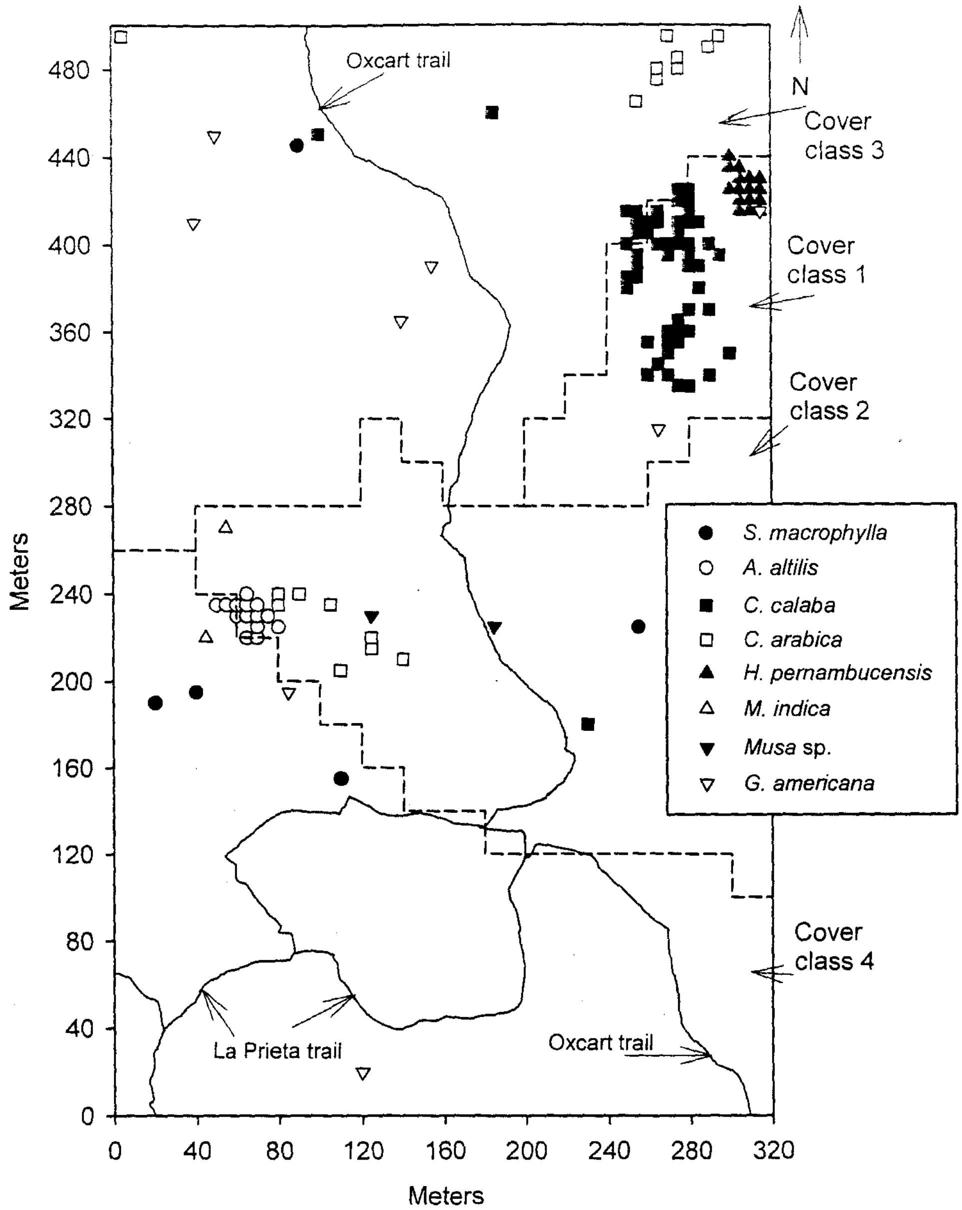

FIG. 3. Historic canopy cover classes, locations of introduced plants (in 5 × 5 m subquadrats with individual stems ≥ 1 cm D_{130}, diameter at 130 cm above ground), and historic trails in the 16-ha Luquillo Forest Dynamics Plot at El Verde, Puerto Rico. Cover classes were differentiated from aerial photographs taken in 1936 and reflect different land uses before 1936. Cover classes 1, 2, and 3 (10–20%, 20–50%, and 50–80% cover, respectively) were clear-cut or heavily logged. and then farmed or locally planted with tree crops: class 4 (80–100% cover) was selectively logged.

Present stand structure and historical cover class

In the 16-ha LFDP in 1989, there were 13 167 stems ≥ 10 cm D_{130}, for an overall density of 822.9 stems/ha and basal area of 36.7 m^2/ha (Table 2). Stems in the 10–30 cm D_{130}, range dominated the diameter class distribution on the LFDP (Fig. 5), especially when the abundant *Prestoea acuminata,* which reaches a maximum diameter of ~20 cm D_{130}, was included. Stem density, basal area. and diameter class distributions were similar among most sections of the LFDP differentiated by historic cover class (Table 2). However, stem densities were lowest in cover class 1, and basal area was highest in class 4. The diameter class distribution in class 1 (Fig. 5) differed significantly (Kolmogorov-Smirnov Tests, $P < 0.002–0.0001$) from that of the other cover classes because of the higher proportion of stems 20–30 cm D_{130} in cover class 1. This may be due to the especially high abundance of *Prestoea acuminata* and the presence of *C. calaba* trees

