

Forest vegetation along environmental gradients in northeastern Puerto Rico

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Forest composition and structure from sea level to the >1000 m summits of the Luquillo Mountains in northeastern Puerto Rico is a function of climatic gradients in rainfall, temperature, and cloud cover as well as regional land use history, including past agricultural activities and conservation efforts. With ascent, mean annual rainfall increases five-fold and mean annual temperature declines by about 6°C. Over the same gradient, six ecological life zones are encountered, ranging from subtropical dry forest to subtropical lower montane rain forest. Forest composition, structure, and dynamics at any particular elevation reflect human influences, environmental variables, and recurrent hurricanes. Urbanization, cleared land, and young secondary forests are prevalent at lower elevations, whereas protected secondary and mature forests predominate at upper elevations. Human activities (logging, clearing, agriculture, and tree plantings) accompanied by secondary regeneration have contributed to species' compositions at lower elevations. Nearly 150 native and introduced tree species have been planted near the Luquillo Experimental Forest (LEF) boundary, including >4 million seedlings at 54 plantation sites on 2000 ha of abandoned farmland. Today, secondary or planted species are represented in the LEF's post-disturbance forests where their signature may remain for a century or more. Recognized forest types along the gradient change from coastal mangroves and dry forest through moist coastal plain and lower slope forests with secondary and plantation species, to four montane types: tabonuco forest from 150 to 600 m; colorado forest between 600 and 900 m; palm brake in ravines and on steep slopes above 450 m; and dwarf forest above 900 m, with a stunted version of the latter growing on LEF summits. Environmental variables include aspect, topography (i.e. ridge, slope, and ravine), and exposure. Recurrent hurricanes maintain forests in constant flux and impacts vary by trajectory, storm attributes, and landscape features, all of which influence the amount of forest damage and subsequent recovery.

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The Luquillo Mountains in northeastern Puerto Rico rise abruptly from sea level to 1074 m at El Toro Peak in the Luquillo Experimental Forest (LEF) (Fig. 1). The simplest classification of forest types along this gradient recognized moist coastal forest surrounding the mountains, and lower and upper forests within the LEF (Little and Wadsworth 1964). During the 1940s, climax forests along the same gradient from shoreline to mountain summit were described in the Lesser Antilles as follows (Beard 1949): edaphic climax formations along the coast (i.e. swamp forest and mangrove woodland); dry evergreen formations (i.e. dry evergreen forest, evergreen bushland, and littoral woodland); seasonal formations (i.e. evergreen seasonal forest, semi-evergreen seasonal forest, and deciduous seasonal forest); rain forest; and montane

formations (i.e. lower montane rain forest, montane rain forest, palm brake, and dwarf forest). The same montane formations were adopted for the LEF with local names: tabonuco forest between 150 and 600 m; colorado forest between 600 and 900 m; dwarf forest above 900 m; and palm brake on steep windward facing slopes and in drainages above 450 m (Wadsworth 1951). Six ecological life zones have also been described for northeastern Puerto Rico (Ewel and Whitmore 1973): subtropical dry forest along the coast; subtropical moist forest and subtropical wet forests surrounding the LEF; subtropical rain forest to the windward; and both lower montane wet and lower montane rain forests at higher elevations. Zonal (i.e. typical or characteristic), edaphic (e.g. palm brake), and atmospheric associations (e.g. cloud forest) are recognized

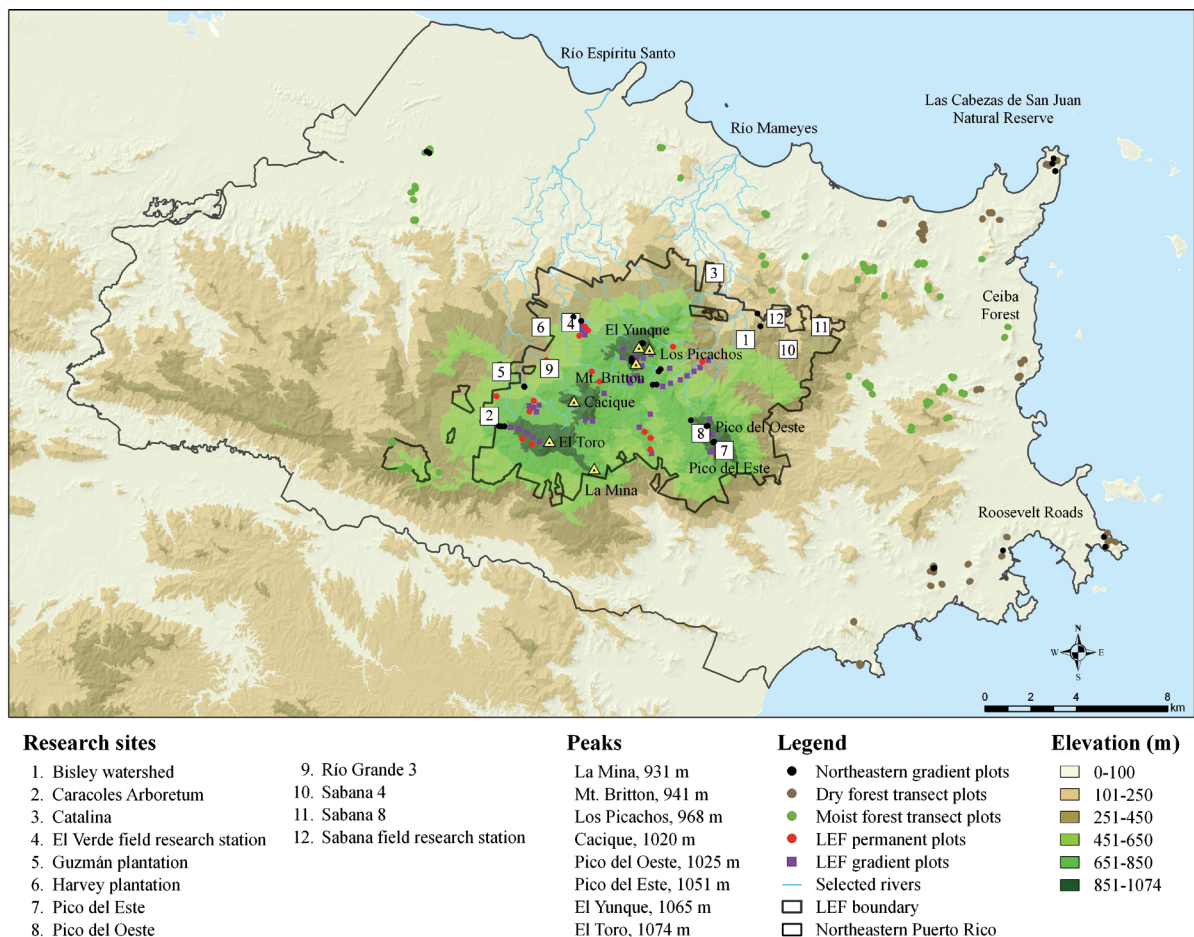


Figure 1. Northeastern Puerto Rico showing the Luquillo Experimental Forest boundary, elevational ranges, sampling sites, and places mentioned in text.

divisions within the broad life zone classification system (Holdridge 1967).

In addition to major forest types associated with elevation, early Caribbean botanists and foresters observed that environmental variation over short distances caused changes in forest structure and composition. Slope forests in Jamaica had vegetative characteristics intermediate between those of ridges and ravines (Shreve 1914). In the mountainous Lesser Antilles, lower montane forest grew at higher elevations on leeward slopes than windward exposures (Beard 1949). In Puerto Rico, dwarf forest was associated with low temperatures, persistent wind and fog, heavy precipitation, and water-soaked soil (Gleason and Cook 1927). Dwarf forest could be considered a subdivision of colorado forest because it has fewer species, none unique to the type, manifesting the adversity of the exposed summits (Wadsworth 1951). Similarly, palm brake occurs on steep slopes with saturated, un-

stable soils, conditions that favor fewer tree species than are typically found in bordering tabonuco and colorado types.

Trees follow numerous pathways to maturity depending on their life cycle strategies (Gómez-Pompa and Vázquez-Yanes 1974). During centuries of human activities, however, >99% of Puerto Rico's native forests were cutover or disturbed, including the lower one-half of the LEF (Wadsworth 1950). Today, forest composition and structure in northeastern Puerto Rico reflect not only environmental variables but also land use history and conservation efforts. The purpose of this report is to describe the island's northeastern vegetation based on existing information and to explore its inherent variation along environmental gradients. The major gradients are elevation with its influence on climate and past human activity, and topography with its differences in slopes, soils, and exposure; moreover, hurricanes recurrently impact the land-

scape. Nomenclature follows relatively recent taxonomic work (Liogier 1985–1997).

Setting

Climatic, landscape, and human influences

Puerto Rico lies in the path of the easterly trade winds and the LEF is their first barrier after traversing the Atlantic. During the year, the island is affected by tropical waves, depressions, storms, and hurricanes that occur from May to October, and by northerly cold fronts during the winter months (Calvesbert 1970). Over a distance of 20 km, mean annual wind velocity changes from 15 km h⁻¹ along the windswept coastline at Roosevelt Roads Naval Base and Las Cabezas de San Juan Natural Reserve through about 4–6 km h⁻¹ at Catalina and El Verde between 200 and 350 m elevation, to 18 km h⁻¹ on the LEF summits (Briscoe 1966, Baynton 1968, Odum et al. 1970). Cloud cover and mean annual rainfall increase with elevation, the latter from 900 mm along the coast to >4500 mm on the peaks (Briscoe 1966). On the summits, mean annual solar radiation averages 60% of that received along the coast, and cloud moisture filtered by the vegetation as clouds pass through adds 10%-more moisture to already saturated soils (Briscoe 1966, Baynton 1968, 1969, Weaver 1972). Over the same gradient, mean annual temperature declines from 25 to 19°C, saturation pressure deficits decrease, and relative humidity ascends from modest midday values to a nearly constant 100%.

About 80% of the Luquillo Mountains are underlain by marine volcanoclastic rocks (i.e. breccia, conglomerate, mudstone, and sandstone) ranging in age from early Cretaceous to mid-Eocene (i.e. about 145 to 45 million yr ago) (Cox and Briggs 1973). LEF soils are highly leached inceptisols and ultisols made up of silty clay loams, silty clays, and clays in different horizons (USDA Natural Resources Conservation Service 2002).