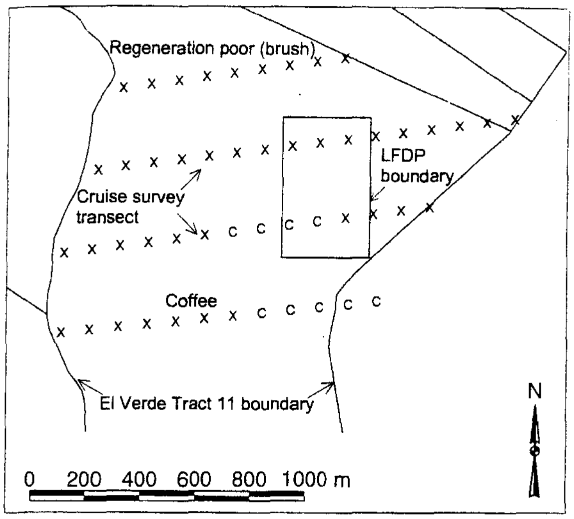

FIG. 4. Timber cruise lines followed in 1934 within Tract 11 at El Verde, Puerto Rico (Gerhart 1934). The rectangle shows the location of the of the Luquillo Forest Dynamics Plot. Each "X" on a transect line indicates where a segment of about 100 m was recorded as "cut over" (recently clearcut), and each "C" similarly indicates "culled" (selectively logged) forest.

planted in this area by the Forest Service in the 1930s before the LFDP was established.

Tree community structure and historical cover class

The LFDP as a whole contained 89 (including six exotic) tree species with stems $\geq$ 10 cm D_{130} in 72 (six exotic) genera and 38 families (see Table 1). The most speciose genera were *Ocotea* (four species) and *Myrcia* (three species). The largest families were Lauraceae and Rubiaceae (seven species each) and Leguminosae (sensu lato) and Myrtaceae (six species each). There were 44.3 ± 5.7 species/ha (mean ± 1 SD) with stems $\geq$ 10 cm D_{130} on the LFDP (range 33–52 species, N = 15 ha^2; Table 2). The LFDP was dominated by the medium-sized (height ~15 m, 10–20 cm D_{130}) palm *P. acuminata* (Table 3). *Prestoea acuminata. Casearia arborea,* and *Dacylodes excelsa* made up nearly 50% of all stems on the LFDP (Table 3). Of the 89 species with stems $\geq$ 10 cm $D_{130,45}$ were rare (< 1 stem/ha; Hubbell and Foster 1986). Ten of these species were represented by only one stem on the LFDP, 14 species were endemic to Puerto Rico, and four of these were endemic to the Luquillo Mountains (Table 2; see Table 1 and the Appendix).

Among the four historic cover classes on the LFDP, the total number of tree species with stems $\geq$ 10 cm D_{130} ranged from 32 (cover class 1) to 76 (cover class 4), with cover class 1 having many fewer species than the other classes (Table 1). Cover class 4 contained more species that were rare (< 1 stem/ha), unique (found only in one cover class), and endemic (Table 2). The Shannon-Wiener measure of species diversity ($H' = \Sigma_i - f_i \ln f_i$, where f is the relative abundance of species i) ranged from 2.18 (class 1) to 2.93 (class 4), with class 1 again much lower than the others (Table 2). Curves of species accumulation per area and per number of individual trees show that rankings of the cover classes by total species richness and H' are maintained when species richness is standardized for sample area and number of trees (Fig. 6).

TABLE 2. Forest structure, species totals, and diversity of trees with stems $\geq$ 10 cm D_{130} in the 16-ha Luquillo Forest Dynamics plot (LFDP) at El Verde, Puerto Rico, in 1989 at the time of Hurricane Hugo.

Forest in 1989	LFDP total	Cover class (canopy cover) in 1936: 1 (0–20%)	2 (20–50%)	3 (50–80%)	4 (80–100%)
Area (ha)	16.00	1.16	3.96	5.64	5.24
No. stems	13167	866	3401	4572	4328
Density (no. stems/ha)†	822.9	746.6	858.8	810.6	826.0
BA (m^2/ha)†	36.7	36.5	35.1	35.4	40.8
Total no. spp: (w/o exotics)‡	89 (83)	32 (30)	66 (63)	62 (60)	76 (15)
No. spp./ha, mean ± 1 SD	44.3 ± 5.7	32	44.5 ± 3.5	42.1 ± 2.5	48.0 ± 2.9
No. spp./ha, range§	33–52		42–41	40–45	45–51
Shannon-Wiener H' (w/o exotics):	2.90 (2.86)	2.18 (2.06)	2.69 (2.68)	2.65 (2.63)	2.93 (2.92)
No. rare spp. (w/o exotics)‖	44 (41)	3 (2)	21 (19)	17 (17)	32 (30)
No. unique spp. (w/o exotics)‡¶	19 (16)	1 (0)	1 (0)	5 (5)	12 (11)
No. spp. endemic to Luquillo Mts.#	4	0	2	1	4
No. spp. endemic to Puerto Rico#.††	14	2	10	8	13

Notes: Data are presented for the whole plot and as a function of canopy cover class. determined from aerial photographs taken in 1936. Cover classes 1–3 had been clear cut or heavily logged and farmed or locally planted with tree crops before 1936. Class 4 was selectively logged before 1936 and from 1944 to 1953.

† Calculated by dividing total stems or basal area by the total area for the LFDP or cover classes.

‡ Totals in parentheses exclude exotic species.

§ Calculated by using species totals in non-overlapping hectares delimited within the LFDP or cover classes. including exotics.

‖ Density < 1 stem/ha in LFDP

¶ Species found in only one cover class in LFDP: total of such species in column LFDP.

\# Little and Woodbury (1976).

†† Includes Luquillo Mountain endemics.