Climatic changes associated with elevation in the LEF affect forest structure, tree species composition, and forest dynamics (Weaver and Murphy 1990) and local factors such as aspect, topography, and exposure are important at any particular elevation (Crow and Grigal 1979, Weaver 1991, 2000). Topography affects soil formation, erosion, organic matter concentrations, soil moisture content, and water movement (Scatena and Lugo 1995). It also affects landslide potential and tree species colonization after disturbance (Guariguata 1990, Simon et al. 1990, Basnet 1992). Past land use at lower elevations in the LEF and temporal conditions (i.e. pre- and post hurricane disturbance) are also critical factors (Walker et al. 1991, 1996). Mature forest species like *Buchenavia pentaphylla* and *Manilkara bidentata* that previously grew in lowland moist or lower slope forests are today largely confined

to tabonuco forest in the LEF (Gill 1931, Wadsworth 1950).

Hurricanes and vegetation impacts

Since 1700, Puerto Rico has experienced at least 33 hurricanes, four of which passed over the mountains and several others close enough to have caused impacts (Salivia 1972, Weaver and Schwagerl 2009). Major hurricanes over or near the LEF during the 20th century include San Felipe (1928), San Cipriano (1932), Hugo (1989), and Georges (1998) (Salivia 1972, Weaver 2002). Hurricane trajectories, storm characteristics (i.e. wind velocity, forward movement, rainfall, and duration), landscape features, and innate differences among tree species all influence the amount of forest damage and recovery rates (Wadsworth and Englerth 1959, Walker et al. 1991, 1996, Basnet 1992, Basnet et al. 1993, Weaver 1999). Observations of forest damage after Hurricane Hugo, however, showed that it was patchy with 'large areas of LEF not damaged at all' (Walker 1991).

Hurricanes maintain the island's vegetation in constant flux. Defoliation, stem breakage, and uprooting of trees occur during the storms (Bates 1929). Post-storm response includes the rapid recovery of tree foliage and lost branches, the regeneration of secondary species, and the growth of vines and herbs in forest openings (Brokaw and GEAR 1991). Within a few years, stand density increases and tree growth is comparatively rapid (Crow 1980, Weaver 1989a). Subsequently, as surviving stems compete, the proportion of suppressed trees in the understory increases, and both stem density and growth decline. Tree species richness is highest a few years after hurricanes when stands contain a mixture of primary and secondary species. During the next 30–35 yr, surviving trees and stands gradually increase in dbh (i.e. diameter at 1.4 m above ground), height, and biomass. Mean specific gravity of the forest also increases because lighter, short-lived secondary species disappear while heavier, longer-lived, mature forest species gradually dominate.

Data sources

Most observations summarized in this report were taken from studies carried out during the past 25 yr, including:

- 1) Northeastern gradient plots: a series of 72 plots each 10 × 10 m located in representative forests ranging from the coast to the LEF summits. Eight different forest types were surveyed, each within three separate sampling sites by using 0.01 ha plots replicated nine times. All plots were set up in mature, representative forest >60 yr old. The sites ranged from subtropical dry forest at the former Roosevelt Roads and Las Cabezas Reserve through six intermediate forest types at different elevations to subtropical lower

montane rainforest (i.e. dwarf forest) at ~1000 m on Pico del Oeste. All tree species ≥ 2 cm in dbh were identified, tagged, and measured. Dbh, and mean and maximum plot canopy heights were recorded along with all vascular species and associated environmental characteristics (Gould et al. 2006).

2) Forest transects: a set of 960 variable radius plots arranged along transects from forest edges to interiors provide information on forest structure and composition of typical secondary lowland moist and dry forests in Puerto Rico, with the majority of the plots in the northeastern region surrounding the Luquillo Mountains. Forest fragments, typically recovering from past agricultural uses, were identified as younger (<30 yr) or older (>30 yr) secondary forest. Plot data included tree species, dbh, height, canopy volume, number of stems, and environmental characteristics. Data summarize both edge and interior plots (Gould et al. 2008). In addition, surveys were conducted in representative dry forests (i.e. secondary semi-evergreen seasonal forest, secondary littoral woodland, and abandoned coconut plantation) along the coast at Las Cabezas Reserve (Weaver et al. 1999, this study). Minimum dbh was 4 cm.

3) LEF permanent plots: permanent plot monitoring in the LEF, beginning in 1943, was carried out on 23 plots in representative tabonuco, colorado, palm brake, and dwarf forests (Crow 1980, Weaver 1983, 1989a, 1991, 1999, 2008, Frangi and Lugo 1985, 1991, 1998). Plot sizes were 0.4 or 0.2 ha in tabonuco (5 plots), 0.4 ha in colorado (9 plots), 0.4 or 0.25 ha in palm (3 plots), and 0.025 ha in dwarf (6 plots) forests. Minimum dbh was 4 cm except for one palm plot with 2.5 cm.

4) LEF gradient sampling: a series of closed forest plots totaling 5.78 ha situated in different parts of the LEF. Plots at each site, spaced from 50 to 100 m apart in elevation, were stratified in groups of three by topography (i.e. ridge, slope, or ravine) and located roughly between 380 and ~1000 m elevation. Plot sizes were 0.05 ha in tabonuco (18 plots), colorado (69 plots), and palm brake (12 plots) forests, and 0.025 ha in dwarf (33 plots) forest (Weaver 1991, 2000, 2008, 2010, this study). Minimum dbh was 4 cm.

All measurements and analyses were in metric units. The difference between monitoring and gradient plots is important. Most monitoring plots were selected to represent mature forest types (i.e. zonal vegetation). Incidentally, they also provide information on hurricane impacts and recovery. Gradient plots were established more recently to explore environmental differences in composition and structure. Considerable variation in plot data was evident, due partly to the variety of habitats sampled and partly to small sample sizes.

Additional observations come from remote sensing analyses and land cover characterization based on Landsat ETM+ imagery obtained between 1999 and 2003 and classified to set of 70 land cover classes for the Puerto Rican Archipelago (Gould et al. 2008). Analyses of the distribution of land cover and forest types along the eleva-

tional gradient in northeastern Puerto Rico indicates both environmental and anthropogenic controls on the landscape patterns, and provides a context in which to better understand patterns of forest species distributions.

Tree species and forest types

Most of the island's 550 native tree species grew within the variety of forest types found in northeastern Puerto Rico at the time of discovery (Little and Wadsworth 1964, Little et al. 1974). Subsequently, dry coastal and lowland moist forests were altered by logging, agriculture, tree planting, urban development, and secondary regeneration. The results of past surveys and gradient sampling provide estimates of tree species richness for northeastern Puerto Rico: 1) littoral woodland and seasonal semi-evergreen forest: at least 88 species (Weaver et al. 1999). 2) Coastal plains and lower foothills: about 200 tree species within a dense, largely evergreen forest at the time of discovery (Wadsworth 1950). 3) Luquillo Mountains: one center of high species richness and endemism in Puerto Rico with at least 830 native species of plants and >250 species of trees (Figuroa Colon 1996). 4) LEF: at least 225 species of native trees in 144 genera and 59 plant families within the upper 57% of the Luquillo Mountains (Little 1970, Little and Woodbury 1976). Of the 88 species classified as either endemic or rare in the LEF, 16 are endemic only to the LEF, another 45 are endemic to Puerto Rico and also found in the LEF, and 20 species are classified as rare in Puerto Rico but also native to areas outside of the island. 5) Tabonuco: 73 tallied on 4 ha and 168 noted during excursions to several sites (Little 1970); also, 69 tallied on 0.9 ha during gradient sampling (Weaver this study). 6) Colorado: 51 tallied on 4 ha (Little 1970) and 73 on 3.75 ha during past gradient sampling (Weaver 1989a). 7) Palm brake: 63 recorded on 4 ha (Little 1970) and 36 tallied on 0.6 ha in gradient sampling (Weaver this study). 8) Dwarf: 54 observed on 0.82 ha during gradient sampling (Weaver 2008).

For purposes of this report, twelve forest types are recognized from sea level to the LEF summits (Fig. 2, 3). They include coastal forests: 1) mangrove, 2) semi-evergreen seasonal (subtropical dry) forests, 3) littoral woodlands, and 4) old coconut palm plantations; lowland moist forests: 5) *Pterocarpus* swamp and riparian forests, 6) lowland moist zonal forests, and 7) lowland moist and lower slope secondary forests; and montane forests: 8) forest plantations with secondary forest, 9) tabonuco forest, 10) colorado forest, 11) palm brake, and 12) dwarf forest.

Coastal forests

Subtle elevational and hydrologic gradients control the occurrence of natural vegetation and also favor certain hu-

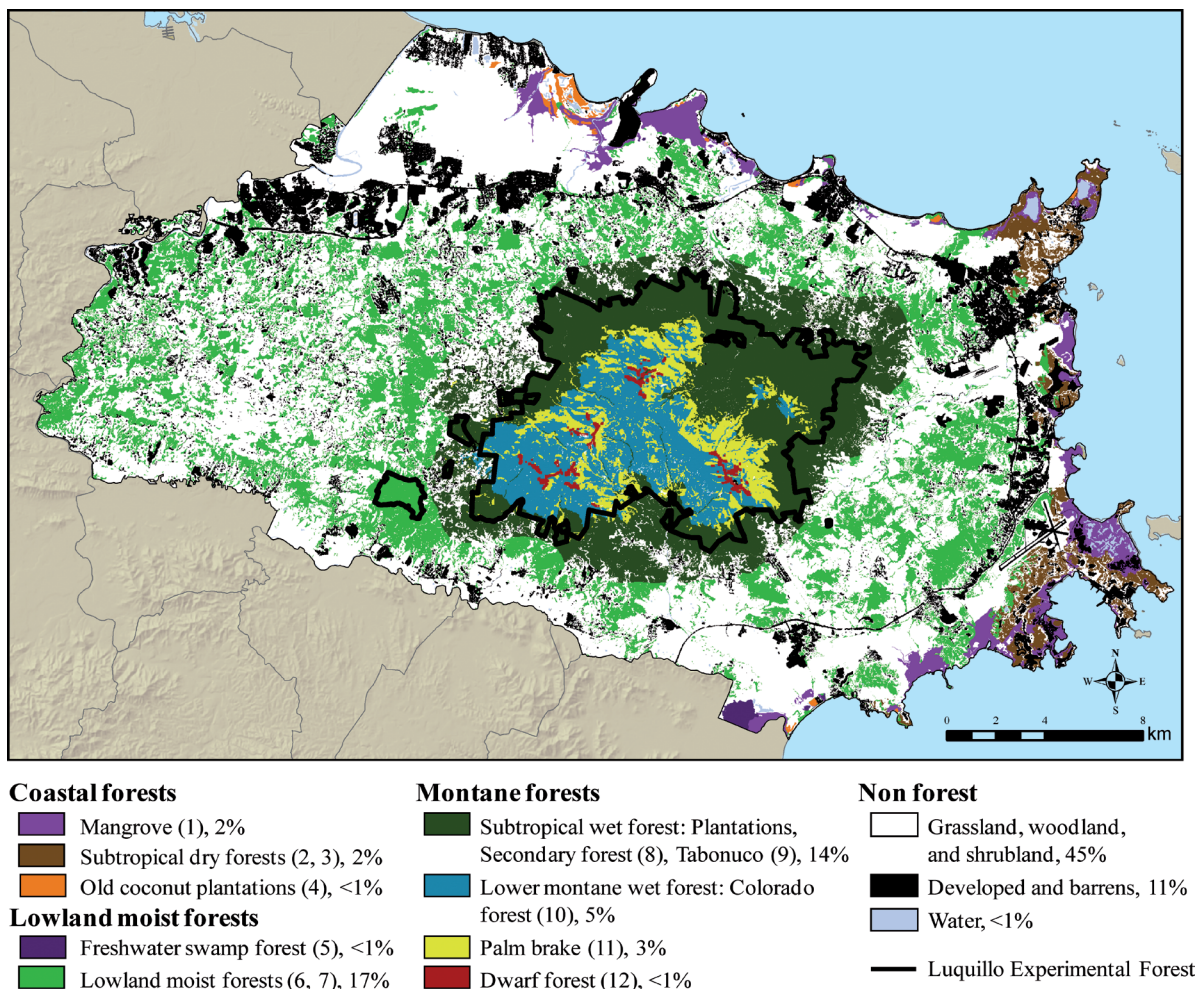


Figure 2. Major land cover types in northeastern Puerto Rico including coastal, lowland moist, and montane forests, which occupy over 50% of the area, and nonforest vegetation, unvegetated developed land and barrens, and water. Classification based on 1999–2003 Landsat ETM+ imagery and modified from Gould et al. (2008). Numbers in parentheses (i.e. 1–12) refer to forest types as described in this chapter.

man activities in the coastal zone. Among them are topographic and associated salinity gradients at or very near sea level that influence the distribution of mangrove species (Lugo and Snedaker 1974); the growth of secondary littoral woodlands under the influence of wind and salt spray along shorelines; the regeneration of secondary semi-evergreen seasonal forest on abandoned pastures and hills up to 100 m; and the development of coconut plantations on relatively level terrain. The northeastern sea coasts were originally occupied by littoral woodland and mangroves (Wadsworth 1950), freshwater swamp forests, and different types of subtropical dry forests. *Pterocarpus* formed extensive stands in freshwater swamps and extended to higher elevations along riparian corridors. Species associated with drier conditions include *Bursera simaruba* and *Guaiacum officinale*, which were likely prevalent on less

protected coastal slopes and hilltops, and *Bucida buceras* which also grows in coastal basins and along streams (Gill 1931, Little and Wadsworth 1964). In protected locations, species associated with moist forests such as *Calophyllum calaba*, *Manilkara bidentata*, *Tabebuia heterophylla*, and *Mastichodendron foetidissimum* were likely common. Today, some protected coastal areas such as the Las Cabezas Reserve, the Commonwealth of Puerto Rico's Ceiba forest, and parts of Roosevelt Roads are recovering in secondary forest (Fig. 1).

1) Mangrove

Mangrove forests have gone through a period of decline and partial recovery related to human activities such as altered hydrology for agricultural practices, urbaniza-



Figure 3. Montane forest types include (a) dwarf, (b) colorado, (c) tabonuco, (d) sierra palm, and (e) mahogany plantations. Coastal and lowland forest types include (f) lowland moist secondary, (g) subtropical dry, (h) *Pterocarpus* swamp and riparian, and (i) *Laguncularia racemosa*–*Avicennia germinans* mangrove.

tion, and the implementation of conservation activities (Martinuzzi et al. 2009). Mangroves cover about 1900 ha in northeastern Puerto Rico and account for 22% of all of the island's mangrove forests. The largest remaining areas are found east of the Río Espíritu Santo, in the Las Cabezas Reserve, in the Ceiba Forest, and at Roosevelt Roads. These mangroves are typically characterized as: *Rhizophora mangle* dominated stands on coastal and estuarine fringes; *Avicennia germinans* and *Laguncularia racemosa* in basins as pure or mixed stands; or *Conocarpus*

erectus and the shrub *Suriana maritima* in mixed stands. Species richness is very low. Mangrove forest structure is strongly affected by salinity, nutrient availability, and storm disturbance. Typical mixed mangrove *Laguncularia racemosa*–*Avicennia germinans* associations growing at the Las Cabezas Reserve and Roosevelt Roads areas had canopy heights of 12 m, stem densities (stems ≥ 10 cm) of 344 stems ha^{-1} , and relatively low basal area (15 $\text{m}^2 \text{ha}^{-1}$) and aboveground biomass (57 t ha^{-1}) (Gould et al. 2006).

2) Subtropical dry forest – secondary semi-evergreen seasonal forest

Subtropical dry forests occur between sea level and up to nearly 100 m elevation in northeastern Puerto Rico (Gould et al. 2008). They are predominantly young secondary forests with some mature stands occurring in reserves. In the Las Cabezas Reserve semi-evergreen forest covers 40% of the area and has the largest component of tree species. Different successional patterns may evolve with some species favoring drier windward slopes and ridges and others moister ravines and protected lower slopes. Topography controls the forest structure as well with shorter trees and higher stem densities on ridges as opposed to slopes and ravines. The following species are well-distributed in different forest types at Las Cabezas Reserve: the exotic *Leucaena leucocephala*, and the natives *Capparis cyanophallophora*, *C. flexuosa*, *C. indica*, *Coccoloba microstachya*, *C. uvifera*, *Cordia laevigata*, *Jacquinia arborea*, *Pithecellobium unguis-cati*, and *Randia aculeata*. In addition, the natives *Acacia farnesiana*, *Bursera simaruba*, *Capparis hastata*, *Cassine xylocarpa*, *Erythroxylum brevipes*, and *Gymnanthes lucida* and the exotics *Gliricidium sepium* and *Tamarindus indica* typically grow in semi-evergreen seasonal forest (Weaver et al. 1999).

In 1998, about 9 yr after the passage of Hurricane Hugo and 4 months after Hurricane Georges, a permanent 0.10 ha plot was established in the reserve's semi-evergreen forest to determine species composition, forest structure, and dbh growth rates. The first tally showed 16 tree species, 2170 stems ha^{-1} , a mean stem height of 5.4 m, and a basal area of 16.5 $\text{m}^2 \text{ha}^{-1}$ (Weaver this study). Measurements in 2008 showed 18 tree species, 2940 stems ha^{-1} , a mean stem height of 6.0 m, and a basal area of 19.5 $\text{m}^2 \text{ha}^{-1}$. Ingrowth during the 10-yr period averaged 115 stems ha^{-1} and mortality 38 stems ha^{-1} . *Leucaena leucocephala*, an aggressive colonizer, increased from 180 to 650 stems ha^{-1} between measurements.

Forest composition and structure sampled in secondary subtropical dry forests recovering after agriculture on low elevation windward coastal hills showed that *Leucaena leucocephala* had the highest stem density in stands <30 yr old while *Guapira fragrans* and *Bursera simaruba* had the greatest basal areas (Gould et al. 2008). In stands >30 yr old the latter two species had the highest stem densities and greatest basal areas. For all stands, mean tree heights were 6.1 m, mean basal area was 9.6 $\text{m}^2 \text{ha}^{-1}$, and mean aboveground biomass was 34 t ha^{-1} . A mature subtropical dry forest association, *Bucida buceras*–*Guapira fragrans*, described from plots along the elevational gradient (Gould et al. 2006) occurs in a few protected areas in the subtropical dry life zone in northeastern Puerto Rico. *Bourreria succulenta* and *Bursera simaruba* were also abundant in these plots, along with *Capparis cynophallophora*, *Erythroxylum brevipes*, *Eugenia biflora*, and *Neea buxifolia*. Mean canopy heights averaged 13 m, stem densities (stems ≥ 10 cm) averaged 478 ha^{-1} , basal area 26 $\text{m}^2 \text{ha}^{-1}$, and aboveground biomass 163 t ha^{-1} .

3) Subtropical dry forest – secondary littoral woodland

Mature littoral woodland may grow on sand dunes, salt flats, and rocky slopes (Beard 1949). The littoral woodland at Las Cabezas Reserve lies behind the beaches and is mainly underlain by loamy sand. In addition to the well-distributed species above, *Cassine xylocarpa* and *Gymnanthes lucida* are representative natives, and *Morinda citrifolia*, *Thespesia populnea*, and *Cocos nucifera* exotics typically found in littoral woodland (Weaver et al. 1999).

4) Old coconut plantations

Abandoned coconut plantations, previously harvested commercially, are scattered along the island's northeastern coast. In addition to the well-distributed species above, the abandoned plantation at Las Cabezas Reserve contains *Conocarpus erecta* and *Krugiodendron ferreum* among the natives, and *Cocos nucifera*, *Gliricidium sepium*, *Morinda citrifolia*, and *Terminalia catappa* among the exotics (Weaver et al. 1999). Plot data for 0.12 ha showed a density of 2260 stems ha^{-1} and basal area of 25 $\text{m}^2 \text{ha}^{-1}$ (Weaver this study). Of the 13 species tallied, 77% were *Leucaena leucocephala*, 6% *Cocos nucifera*, 5% *Terminalia catappa*, and 4% *Ficus citrifolia*. Mean height of dominant and codominant trees averaged 9 m with the tallest *Cocos nucifera* trees averaging 17 m.