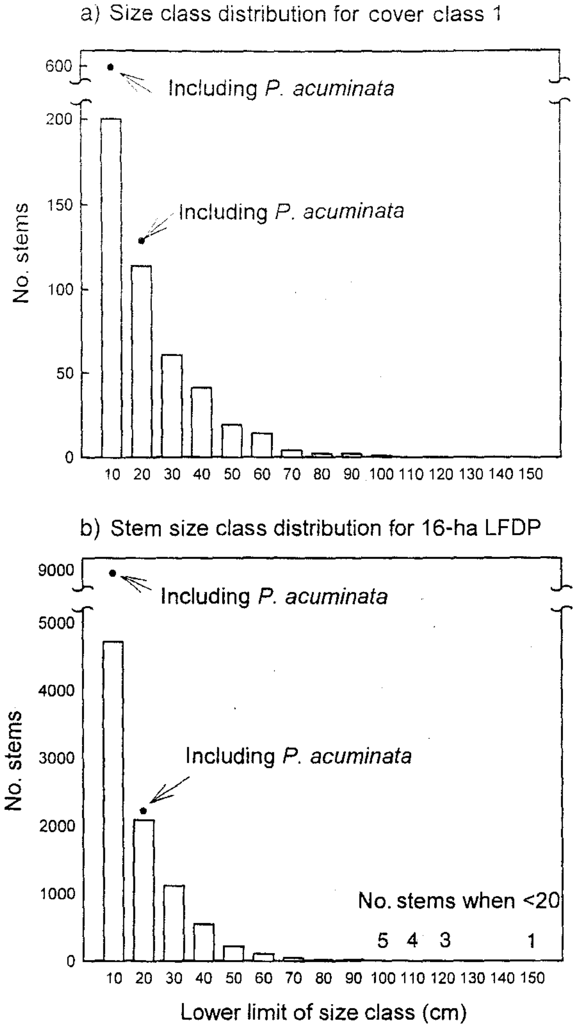

FIG. 5. Diameter class distributions of trees ≥ 10 cm D_{130}, at El Verde, Puerto Rico in (a) cover class 1 of the Luquillo Forest Dynamics Plot (LFDP) and (b) in the entire LFDP. See Fig. 3 for an explanation of cover classes representing different historic land uses.

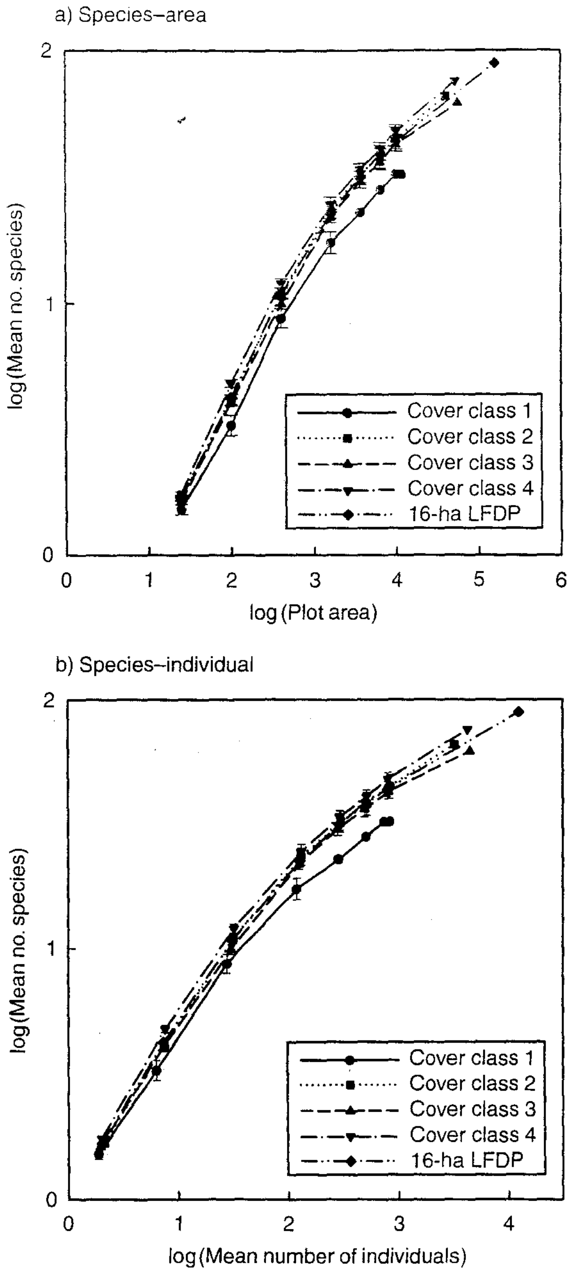

FIG. 6. Species accumulation (a) per unit area and (b) per number of stems ≥ 10 cm D_{130} in the 16-ha Luquillo Forest Dynamics Plot (LFDP) at El Verde, Puerto Rico. and in sections of the LFDP distinguished by historic cover classes indicating different historic land uses. See *Methods: Analysis* for computation methods. Cover classes are defined in Fig. 3.

Tree community composition, historical cover class, and environment

Ordination of tree species composition using NMS (Fig. 7) separated the 400 20 × 20 m quadrats of the LFDP primarily by historic canopy cover class. which reflects land use history. This considerable role of land use history was indicated by the strong correlation of cover class with Axis 1 of the ordination. explaining 46.5% of the variance in the community distance matrix (McCune and Mefford 1997) of the quadrats (Table 4). All quadrats in cover class 1 were clearly grouped to the right in the ordination figure (Fig. 7), whereas the other cover classes overlapped one another, but with a trend of increasing canopy cover toward the left.

The present distribution of stems of several species recorded in this census of the LFDP accounted for the strong effect of historic cover class. Most dramatic were the distributions of *Dacryodes excelsa*, characterizing less disturbed sections, and *Casearia arborea*. in more disturbed sections (Fig. 8). Additionally, cover class 1 was dominated by the palm *P. acuminata* (Fig. 9a) and otherwise lacked many species represented in the other cover classes. The least disturbed section,

TABLE 3. (A) The ten most abundant and (B) the ten most important tree species (stems ≥ 10 cm D_{130}; 89 total species) in the 16-ha Luquillo Forest Dynamics Plot (LFDP) at El Verde. Puerto Rico, at the time of Hurricane Hugo in 1980

A) Ten most abundant species				B) Ten most important species		
Species	Total no. stems	Relative abund.†	Cumul. stems (%)	Species	Import. value‡	Cumul. imp. value
Prestoea acuminata	4265	32.4	32.4	*Prestoea acuminata*	45.7	45.7
Casearia arborea	1109	8.4	40.8	*Dacryodes excelsa*	20.4	66.1
Darcryodes excelsa	1037	7.9	48.7	*Casearia arborea*	13.2	79.3
Manilkara bidentata	692	5.3	54.0	*Manilkara bidentata*	11.3	90.5
Inga laurina	566	4.3	58.3	*Inga laurina*	11.0	101.5
Sloanea berteriana	531	4.0	62.3	*Buchenavia tetraphylla*	9.4	110.9
Tabebuia heterophylla	338	2.6	64.9	*Guarea guidonia*	8.0	118.9
Guarea guidonia	308	2.3	67.2	*Sloanea berteriana*	7.4	126.3
Matayba domingensis	267	2.0	69.2	*Tabebuia heterophylla*	5.4	131.7
Casearia sylvestris	231	1.8	71.0	*Matayba domingensis*	4.6	136.3

Note: See the Appendix for a complete list of species and botanical authorities.

† Relative abundance is the percentage of the total stems in LFDP.

‡ The importance value (IV) is the sum of relative abundance and relative basal area (which is the percentage of the total basal area in the LFDP). The total IV is 200.

cover class 4, had high densities of *Dacryodes excelsa* (Fig. *8), Manilkara bidentata, Sloanea berteriana,* and *Tetragastris balsamifera* (Fig. 9b–d). Some secondary species did not sort by cover class on the LFDP; for example, *Cecropia schreberiana* and *Schefflera morototoni* were distributed more evenly throughout the plot (Fig. 9e, f). *Casearia arborea,* also considered a secondary species, was an exception (Fig. 8).

Significant correlations with Axis 2 of the NMS (17.7% of the variance in the community distance matrix) included, in order of decreasing strength of correlation: rockiness. canopy cover class in 1936, Prieto

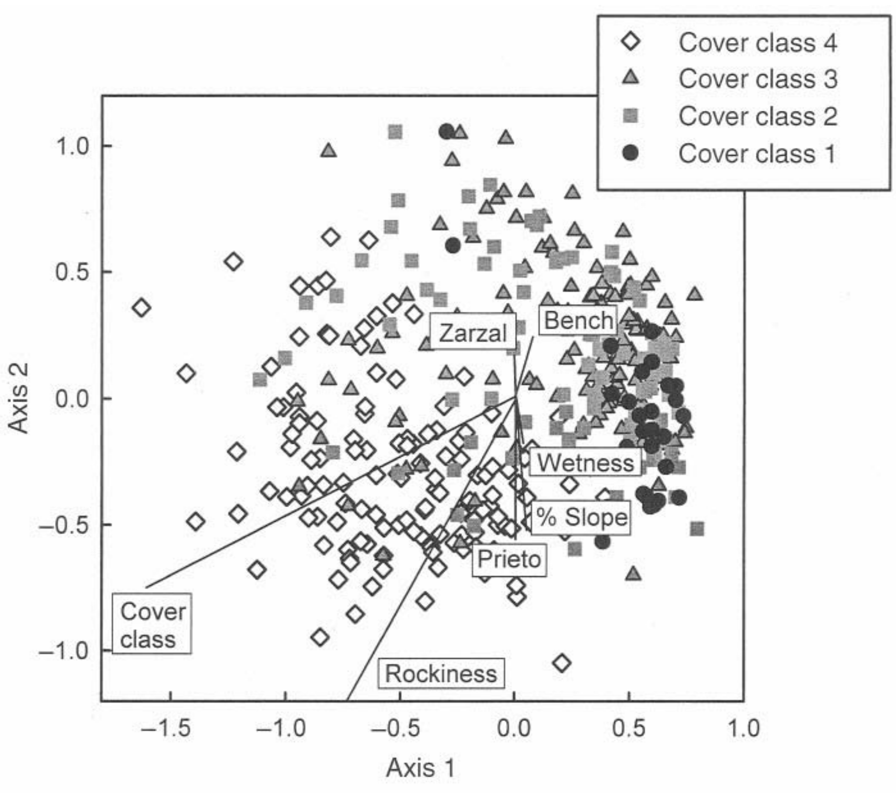

FIG 7. Nonmetric multi-dimensional scaling (NMS) of 400 20 × 20 m quadrats in the 16-ha Luquillo Forest Dynamics Plot at El Verde, Puerto Rico, according to species composition of trees ≥ 10 cm D_{130}. The historic cover class is significantly correlated with Axis 1 of the array (Table 3). Cover classes are defined in Fig. 3.

TABLE 4. Correlations (Kendall's tau) of canopy cover (1936 classes) and environmental variables with composite species distributions of all stems ≥ 10 cm D_{130} for the 16-ha Luquillo Forest Dynamics Plot (LFDP) and two cover class subsections, El Verde, Puerto Rico, at the time of Hurricane Hugo in 1989. Correlations are shown for two axes of the Nonmetric Multi-dimensional Scaling (with percentage of variance in parentheses).