Lowland moist forests

Historically, the lowland moist forests probably had two principal layers with canopy trees reaching 25 m or more in height (Wadsworth 1950). Among the major species were *Andira inermis*, *Brysonima spicata*, *Bucida buceras*, *Calophyllum calaba*, *Coccoloba pubescens*, *Cedrela odorata*, *Citharexylum fruticosum*, *Cordia alliodora*, *Guarea guidonia*, *Hymenaea courbaril*, *Hyeronima clusoides*, *Manilkara bidentata*, *Masticodendron foetidissimum*, *Montezuma speciosissima*, *Petitita domingensis*, *Pouteria multiflora*, *Stahlia monosperma*, *Tabebuia heterophylla*, *Tetragastris balsamifera*, *Vitex divaricata*, and *Zanthoxylum flavum*. A deciduous species formerly prevalent within this type was *Buchenavia tetraphylla* (Gill 1931). Variation within these forests was likely related to substrate and topography. *Pterocarpus* swamp forests grew in lowland areas and along riparian corridors. Moist forests intergraded with dry forests at lower elevations and with wet forests at higher elevations along edaphic and moisture gradients related to topography and exposure. Logging, agriculture, and urbanization heavily impacted the lowland moist forest, which has been partially replaced by secondary forest in various stages of development.

5) Freshwater swamp forests

Pterocarpus officinalis is the dominant freshwater swamp and riparian tree species in the Caribbean (Bacon 1990)

and was historically abundant on the coastal plains of Puerto Rico. Stands of *Pterocarpus* extended inland to higher elevations along riparian corridors. Anthropogenic disturbance of the lowland landscape has reduced the distribution of the species to a relict set of about 15 stands (Cintrón 1983), which are typically associated with the landward side of mangroves where salinity is lower due to high rainfall or other freshwater inputs (Medina et al. 2007). *Pterocarpus* also survives in relict riparian stands in the LEF above 300 m in elevation (Francis and Lowe 2000). *Pterocarpus* swamp and riparian forests are a historically important component of the Puerto Rican landscape and represent important elements for preservation, conservation, and restoration.

Variation in the composition and structure of *Pterocarpus* forests along gradients are difficult to assess because the remaining stands survive in marginal habitats relative to the former range of the species. Little ecophysiology research has been conducted on the *Pterocarpus* stands in the northeast. Studies at nearby *Pterocarpus* stands, however, indicate that litterfall, fruiting, and flower production varied along a salinity gradient with all declining as salinity increased (Eusse and Aide 2005). The greatest basal areas, tree heights, and stand species richness were found in montane sites relative to coastal sites (Alvarez-Lopez 1990). One coastal *Pterocarpus officinalis*–*Acrostichum aureum* community occurring as a monoculture of *Pterocarpus* trees with the fern *A. aureum* growing in the understory had a mean canopy height of 34 m and a mean stem density (stems ≥ 10 cm) of 700 ha^{-1} (Gould et al. 2006).

6) Lowland moist forest

Mature lowland moist *Manilkara bidentata*–*Ocotea leucoxylon* associations (Gould et al. 2006) found in a few relict sites are likely similar to formerly extensive moist lowland forests converted to agriculture during the preceding century. Sampled stands occur on the alluvial plain of the northeast coast and the lower foothills within the lowland subtropical moist life zone. *Manilkara bidentata* is dominant in the overstory with *Faramea occidentalis* as the most abundant understory species. Composition of these plots was more variable than that of all other forest types along the elevational gradient, reflecting a long history of anthropogenic disturbance in the lowlands. Mean canopy heights were 26 m, stem density averaged 478 ha^{-1} , mean basal area was 50 $\text{m}^2 \text{ha}^{-1}$ and mean aboveground biomass was estimated at 330 t ha^{-1} .

7) Lowland and lower slope moist forests

Summaries from forest transects in typical secondary moist forests recovering from past agriculture in the lower elevations and coastal plains of northeastern Puerto Rico (Gould et al. 2008) indicate that two native trees, *Tabebuia heterophylla* and *Andira inermis* had the highest stem den-

ties, followed by two exotic species, *Spathodea campanulata* and *Mangifera indica*, and the native *Hura crepitans*. These same species, as follows, also had the greatest basal areas: *Mangifera indica*, *Hura crepitans*, *Tabebuia heterophylla*, *Spathodea campanulata*, and *Andira inermis*. Mean tree heights were 8.7 m, mean basal area 11.3 $\text{m}^2 \text{ha}^{-1}$ and mean tree biomass 50 t ha^{-1} .

In addition to deforestation of the lowlands, past human involvement near the LEF border was extensive and has affected the structure and composition of the montane forests to varying degrees. Tree cutting was common along the border and in river valleys where >50 tree species were considered satisfactory for furniture, construction, and posts (Wadsworth 1952). From the mid-1930s to the mid-1940s, about 3500 ha of open land in the LEF reforested naturally, including areas of previous planting trials (Wadsworth 1970).

In the mid-1990s, researchers examined secondary forest stands growing on abandoned pastures on the lower northern slopes of the Luquillo Mountains (Aide et al. 1996). After 40 yr of recovery, these stands could not be distinguished from undisturbed sites in terms of density, basal area, species numbers, or diversity; however, centuries would be required before the species compositions were similar. Moreover, abandoned pastures ranging from about 50 to 80 yr old had tree species distinct from those on old growth forest sites >80 yr old (Aide et al. 2000). On another site cutover for timber around 1900 and abandoned in the 1930s, the basal area and litterfall rates 50 yr later were similar to undisturbed tabonuco forest in the vicinity; the dominant species, however, were successional (Zou et al. 1995). Secondary forests recovering after disturbance on the lower slopes of the Luquillo Mountains will most probably carry the signature of past land use for several centuries, at least with regard to species composition.

Montane forests

8) Subtropical wet forest – plantations and secondary forests

Timber and ornamental trees introduced from other countries, both tropical and temperate, were propagated and tested in Puerto Rico (Francis 1987, 1995). Since the 1920s, at least 120 tree species were introduced into the LEF, including 112 exotics and 8 species native to other areas in Puerto Rico. Most were planted along the LEF's northeastern, western, and southern borders for timber production and watershed protection. In 1960, an arboretum was established on the lower western flank of El Toro Peak, one of the driest parts of the LEF (Francis 1989). A 1987 inventory showed 68 species from 25 countries.

Reforestation was most active between 1934 and 1945 when >4 million seedlings of 27 species were planted at 54

plantation sites on 2000 ha of recently abandoned farmland (Marrero 1948). Ten species accounted for >94% of the planted seedlings: *Swietenia macrophylla* and *Swietenia mahagoni* totaled 51%; and *Casuarina equisetifolia*, *Cedrela odorata*, *Cordia alliodora*, *Guarea guidonia*, *Montezuma speciosissima*, *Petitita domingensis*, *Tabebuia heterophylla*, and *Tectona grandis* accounted for >43%. *Byrsonima spicata*, *Calophyllum calaba*, and *Tabebuia heterophylla*, tree species that easily invade degraded secondary sites throughout the island, were also used (Marrero 1950). Tree densities and dimensions varied with species and planting techniques. About 60% of the plantations were well-stocked. Among the surviving plantings today are:

1) *Calophyllum calaba*, *Swietenia macrophylla*, and *Swietenia* hybrid (i.e. *S. macrophylla*–*S. mahagoni*) established in agroforestry plantings in the late 1930s, to convert abandoned agricultural land into timberland (Holdridge 1940). After 50 yr, *Swietenia* hybrid at the Harvey farm averaged 400 m³ ha⁻¹, about twice the volume of nearby *Calophyllum calaba* over the same period (Weaver 1989b).

2) *Pinus caribaea* planted in spacing trials at Guzmán and the Caracoles arboretum located along the western and southwestern boundaries of the LEF (Liegel et al. 1985). Various spacings averaged >20 m tall after 20 yr.

3) *Anthocephalis chinensis* in spacing studies at El Verde, line plantings at Jiménez, and plantations at Catalina (Lugo and Figueroa 1985). Initial height growth averaged about 15–20 m after 10–22 yr.

4) *Hibiscus elatus* in the arboretum and near the Sabana research station (Francis and Weaver 1988). The species appeared adapted to the wet sites of the LEF, in some instances reaching basal areas of ~50 m² ha⁻¹ after 25 yr.

5) *Tectona grandis* at 120 m elevation near the Sabana research station (Weaver and Francis 1990). Growth was satisfactory with several trees reaching merchantable volume in 50 yr.

6) *Swietenia* hybrid in 1275 ha of line plantings (sometimes called under-planting or enrichment planting) trials in degraded secondary forest at low elevations along the northeastern LEF border (Weaver and Bauer 1986). Trees on bottomlands and lower slopes averaged ~20 m in height after 18 yr, when total aboveground biomass was 170 t ha⁻¹. Dbh growth on mid-slopes and ridges was slower. Better light conditions and lower surrounding basal areas positively influenced growth. The hybrid produced significant regeneration under closed canopy wherever it was planted.

Many of the planted natives and exotics were not well-adapted to the Luquillo Mountains and site differences, notably topography and the amount of erosion, were recognized as important to survival and growth (Marrero 1948). At least 41 exotic tree species have become naturalized to varying degrees within Puerto Rico and 35 appear adapted to the climate and soils of the LEF (Francis 1987, Francis and Liogier 1991). Two exotics not associated with plantations survive well in the LEF: *Syzygium*

jambos, native to southeast Asia, was introduced to Puerto Rico nearly 200 yr ago (Brown et al. 2006); and *Bambusa vulgaris*, planted to help stabilize soils during the 1930s and 1940s, is visible in ravines and along the roadside (Little and Wadsworth 1964). Specimens of *Castilla elastica*, *Mangifera indica*, and *Psidium guajava*, all shade or fruit trees, were noted at least once near roads. Although secondary forest has regenerated throughout the lower LEF during the past 70 yr, much of boundary area still contains numerous introduced native and exotic trees.

9) Subtropical wet forest – tabonuco forest

The tallest trees in mature tabonuco forest grow at lower elevations on protected ridges and slopes (Wadsworth 1951). The forest contains three layers of trees with canopy species reaching 30 m in height and occasionally >1 m in dbh. Shrubs and herbs are usually unimportant. *Dacryodes excelsa*, *Prestoea montana*, *Sloanea berteriana*, *Cordia boricuensis*, *Manilkara bidentata*, *Schefflera morototoni*, *Cecropia schreberiana*, *Micropholis garciniiifolia*, *Henriettea squamulosa*, and *Quararibea turbinata* were the 10 most common of >80 species recorded on 4 ha of plots established in 1946 (Briscoe and Wadsworth 1970). *Dacryodes excelsa*, which reaches 1 m in dbh in ~500 yr, and *Sloanea berteriana* are indicator species for the type (Wadsworth 1951). *Buchanania tetraphylla*, considered to be a 'late secondary' species (Sastre-De Jesús 1979), grows rapidly and may reach 1 m in dbh within a couple of centuries. *Manilkara bidentata*, the remaining large species in tabonuco forest, is a shade tolerant, slow growing tree that attains >1 m in dbh (Little and Wadsworth 1964). It is likely that the largest specimens cut by loggers in the past, >1 m in dbh, were ~500 yr old.