	Whole LFDP		Cover classes 2 and 3		Cover class 4	
Variables	Axis 1 (46.5%)	Axis 2 (17.7%)	Axis 1 (39.8%)	Axis 2 (24.1%)	Axis 1 (41.7%)	Axis 2 (17.2%)
Cover class in 1936†	−0.469**	−0.260**				
Rockiness	−0.289**	−0.304**	−0.123**	0.226**	0.133*	−0.074
Slope	−0.098**	−0.099**	0.017	−0.003	−0.170**	0.086
Bench	0.095**	0.146**	0.045	−0.186**	0.038	−0.126*
Elevation$	−0.063	0.033	0.082	0.013	−0.338**	−0.175**
Coloso 4	0.061	0.023	0.078	0.010		
Valley	0.052	−0.065	−0.045	0.222**	0.188**	0.054
Ridge	−0.032	0.075*	−0.029	−0.065	0.014	−0.082
Percentage slope‡	0.027	−0.209**	0.070	0.237**	0.156**	0.149*
Zarzal 1	−0.018	0.124**	0.158**	−0.145**	−0.323**	0.018
Wetness	0.017	−0.141**	−0.140**	0.162**	0.311**	−0.035
Exposure	−0.013	−0.055	−0.037	0.073	−0.057	−0.082
Cristal 2	0.013	−0.006	−0.195**	0.050	0.175**	0.069
Prieto	−0.004	−0.219**	0.127**	0.153**	0.273**	−0.080
Fluvaquents	0.004	−0.047	−0.063*	0.130**	−0.046	−0.046

Notes: Ordinal variables include soil type (from driest to wettest: Zarzal, Cristal, Prieto, Coloso, and Fluvaquents); topographic classes (valley, slope, ridge, and bench), and rockiness. Coloso 4 was not found in the section of cover class 4. Tree data for the 1989 NMS ordination are from a sample size of 400 20 × 20 m quadrats.

* $P < 0.05$; ** $P < 0.01$.

† Cover class in 1936 was determined from aerial photographs. Cover classes 1 (10–20%), 2 (20–50%), and 3 (50–80%) had been clearcut or heavily logged, and farmed or locally planted with tree crops before 1936. Cover class 4 (80–100% cover) had been lightly selectively logged.

‡ Percentage slope and elevation were calculated as the means of values at the four corner points of each 20 × 20 m quadrat.

soil, and percentage slope (Table 4). Cover class and rockiness produced the strongest correlations with both Axis 1 and Axis 2, because tree felling and farming occurred on the least rocky and flatter part of El Verde Tract, where historic cover classes 1, 2, and 3 on the LFDP were located.

Environmental influences on species distributions were further evaluated by removing the influence of historic cover class (and thus land use history). We conducted NMS and correlation analysis on a combined data set of cover classes 2 and 3 (combined because their land use histories appeared similar; cover class 1 included too small an area) and separately on cover class 4. When the effect of cover class was removed, the strength and number of correlations with environmental characteristics generally increased (Table 4). Plots within classes 2 and 3 were separated primarily by percentage slope and rockiness, with the highest environmental correlations on Axis 2 (24.1% of the variance; Table 4) identifying flatter and less rocky areas occupied by *Casearia arborea* (Fig. 8) and *Tabebuia heterophylla* (Fig. 9g). Within class 4, the most important variables correlating with Axis 1 (41.7% of the variance) were elevation and soil characteristics (Table 4), mainly as a result of the occurrence of *Cyrilla racemiflora* and *Matayba domingensis* in the highest (southeastern) portion of this cover class (Fig. 9h, i).

DISCUSSION

Ecologists are well aware that human disturbance in the past has influenced the tree species composition of some present-day tropical forests (Clark 1996, Whitmore and Burslem 1998). Given the long life-spans of trees, we should expect a long-term effect of human disturbances. Ecologists are also aware that the environment influences present forest stand characteristics. Our study, however, has shown that the effects' of human disturbance have persisted for more than 60 yr and have overridden the effect of environmental gradients on species composition. We will now compare the LFDP to other tropical forests and discuss how specific land uses and environmental features affected stand structure and composition. We also will weigh the relative effects of human vs. natural disturbance on this forest stand, and will draw lessons from our results for biodiversity conservation.

Comparison with other tropical forests

In the LFDP, stem density was higher and basal area was similar to the values of other tropical forests: (822.9 stems/ha and 36.7 m^2/ha basal area in the LFDP vs. means of 497.4 stems/ha and 36.6 m^2/ha from many forests (Meave and Kellman 1994; see Leigh 1999). The LFDP had a higher density of small-diameter trees than did most tropical forests, probably due to disturbance-