Gradient sampling in tabonuco forest disclosed 69 tree species, 10 of which accounted for 65% of the total stems (Weaver 2010a, Table 1). For all sampled plots, mean stem density was 1560 ha⁻¹, mean canopy height 19 m, and mean woody biomass 245 t ha⁻¹. *Prestoea montana*, with 20% of the total, was the most common species and *Dacryodes excelsa* second with 11%. Of the remaining species, the 38 least common accounted for only 9% of the tallied stems. Certain species showed topographic preferences. *Cecropia schreberiana*, *Croton poecilanthus*, and *Prestoea montana* favored ravine topography and *Cyrilla racemiflora*, *Dacryodes excelsa*, *Matayba domingensis*, *Schefflera morototoni*, and *Tetragastris balsamifera* grew mainly on ridges and upper slopes. *Manilkara bidentata* appeared to favor slopes and ridges, and *Cordia boricuensis* slopes and ravines. *Sloanea berteriana*, although well represented on all topographies, slightly favored ravines (Table 1). Comparison between the Mameyes and the Espiritu Santo watersheds revealed differences in species composition. The Mameyes contained *Clusia clusioides*, *Eugenia boricuensis*, *Ocotea spathulata*, and *Tabebuia rigida*, species normally associated with cooler and wetter sites at higher elevation

(Weaver 2010a). These species are abundant in the dwarf forest, but survive scattered at mid-elevations in tabonuco forest, mainly on upper slopes and ridges (Weaver 1983, 1994, 2002).

Sampling species distributions in the previously disturbed Bisley watershed between 260 and 450 m in elevation showed that *Alchorneopsis portoricensis*, *Casearea arborea*, *Dacryodes excelsa*, *Inga laurina*, and *Manilkara bidentata* were more frequent on ridges and slopes, and *Guarea guidonia* and *Prestoea montana* in ravines (Basnet 1992). The dominance of *Dacryodes excelsa* on ridges was attributed to better soil drainage and root grafting, which helped to stabilize them against wind throw (Basnet et al. 1993). In addition, ridges and slopes contained a greater number of tree species than ravines (Scatena and Lugo 1995).

Past monitoring of tabonuco plots in the Espiritu Santo and Mameyes watersheds provided a 30-yr post-hurricane history. During the observation period, both stands decreased in stem density and species numbers, and increased in basal area (Weaver 1983). Secondary species like *Alchorneopsis portoricensis*, *Cecropia schreberiana*, and *Schefflera morototoni* and the understory *Psychotria berteriana* all declined considerably in stem numbers whereas mature forest species like *Dacryodes excelsa* and *Manilkara bidentata* remained relatively stable in both stem numbers and basal area (Crow 1980, Weaver 1983, 2000).

Species-site relationships were investigated on permanent plots in three other areas of tabonuco forest (Crow and Grigal 1979): at Sabana 4, between 210 and 600 m, in undisturbed forest; at Río Grande between 420 and 600 m, with secondary forest at lower elevations and undisturbed forest above; and Sabana 8, between 180 and 360 m, mainly in secondary forest. At Sabana 4 and Río Grande, *Dacryodes excelsa* grew best on ridges, *Cyrilla racemiflora* and *Micropholis garciniifolia* on slopes and ridges, and *Prestoea montana*, *Cecropia schreberiana*, and *Sloanea berteriana* on bottomlands and riverbanks. *Prestoea montana* was well distributed in both areas. At Sabana 8, *Ormosia krugii*, *Tabebuia heterophylla*, and *Schefflera morototoni* were most common on ridges, and *Buchenavia tetraphylla* and *Manilkara bidentata* were found together on upper slopes. *Inga laurina*, previously planted as coffee shade, grew on a variety of sites. Moreover, secondary species like *Alchornea latifolia* and *Tabebuia heterophylla* sometimes dominated young stands.

Thinning, which simulates hurricane impacts in some respects, was implemented on the secondary forest plots at Río Grande and Sabana 8 (Crow and Weaver 1977). Dbh increment on mature forest species, *Buchenavia tetraphylla*, *Dacryodes excelsa*, *Manilkara bidentata*, *Micropholis garciniifolia*, *M. guyanensis*, and *Sloanea berteriana*, nearly doubled over 18 yr, approaching twice the average for the same species in undisturbed forest. In comparison, the dbh growth of species common in secondary forest, *Byrsonima coriacea*, *Homalium racemosum*, *Inga laurina*, *Chionanthus domingensis*, *Matayba domingensis*, and *Ormosia kru-*

gii, increased by about 50%. Dbh growth for *Alchornea latifolia*, *Cecropia schreberiana*, *Schefflera morototoni*, and *Tabebuia heterophylla*, all pioneer species, increased by only 10% (Weaver 1983). The results provide some indication of typical species' responses to improved growing conditions.

10) Lower montane wet forest – colorado forest

Mature colorado forest was first characterized as dense stands of pole-size trees reaching 15 m in height, with two-thirds of the diameters between 10 and 15 cm (Wadsworth 1951). Trees are typically short and crooked, and crowns consist of heavy branches that emerge low on the trunk. Grasses and sedges grow in openings. The two largest species, *Cyrilla racemiflora* and *Magnolia splendens*, may survive for centuries and attain diameters between 1 and 2 m (Weaver 1986, 1987). Their regeneration occurs mainly in canopy openings after disturbance (Weaver 1992). *Henriettea squamulosa*, *Micropholis garciniifolia*, and *M. guyanensis*, which may attain relatively large sizes, are also common within the forest.

Gradient sampling of colorado forest disclosed 65 tree species, 10 of which accounted for 71% of the total stems (Table 1). For all sampled plots, mean stem density was 2060 ha⁻¹, mean canopy height 13 m, and mean woody biomass 190 t ha⁻¹. *Prestoea montana* with 17% of the stems and *Henriettea squamulosa* with 14% were the most common species. Certain tree species showed topographic preferences (Weaver 1991). Species commonly found in drainages and ravines included: *Citharexylum caudatum* at high elevations and *Sapium laurocerasus* at lower elevations; and *Cecropia schreberiana*, *Croton poecilanthus*, and *Prestoea montana*, which were well distributed throughout the forest. Species that were common on ridge topography were: *Calyptanthus krugii*, *Clusia clusoides*, and *Ocotea spathulata* at high elevations; *Byrsonima wadsworthii*, *Cyrilla racemiflora*, and *Haenianthus salicifolius* at mid-elevations; and *Dacryodes excelsa*, *Matayba domingensis*, and *Micropholis guyanensis* at lower elevations. *Cordia borinquensis* was well distributed with regard to topography (Table 1). Understory species such as *Daphnopsis philippiana* and *Garcinia portoricensis* were more common on ridges and upper slopes, and *Ditta myriocoides* on slopes and in ravines.

Gradient sampling also showed that tree height decreased with elevation on both windward and leeward exposures (Weaver 2000). Also, aboveground woody biomass decreased significantly with elevation on ridges to the windward and soil organic matter significantly with elevation to the leeward. Tree density was greatest on ridges and least in ravines. Species-area curves showed that the greatest number of species was found on ridges and slopes, and the fewest in ravines. An earlier field survey carried out on both sides of a line that separated parent geological materials within colorado forest did not detect

a change in tree species composition (Wadsworth and Bonnet 1951).

During the 35-yr period of post-hurricane observation on permanent plots, small secondary species like *Hedyosmum arborescens* and *Psychotria berteriana* virtually disappeared (Weaver 1989a). Larger secondary species, *Cecropia schreberiana*, *Schefflera morototoni*, and *Miconia laevigata* also declined considerably in stem numbers although their basal areas remained relatively stable because of subsequent growth on residual stems. In comparison, mature forest species showed variable trends. *Cyrtilla racemiflora* remained constant in stem numbers but declined in basal area due to the loss of a few large trees. Stem numbers and basal areas remained relatively constant for *Prestoea montana*, but increased to varying degrees for *Cordia boricuensis*, an understory species, and *Micropholis garciniifolia* and *M. guyanensis*, both canopy species.

A 50% basal area thinning was carried out in colorado forest to determine its effect on residual stems. No differences were apparent after 10 yr (Anonymous 1957). After 35 yr, however, the stand had experienced a massive influx of *Clusia clusioides*, *Cyrtilla racemiflora*, and *Miconia tetrandra* (Weaver 2001). *Micropholis garciniifolia* and *Tabebuia rigida* also showed gains. Thinning did not stimulate dbh growth on the slow-growing residual stems; instead, available space was colonized by new stems.

11) Palm brake

Prestoea montana is ubiquitous in the LEF, reproducing in closed forest, gaps, and on landslides. Palm seedlings are adapted to low light conditions on the forest floor and survive in humid conditions for long periods (Bannister 1970). Palm brakes, dominated by *Prestoea montana*, grow on steep, east-facing slopes and in ravines above 450 m (Wadsworth 1951). Ground cover consists of a sparse herbaceous layer and, in the case of drainages, rocks and boulders. Previously, palm brakes were considered as a secondary, or sub-climax communities on steep soils subject to landslips or soil movement (Beard 1949). Palms may reach 20 m in height and 20 cm in dbh, and may persist for ~180 yr (Van Valen 1975).

Gradient sampling of palm brake showed that 10 species accounted for 90% of the total stems (Table 1). For all sampled plots, mean stem density was 1890 ha⁻¹, mean canopy height was 12 m, and mean woody biomass was 105 t ha⁻¹. *Prestoea montana* was the most common species with 57% of the total stems and *Cecropia schreberiana* followed with 12%. Slight increases in local relief within palm brakes are associated with species' differences. *Prestoea* dominates palm brakes but is especially common in ravines whereas associated broadleaf species favor slightly elevated sites.