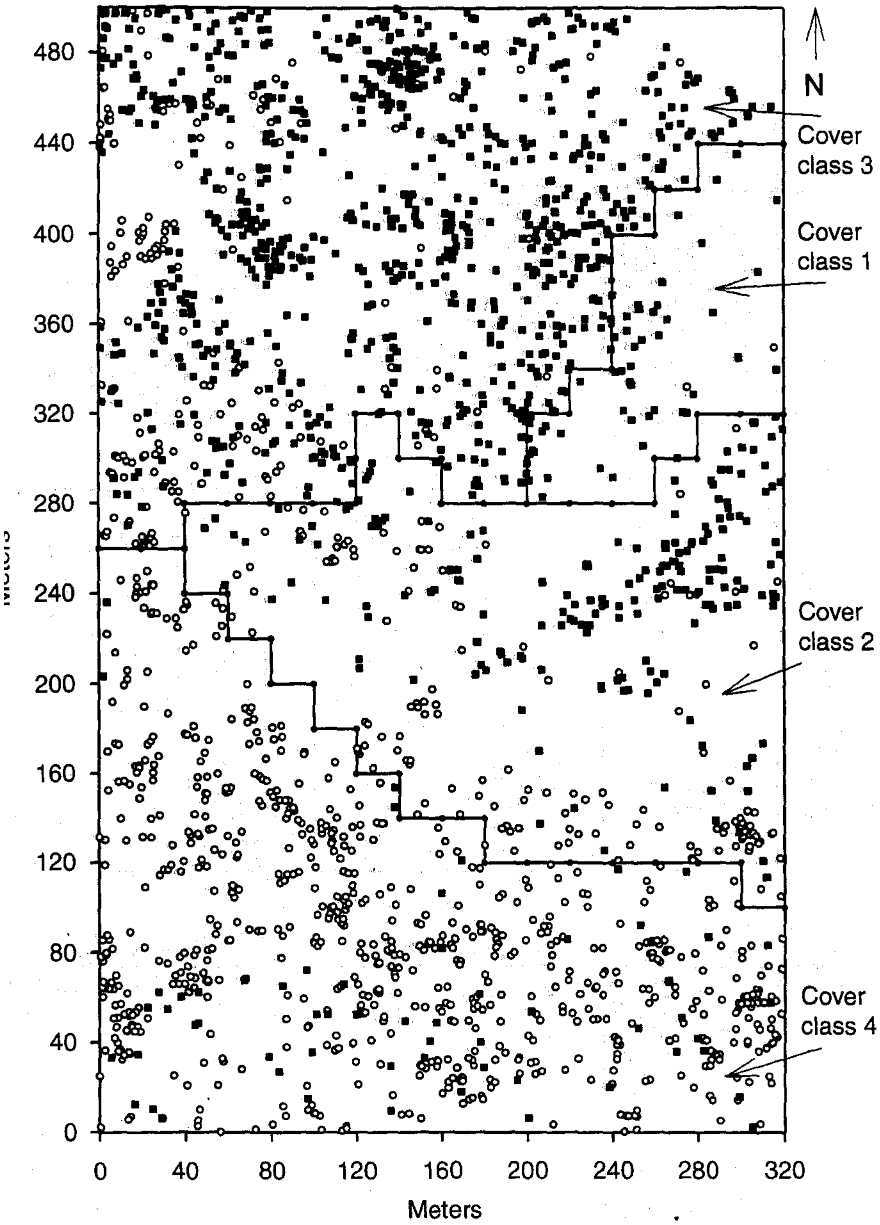

FIG. 8. Distributions of *Dacryodes excelsa* (open circles), a mature forest tree species, and *Casearia arborea* (solid squares), a secondary species, on the 16-ha Luquillo Forest Dynamics Plot at El Verde, Puerto Rico. Lines show boundaries of historic Cover classes, defined in Fig. 3. (Modified from Willig et al. [1996], copyrighted 1996 by the Association for Tropical Biology, P.O. Box 1897, Lawrence, Kansas 66044-8897. Reprinted by permission.)

related regeneration and to the abundance of the relatively small *Prestoea acuminata.* Basal area and stem density in cover class 4 (826 stems/ha and 40.8 m^2/ha) were similar to those reported for tabonuco forest near the LFDP at El Verde, and twice those recorded at another site in the Luquillo Mountains (Soriano-Ressy et al. 1970). Tree size and basal area in cover class 4, however, are about half those of tabonuco forest in Dominica, where there has been less hurricane and human disturbance (Perez 1970, Soriano-Ressy et al. 1970).

Compared with most other humid tropical forests at low to middle elevations, the LFDP had fewer species per hectare with stems $\geq$ 10 cm D_{130} (44.3 spp./ha in LFDP vs. 46–283 species/ha in other forests; Brokaw et al. 1997, Leigh 1999). In cover class 4, the least disturbed section, the mean of 48 species/ha was slightly higher than for the whole LFDP (mean 44.3 spp./ha, range 33–52 species/ha) but was still low relative to other forests. The low species numbers compared to other tropical forests may be a result of the island bio-