Prestoea montana accounted for 54–63% of the stems and basal area on a permanent plot measured between 1947 and 1975, demonstrating that palms survive hur-

ricanes well and persist over long periods (Weaver 1983). Common broadleaf stems recorded on the plot were *Cordia boricuensis*, *Croton poecilanthus*, *Henriettea squamulosa*, and *Psychotria berteriana*. In comparison, palms on four typical tabonuco and colorado forest permanent plots accounted for 6–23% of both stems and basal area. Dbh increment for broadleaf species on palm plots averaged double the rates of those growing on either tabonuco or colorado plots (Weaver 1983). This difference may be due to lower stem densities, lower basal areas, and a more open canopy that typically characterize palm brakes. On another permanent plot in the headwaters of the Río Espíritu Santo, *Prestoea montana* accounted for 40% of the tallied stems (Frangi and Lugo 1985, 1991, 1998). Periodic flooding, poor soil aeration, heavy annual rainfall, and low atmospheric saturation pressure deficits were suggested as the factors controlling palm growth. After Hurricane Hugo, the palm plot, protected by topographic position, lost only 1% of its trees.

12) Dwarf forest

Dwarf forest is characterized by a single story of trees that commonly range from 1 to 6 m in height depending on exposure (Wadsworth 1951). Trees are branchy and trunks are seldom straight. The upper canopy is uniform in height and leaves are generally small, thick, and concentrated at the ends of branches. Mosses and liverworts cover branches, trunks, and leaves; moreover, nearly all species of flowering plants are found as epiphytes (Howard 1968). Soils in dwarf forest are saturated and contain about 50% organic matter (Lyford 1969). Tree roots are generally superficial and aerial have been recorded on 22 arborescent species (Gill 1969). Although no tree species is confined to dwarf forest, only a few are adapted to survive on the exposed summits (Nevling 1971). El Yunque peak, Los Picachos, Pico del Este, Pico del Oeste, El Toro peak, and the steep east-facing slopes below Mt. Britton are among the most notable and accessible examples of stunted, windswept dwarf forest. This impoverishment of forests on small, wet, tropical mountains has been attributed to the 'Massenerhebung effect' where cool temperatures, frequent fog, and heavy precipitation interact to retard the mineralization of organic matter (Grubb 1971).

Gradient sampling within dwarf forest showed that four species accounted for nearly 70%, and 10 species for >93% of the total stems (Weaver 2010b, Table 1). For all sampled plots, mean stem density was 3330 ha⁻¹, mean canopy height <9 m, and mean woody biomass 170 t ha⁻¹. *Cyathea bryophila*, *Eugenia boricuensis*, *Ocotea spathulata*, and *Tabebuia rigida* were not only the most abundant species, but also those that favored windward rather than leeward exposures at high elevations within the LEF (Weaver 2010b). Earlier studies suggested that *Weinmannia pinna-* along with the last three species above composed 75% of the dominant trees in dwarf forest (Gleason and Cook

Table 1. Gradient sampling tally – occurrence of 45 native tree species by forest type and topography within the Luquillo Experimental Forest (LEF). Selected species account for ≥90% of the stems tallied in each forest type and >95% of all stems tallied for all forest types combined.¹

Species name	Entire LEF		Species occurrence by topography ²				
	Stems		Elevation ³ (m)	Tabonuco		Colorado	
	Total	(%)		R-S-V	R-S-V	R-S-V	R-S-V
<i>Alchornea latifolia</i> Sw.	64	0.49	350–915	4-4-0	19-8-18	8-2-1	0
<i>Byrsonima wadsworthii</i> Little	74	0.56	350–950	1-2-0	44-19-6	0	1-0-1
<i>Calypttranthes krugii</i> Kiaersk.	99	0.75	640–1000	0	30-2-6	0	30-21-10
<i>Cecropia schreberiana</i> Mig.	235	1.80	350–950	10-14-24	7-9-37	47-50-32	0-0-5
<i>Clibadium erosum</i> (Sw.) DC.	13	0.10	730–880	0	0	5-2-6	0
<i>Clusia clusioides</i> (Griseb.) D’Arcy	220	1.67	450–1000	1-6-0	66-69-1	0-0-1	24-34-18
<i>Cordia borinquensis</i> Urban	432	3.28	350–960	4-10-9	135-114-97	14-16-8	0-4-21
<i>Croton poecilanthus</i> Urban	393	2.99	360–960	7-4-40	22-74-219	1-4-11	0-2-9
<i>Cyathea arborea</i> (L.) J.E. Smith	121	0.92	460–970	0-2-2	30-25-15	0-1-3	10-25-8
<i>Cyathea bryophila</i> (R. Tryon) Proctor	435	3.30	850–1000	0	0-0-8	6-0-0	41-176-204
<i>Cyathea portoricensis</i> Spreng ex Kuhn	13	0.10	720–870	0	0	0-8-5	0
<i>Cynilla racemiflora</i> L.	274	2.08	450–970	17-18-1	113-82-11	2-0-0	22-7-1
<i>Dacryodes excelsa</i> Vahl	192	1.46	350–850	83-65-2	21-15-5	0-1-0	0
<i>Daphnopsis philippiana</i> Krug & Urban	234	1.78	450–970	19-24-6	48-74-18	2-0-0	14-22-7
<i>Ditta myricoides</i> Griseb.	79	0.60	450–950	2-0-0	10-27-24	11-0-0	0-0-5
<i>Drypetes glauca</i> Vahl	103	0.78	350–800	16-30-9	4-28-16	0	0
<i>Eugenia borinquensis</i> Britton	572	4.35	550–1000	0-0-1	63-21-27	22-0-6	173-183-76
<i>Garcinia portoricensis</i> (Urban) Alain	60	0.46	350–750	5-0-0	43-10-2	0	0
<i>Guarea glabra</i> Vahl	13	0.10	450–780	2-3-7	0	1-0-0	0
<i>Guatteria caribaea</i> Urban	8	0.06	350–470	6-2-0	0	0	0
<i>Haenianthus salicifolius</i> Griseb.	231	1.76	350–1000	0-2-1	82-70-19	5-3-1	23-12-13
<i>Henriettea squamulosa</i> (Cogn.) Judd.	1401	10.64	350–1000	4-20-10	309-454-174	34-24-15	129-96-132
<i>Hirtella rugosa</i> Pers.	134	1.02	360–860	5-7-1	84-36-1	0	0
<i>Inga laurina</i> (Sw.) Willd.	37	0.28	350–680	2-5-2	26-1-1	0	0
<i>Ixora ferrea</i> (Jacq.) Benth.	26	0.20	350–780	4-4-0	14-4-0	0	0

Table 1. Continued.

Species name	Entire LEF		Species occurrence by topography ²				
	Stems		Elevation ³ (m)	Tabonuco R-S-V	Colorado R-S-V	Palm R-S-V	Dwarf R-S-V
	Total	(%)					
<i>Magnolia splendens</i> Urban	88	0.67	350-990	6-0-1	25-28-6	0	9-6-7
<i>Manilkara bidentata</i> (A.DC.) Chev.	82	0.62	350-650	31-38-11	1-0-1	0	0
<i>Matayba domingensis</i> (DC.) Radlk.	122	0.93	370-875	10-4-0	58-44-6	0	0
<i>Meliosma herbertii</i> Rolfe	30	0.23	350-800	5-8-0	16-1-0	0	0
<i>Miconia tetrandra</i> D. Don	147	1.12	450-915	1-5-2	73-26-39	0	0-1-0
<i>Micropholis garcinifolia</i> Pierre	1097	8.33	350-1000	31-49-3	295-319-29	7-2-0	166-169-27
<i>Micropholis guyanensis</i> (A. DC.) Pierre	369	2.80	370-900	11-8-0	206-122-21	0	1-0-0
<i>Myrcia fallax</i> (A. Rich.) DC.	104	0.79	470-970	3-0-0	73-21-3	1-0-0	3-0-0
<i>Myrcia leptoclada</i> DC.	20	0.15	380-560	7-12-1	0	0	0
<i>Ocotea leucoxylon</i> (Sw.) Mez	75	0.57	350-970	7-2-4	34-8-4	4-2-0	4-3-3
<i>Ocotea spathulata</i> Mez	931	7.07	350-1000	13-6-0	215-105-17	8-0-1	292-215-59
<i>Ormosia krugii</i> Urban	27	0.21	380-780	5-4-0	16-2-0	0	0
<i>Prestoea montana</i> (R. Grah.) Nichols	2366	17.97	350-970	48-42-195	217-254-838	203-202-232	0-5-130
<i>Psychotria berteriana</i> DC.	108	0.82	450-970	12-2-7	27-10-19	9-8-2	0-2-10
<i>Sapium laurocerasus</i> Desf.	50	0.38	450-950	0-1-4	2-3-24	5-6-3	0-0-2
<i>Schefflera morototoni</i> (Aubl.) Mcguire	42	0.32	350-790	13-8-2	9-4-1	4-0-1	0
<i>Sloanea berteriana</i> Choisy	90	0.68	350-890	19-17-24	9-8-11	2-0-0	0
<i>Tabebuia rigida</i> Urban	1303	9.90	450-1000	15-12-5	177-190-20	36-4-0	378-372-94
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	53	0.40	360-780	32-17-3	1-0-0	0	0
<i>Tetrazygia urbanii</i> Cogn.	25	0.19	350-750	8-6-3	7-1-0	0	0
Subtotals	12592	0.96	350-1000	469-463-380	2631-2288-1744	437-335-328	1320-1355-842
Remaining 44 species	573	0.04	350-1000	35-21-26	119-129-119	9-3-10	56-28-18
Totals	13165	100.00	350-1000	504-484-406	2750-2417-1863	446-338-338	1376-1383-860

¹Sampling intensity varied by forest type. Tabonuco, species ≥ 8 stems (91.2% of total); colorado, species ≥ 13 stems (90.9%); and dwarf, species ≥ 48 stems (91.2% of total) (Weaver this study).

²Sampling intensity varied by forest type. Total number of plots = 132 in LEF (5.77 ha), including 18 in tabonuco (0.90 ha), 69 in colorado (3.45 ha), 12 in palm brake (0.60 ha), and 33 in dwarf (0.82 ha). Occurrence by topography = 44 plots each on ridges (R), slopes (S), and in ravines (V).

³Elevational range for species occurrences on sampling plots.

1927). On Pico del Oeste, *Ocotea spathulata* and *Tabebuia rigida* made up 70% of the canopy (Howard 1968).