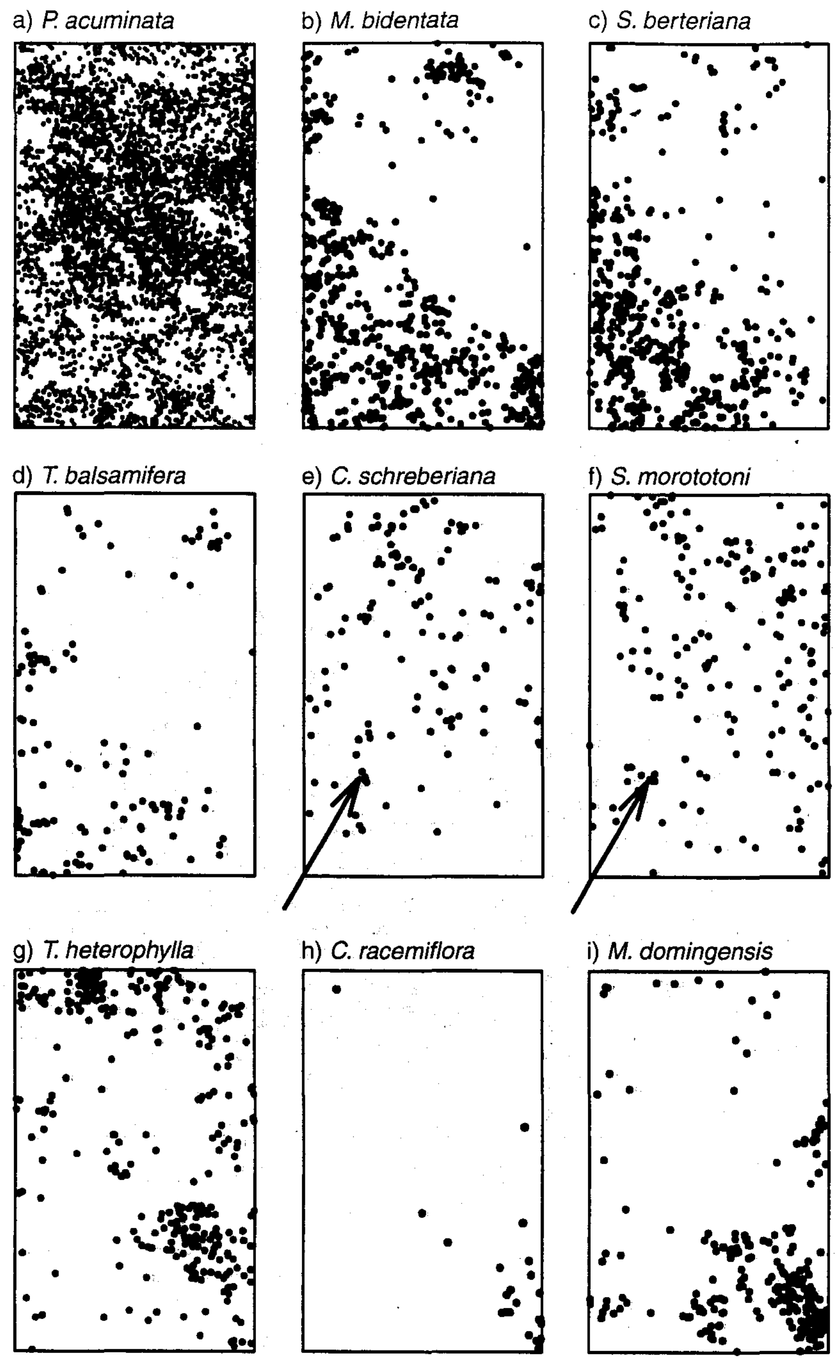

FIG. 9. Distribution of stems ≥ 10 cm D_{130} for a sample of nine species on the Luquillo Forest Dynamics Plot at El Verde. Puerto Rico: (a) *Prestoea acuminata,* (b) *Manilkara bidentata,* (c) *Sloanea berteriana,* (d) *Tetragastris balsamifera,* (e) *Cecropia schreberiana,* (f) *Schefflera morototoni,* (g) *Tabebuia heterophylla,* (h) *Cyrilla racemiflora,* and (i) *Matayba domingensis.* Arrows in (e) and (f) mark the location of the "Cut Center," a gap created in 1963 (Odum and Pigeon 1970).

geographic effect that predicts lower species richness on small islands (Whittaker 1998). The LFDP is typical of tropical forests, however, in showing some degree of dominance by a few species and having a high proportion of rare species (Brokaw et al. 1997, Pitman et al. 1999).

Historic canopy cover, present stand structure, and land use history

Canopy cover as seen in aerial photographs from 1936 reflected the extent of forest clearing and time for recovery, the intensity and type of subsequent farming or other human disturbance, and environmental characteristics. The section of historic cover class 1 was at a higher elevation and potentially less accessible than other sections, and may have been the last area cleared of forest. Its more fertile soils of Crista1 clay may have encouraged farming, while its slopes may have increased erosion and slowed canopy recovery. The section of cover class 2 had similar fertile soil, was at a lower elevation and potentially more accessible, and therefore probably was cleared earlier than class 1. Although cover class 3 had wetter and less fertile Zarzal clay soil than cover classes 1 and 2, it was also less rocky, had not so rugged topography, and was at a lower elevation closer to the sawmill. Cover class 3 is likely, therefore, to have been the first part of El Verde Tract 11 to be cleared. A longer recovery time and lower intensity farming may explain the greater canopy cover in cover class 3 than in classes 1 and 2. The section of cover class 4, perhaps as a result of its distance from the sawmill, higher elevation, low fertility, and rocky soil, was apparently never cleared and so had the highest canopy cover in 1936.

Historic land uses have apparently also affected present stem density and diameter class distributions. In the LFDP census, the section of historic cover class 1 had the lowest stem density, consistent with the low density in a formerly clear-felled site near the LFDP (Zou et al. 1995). An even-aged stand of *Calophyllum calaba,* resulting from Forest Service planting, and the high proportion of *P. acuminata* probably contributed to the difference in diameter class distributions between cover class 1 and the other classes. Cover class 4, which was selectively logged and silviculturally "improved," had the highest basal area. This may reflect, in part, the "stand improvement" by the Forest Service some 40 yr before this study, which was intended to produce a greater basal area.

Present tree communities, land use history, and environment

The location of sections with different percent canopy cover in 1936, reflecting land use history, accounted for more of the statistical variance in the NMS ordination of tree species composition on the LFDP than did environmental factors. The species now present in the different historic cover classes reflect land use intensity or time since abandonment. In cover class 1, which had been cut over by Bliss Plywood Corporation, there was a high density of *Prestoea acuminata.* This species has been associated with the intense human disturbance of charcoal production in another tabonuco forest area (García-Montiel and Scatena 1994). In cover classes 2 and 3, which were also cut over by Bliss Plywood, we found abundant *Casearia arborea*, as also observed in other formerly clear-felled areas at El Verde (Zou et al. 1995). Cover classes 2 and 3 also contained abundant *Inga laurina* and relatively few *Dacryodes excelsa* and *Manilkara* bidentata This pattern is seen in coffee areas in Puerto Rico where growers plant the legumes *Inga* spp. to supply soil nitrogen and cast light shade, and remove *D. excelsa* and *M.* bidentata because they cast heavy shade and are valuable for timber (García-Montiel and Scatena 1994, Wadsworth 1997). In cover class 4, "timber stand improvement" would have favored mature forest species such as *D. excelsa* and *M. bidentata* (E Wadsworth, cited by Odum 1970) that characterize the forest in that section of the LFDP. Stand improvement may thus have accentuated the differences in species composition between this and the other cover classes.

Land use also can account for differences in species diversity. The section of historic cover class 1 had markedly lower richness and diversity and fewer unique, rare, or endemic species than the other classes. Species accumulation curves showed that these differences were not due to unequal sample sizes of plot area or number of individual trees. Instead, the lower species richness in cover class 1 is probably related to its being the most recently and, perhaps, most intensely disturbed section. Cover class 4, the least disturbed section, had somewhat higher species richness and diversity and more unique, rare, and endemic tree species than cover classes 1, 2, and 3. Cover class 4 was selectively logged and thinned, but never cleared. Selective logging can affect relative abundances but does not necessarily reduce species richness (Grieser Johns 1997, Cannon et al. 1998). Some, but not the majority (N. Brokaw, personal observation), of the unique, rare, and endemic tree species in cover class 4 are habitat specialists, e.g., species characteristic of higher elevations (Weaver 2000). The absence of characteristically high-elevation species at lower elevations in the forest cannot, therefore, necessarily be attributed to land use, but disturbance may have eliminated them from the higher elevations of cover classes 1 and 2.

Our results are consistent with patterns in a successional sequence in Venezuela, where the oldest, least disturbed forest had more unique species than younger forests (Saldarriaga et al. 1988), and with observations that endemic species are lacking in secondary vegetation in the Philippines (Brosius 1990). In a Puerto Rican study, however, species number and diversity in forests regrown in pastures and abandoned coffee plantations in the Luquillo Mountains were similar in number and diversity to nearby, relatively undisturbed forest (Zimmerman et al. 1995, Aide et al. 1996; but see Brown and Lugo 1990, Finegan 1996). We note, however, that the species present in these old pastures and coffee plantations were different from those in the undisturbed forest (Zimmerman et a]. 1995, Aide et al. 1996; but see Fujisaka et al. 1998), confirming that land use is a major determinant of forest composition.

Although second in importance to past land use, as reflected by historical cover class, environmental features significantly influenced tree distributions on the LFDP (cf. Wadsworth 1970, Crow and Grigal 1979, Basnet 1992, Johnston 1992). The environmental correlations were stronger when the effect of canopy cover class was removed from the NMS ordination. In the ordination of all LFDP quadrats, rockiness was second in importance to cover class on Axis 1 of the NMS ordination, and first in importance on Axis 2. Rocks are exposed in stream channels, reduce the area for tree establishment, and influence soil water availability. Environmental features such as rockiness are, of course, related to land uses; people select particular topographies and soil types for particular land uses (Foster 1992, García-Montiel and Scatena 1994).

Present tree communities and natural disturbance

As mentioned previously, natural disturbances at El Verde include hurricanes, small-scale treefalls, floods, and landslides. The impacts of these vary at landscape and stand scales (Boose et al. 1994, Scatena and Lugo 1995) and affect stand structure and species composition (Weaver 1989). There is no indication, however, from data on spatial distribution of natural disturbances (Guariguata 1990, Scatena and Lugo 1995, Everham 1996) that these disturbances, including the hurricanes of 1928 and 1932, could have produced the differences in canopy cover in 1936 (and especially some well-delineated boundaries between cover classes). A study over the whole of the Luquillo Mountains showed no obvious correlation between canopy cover and the 1928 and 1932 hurricanes (Foster et al. 1999). Hurricanes can, however, reinforce the dominant effect of land use on tree composition, because they damage pioneers more than mature forest species (Zimmerman et al. 1994; but see Willig et al. 1996). Thus storms can reopen secondary forests of pioneer species in human-disturbed areas to renewed pioneer colonization.

Natural disturbance in the Luquillo forests mainly affects populations of secondary species (Doyle 1981, Zimmerman et al. 1994, Brokaw 1998). Of the three common secondary species in the LFDP, *Cecropia schreberiana* and *Schefflera morototoni* were fairly evenly distributed across the LFDP (Fig. 9e, f) as a result of their colonization of treefall gaps. Although there are somewhat more individuals of these species in cover classes 1, 2, and 3, they contributed little to the patterns in the NMS ordination. *Casearia arborea* is also a secondary species associated with human disturbance (Zou et al. 1995) and did help to group quadrats in the NMS ordination.

Future tree communities and biodiversity

At one time reduced to only 6% of the landscape in Puerto Rico, forests had reclaimed cleared areas and covered 30% of the landscape by 1980 (Birdsey and Weaver 1987, Thomlinson et al. 1996). Our results, however, suggest that secondary forests, represented by historical cover classes 1–3 on the LFDP, harbor few rare and endemic tree species, whereas less disturbed forest represented by cover class 4 harbors more. In Singapore, similarly, species richness accrued slowly in secondary forests (Turner et al. 1997). If forest is allowed to regrow on cleared and abandoned lands, the area of second-growth forests could increase elsewhere in the tropics, in a similar manner to that in Puerto Rico (Brown and Lugo 1990). Our results suggest that forests regrowing after human disturbance are likely to have few rare and endemic species. Fortunately, the ecosystem function, tree diversity, and composition of secondary forests may resemble those of older forests (Brown and Lugo 1990, Aide et al. 1996), and thus, in time, forests may have the potential to fully recover their original species composition.

Conclusion

We have demonstrated the paramount effect of human land uses that ended 40–60 yr prior to our study on the patterns of tree species composition in a 16-ha tropical forest plot. The legacy of different land use in the plot is discernible in the patterns of species distributions. When considering the whole plot, these legacies overrode variation due to environmental gradients, such as soils and topography, which are known to affect tree distributions. Both environmental variation and natural disturbance shape the LFDP tree community, but human disturbance, such as clearing for agriculture, created more extreme environmental conditions than those represented by either natural gradients or natural disturbance. Thus human land uses have the greater effect and longer legacy.

Margalef (1968) would rightly assert that there is a negligible possibility of our predicting, in detail, the future state of a tropical forest. Our study demonstrated the dominant effect of past land use on the species composition within this tropical tree community and described details of the composition that may characterize future forests that regrow in Puerto Rico after human disturbance. This information is critical to biodiversity conservation. Rare and endemic species may need to be reintroduced to reforested areas, and the less disturbed communities, which have retained such species, merit special protection in order to survive. We suggest that studies of tropical forests carefully assess land use history, both for clues to present conditions and for guidelines for conservation.

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APPENDIX

A table providing stem density and basal area of all tree species in each of the cover classes of the 16-ha Luquillo Forest Dynamics Plot at El Verde, Puerto Rico, at the time of Hurricane Hugo, is available in ESA's Electronic Data Archive: *Ecological Archives* A012-013-A1.