Previous stratified sampling of dwarf forest vegetation by topography near Pico del Este indicated that common tree species showed topographic preferences (Weaver 1999). *Prestoea montana* occurred exclusively in ravines and *Cyathea bryophylla* favored slopes and ravines. In contrast, *Calyptranthes krugii*, *Clusia clusioides*, *Micropholis garciniaefolia*, and *Ocotea spathulata* had >90% of their combined occurrences on slopes and ridges. *Henriettea squamulosa* had a more equitable distribution by topography.

Monitoring of dwarf forest after an airplane wreck showed that recovery passed through several stages, probably indicative of typical changes after major soil disturbance. First, grass, ferns, and fern allies regenerated but woody seedlings were scarce (Byer and Weaver 1977). About 20 yr later, ferns and broadleaf species were prominent, and after 37 yr *Clusia clusioides*, *Eugenia borinquensis*, *Micropholis garciniaefolia*, *Ocotea spathulata*, and *Tabebuia rigida* were the largest broadleaf trees (Weaver 1990, 2008). The time required for complete biomass recovery was estimated at two centuries. Slow dbh growth rates on the summits suggests that the largest dwarf forest specimens of *Cyrtilla racemiflora* and *Magnolia splendens* may be among the oldest plants on the island (Weaver 1983, 1986a, 1987). Other trees with small dbhs could be a century or more in age.

Post-Hurricane Hugo tree monitoring showed that about 10% of the biomass was lost during the storm event; moreover, delayed mortality (i.e. gradual death of trees damaged by the hurricane) continued for many years after the storm (Weaver 2000, 2008). The forest's high stem density is partially due to fallen trees from which lateral branches or adventitious shoots subsequently develop (Table 1; Howard 1969). The alpine meadows occasionally seen in summit areas may be caused by landslides or hurricane disturbances which expose the subsoil. Subsequently, grass and ferns invade and once established may persist for decades.

Regional gradients

Forest structure and composition in northeastern Puerto Rico are heavily influenced by climate, past land use, spatial (i.e. elevation and landscape) features, and temporal (i.e. pre- and post disturbance) conditions. Remote sensing of forest cover reveals some landscape patterns related to the elevational gradient while plot sampling within the region has elucidated relationships of composition and structure with elevation.

Landscape patterns

The relative extent of forest cover varies with elevation in the LEF and surrounding lowlands due mainly to hu-

man use of the landscape. The chief natural process affecting the rate of forest recovery on abandoned agricultural lands is storm damage. More important human impacts on forest extent include recurrent clearing and continued grazing of pastures, new land development, and land protection. The region is 45% grasslands, woodlands and shrubland, 43% forested, 11% developed and natural barrens, and 1% water (Fig. 2). The relative amount of forest cover shifts from 20% at elevations below 100 m to nearly 100% at elevations above 700 m. Forests become relatively more abundant than grasslands above 150 m. Land area decreases with elevation with about two-thirds occurring below 150 m elevation and the remainder above 150 m (Fig. 4).

Twelve forest types are among the land cover classes mapped in northeastern Puerto Rico using remote sensing (Gould et al. 2008). The relative amounts of forest type vary according to elevation (Fig. 4). Over 50% of the forests below 15 m are mangrove, followed in abundance by moist lowland forest (26%), semi-evergreen seasonal (subtropical dry) forest (18%), and *Pterocarpus* forest (3%). Lowland moist forests dominate up to 200 m and most seasonal evergreen forests occur below 100 m, occupying about 20% of the forest cover. Tabonuco forests and lower slope secondary forests and plantations dominate between 200 and 600 m elevation, colorado forest between 600 and 900 m, and dwarf forest above 900 m. Palm brakes make up about 30% of the mapped forest types between 500 and 900 m (Fig. 2).

Forest structure

Canopy tree height in the moist forests decreases linearly along the entire elevational gradient. Mangroves and dry forests are of shorter stature and similar to the upper elevation dwarf forest in canopy height (Fig. 5). When canopy height is partitioned by topography within the LEF, the rate of decline is greatest on ridges, intermediate on slopes, and least in ravines (Fig. 6). Plots <650 m elevation, mainly ridges and slopes, have the tallest trees and high elevation dwarf forest ridges the shortest trees.

Stem densities increase linearly within the LEF but show a unimodal relationship along the entire elevational gradient, with lowest stem densities at mid elevations (Fig. 7). High stem densities near the coast are likely due to the presence of younger forests and occasional storm disturbance, while higher stem densities at upper elevations may reflect long term climatic controls on forest structure. When stem density values are partitioned by topography within the LEF, they are more similar at the lowest elevations (Fig. 8). The rates of stem density increase for ridges and slopes were parallel and at higher elevations they tended to average nearly double the average for ravines. At elevations above 900 m, a few slope and ridge plots within dwarf forest had densities >4500 stems ha⁻¹. Extreme den-

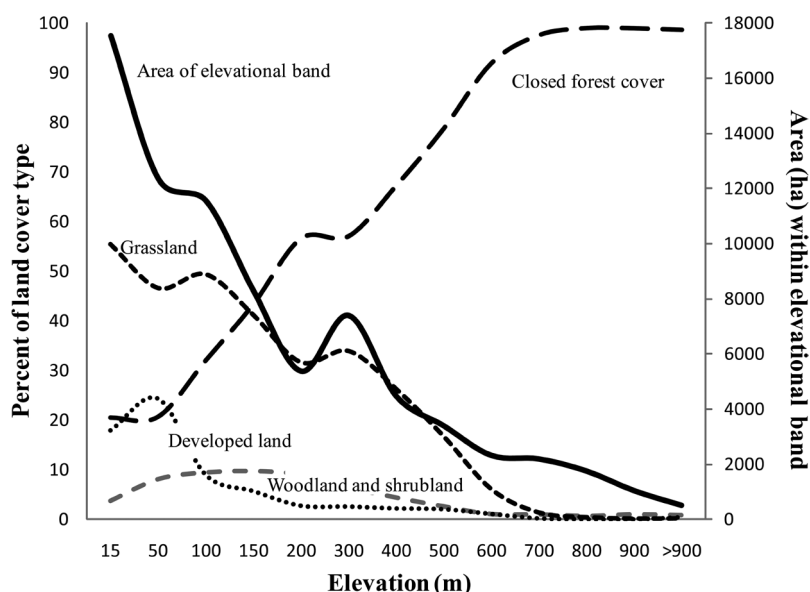


Figure 4. Relative area of forest, woodland and shrubland, grasslands, and developed areas by elevational bands in northeastern Puerto Rico (left axis). Grasslands dominate up to 150 m in elevation, above which forests dominate. Forests cover 90–100% of the landscape at elevations above 600 m. Grasslands decline linearly with elevation. Woodland and shrubland are most abundant between 15 and 200 m. Developed land is most abundant between 15 and 100 m. The absolute area within each elevational band decreases with elevation (right axis).

sities characterize dwarf stands on exposed sites or those recovering from major disturbance.

Above ground biomass has a weak relationship with elevation, declining linearly within the LEF and having a unimodal relationship along the entire elevational gradient, with highest values at mid elevations (Fig. 9). Forest biomass is greatest in coastal lowland, lower slope and tabonuco forests, declining at the extremes along the elevational gradient

(i.e. mangrove, coastal dry forest and dwarf forests). Biomass varies considerably <650 m in tabonuco and colorado forests where a few large trees, often *Dacryodes excelsa* or *Cyrilla racemiflora*, may inflate plot values. Plot biomass on ridges and slopes decreased with elevation but with considerable variation; biomass in ravines, in contrast, showed no elevational trend (Fig. 10). Mean biomass values within all forest types declined from ridge through slope to ravine topo-

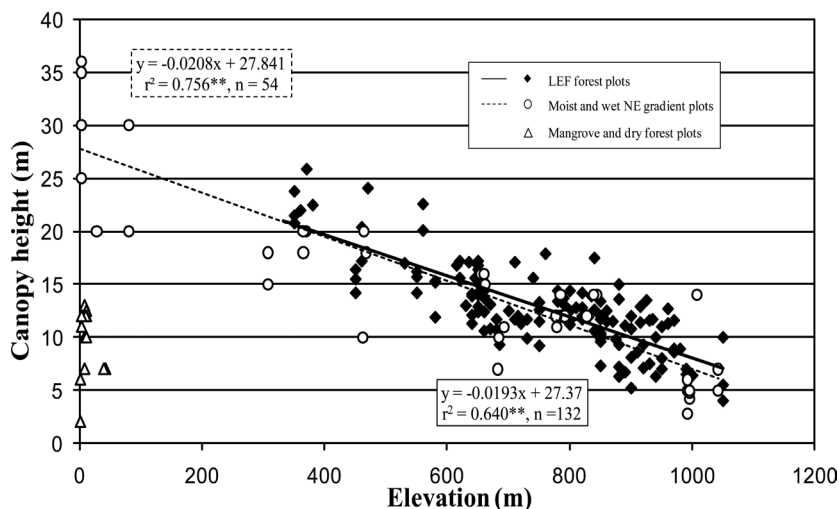


Figure 5. Linear regressions of plot canopy heights vs elevation for two separate data sets in northeastern Puerto Rico: mean values per plot in both the northeastern gradient sampling and within the Luquillo Experimental Forest. Note that canopy heights for mangrove and dry forest plots at lower left are not included in the regression.

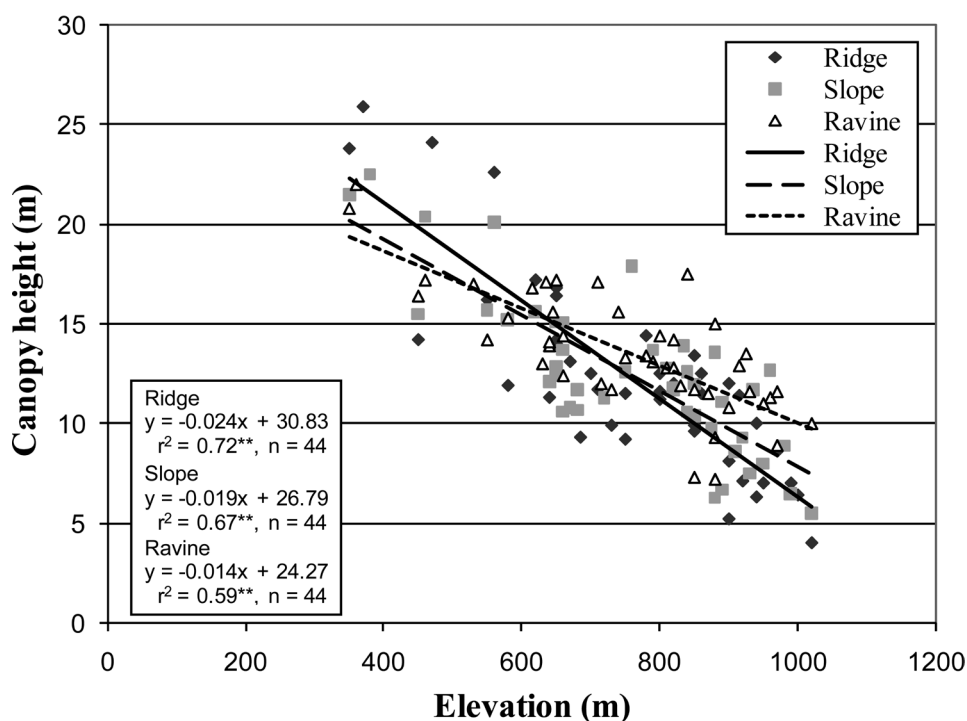


Figure 6. Linear regressions of mean canopy heights per plot vs elevation, by topography, within the Luquillo Experimental Forest.

graphy. Also, biomass is least immediately after hurricanes, gradually increasing for ~50 yr during post-storm recovery.

An early gradient study within the LEF was carried out on ridge topography between 600 and 1020 m el-

elevation on the LEF's northwestern slopes (White 1963). The survey showed that stem density increased with elevation whereas the mean height of canopy trees, mean and maximum tree diameters, plot basal areas, and the

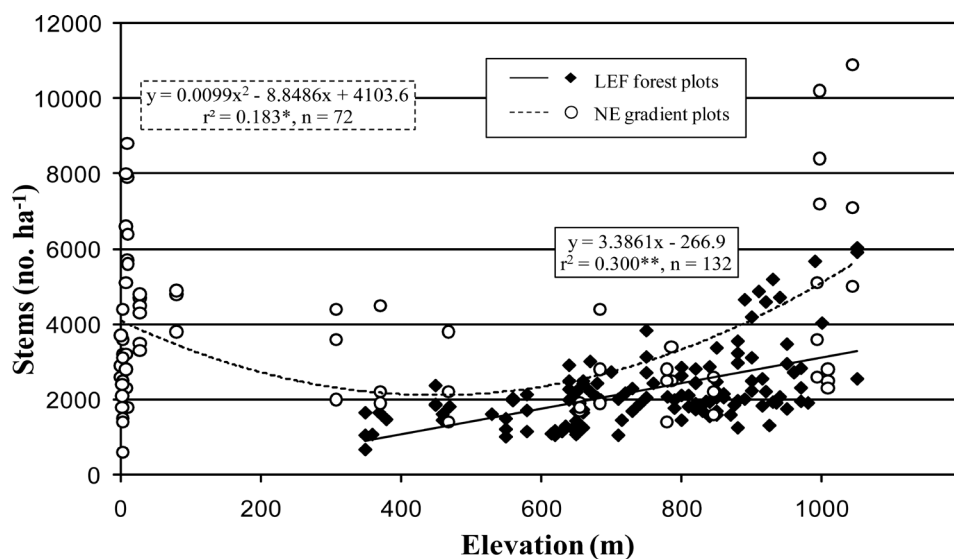


Figure 7. Regressions of stem densities vs elevation for two separate data sets in northeastern Puerto Rico: unimodal relationship for individual plot values in northeastern gradient sampling; and linear relationship for individual plot values within the Luquillo Experimental Forest.

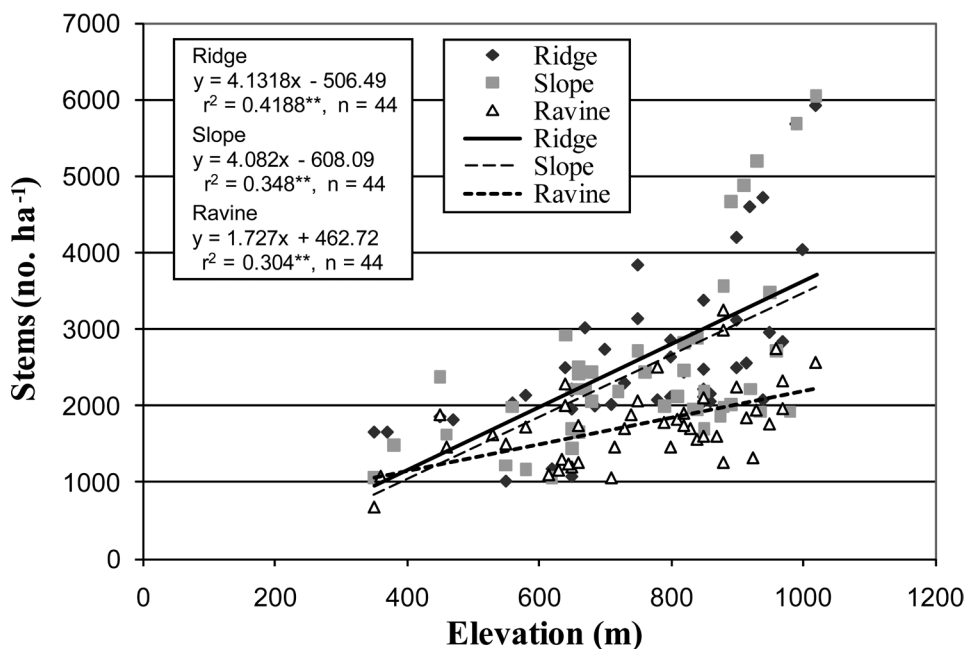


Figure 8. Regression of stem densities per plot vs elevation, by topography, within the Luquillo Experimental Forest.

number of tree species per plot all declined. Another survey between 350 and 1025 m within the Baño de Oro Natural Area showed that the tallest trees in tabonuco forest grew on ridges and the tallest in dwarf forest grew in ravines (Weaver 1994). Only 10% of the dwarf forest trees were >9 m tall; comparable figures for colorado and tabonuco forests were 44 and 54%. Similarly, 32% of the dwarf forest trees were >10 cm in dbh and comparable

figures for colorado and tabonuco forests were 60 and 65%.

Species relationships

Species richness has weak relationships with elevation, declining linearly within the LEF and having a unimodal

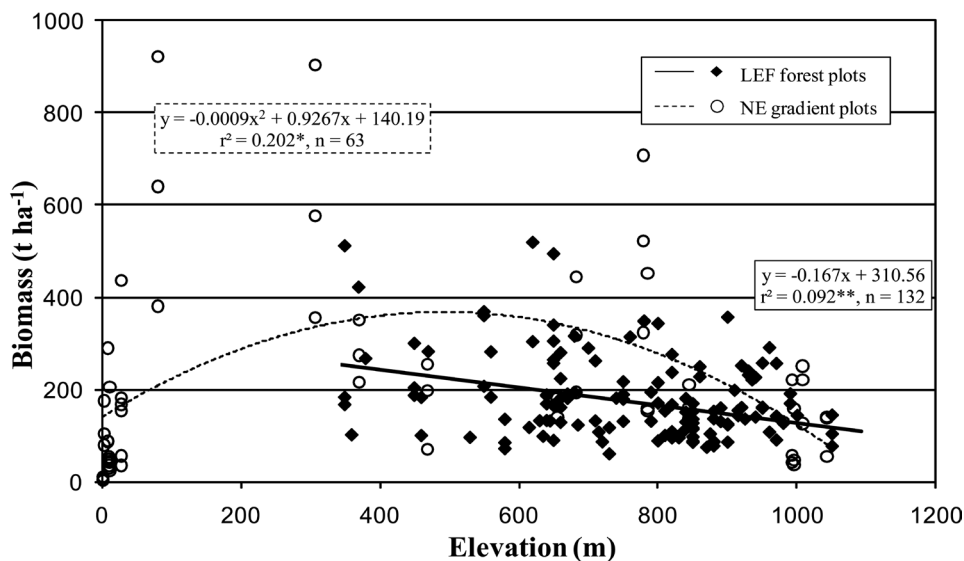


Figure 9. Regressions of mean plot biomass vs elevation for two separate data sets in northeastern Puerto Rico: unimodal relationship of individual plot values in northeastern gradient sampling (excluding freshwater swamp plots); and linear relationships for individual plot values within the Luquillo Experimental Forest.

pattern along the entire gradient, with the highest values at mid elevations (Fig. 11). Native tree species distributions <350 m in northeastern Puerto Rico have been altered by human activity. Many mature forest species like *Buchena-via pentaphylla*, *Dacryodes excelsa*, and *Manilkara bidentata* that previously grew in lowland moist or lower slope forests are largely confined to the LEF.

Within the LEF, tree species richness declines with an increase in elevation or with more stressful growing conditions, being greater in tabonuco and colorado forests and notably less in palm brake and dwarf forests. Also, it tends to be greatest about 15–20 yr after major hurricane disturbance when both secondary and mature tree species grow in proximity. With regard to topography, species richness follows the pattern ridges \geq slopes $>$ ravines (Fig. 12). Species richness declines with elevation, most rapidly and similarly for ridge and slope plots; species richness on ravine plots decreases more slowly. The greatest species richness is on ridge and slope plots between 600 and 800 m elevation, the ecotone between tabonuco and colorado forests. Above 900 m, more stressful climate and saturated soils filter out many species. In the aforementioned Baño de Oro study, total tree species richness declined by more than one-half along the elevational gradient from tabonuco forest to dwarf forest (Weaver 1994).

The gradient study has provided information regarding contrasting species distribution patterns within and among forest types in the LEF (Table 1). For example: 1) some forest species are largely confined to one or two forest types such as *Dacryodes excelsa* and *Manilkara bidentata* in tabonuco, *Brysonima wadsworthii* and *Micropholis guyanensis* in colorado, and *Cyathea bryophylla* in dwarf; and *Eugenia borinquensis*, *Ocotea spathulata*, and *Tabebuia rigida* in dwarf and colorado. 2) Some intermediate-size species like *Henriettea squamulosa*, *Micropholis garciniifolia*, and *Prestoea montana* have ample elevational ranges within the LEF, growing in the second story at lower elevations and reaching the canopy at higher elevation. 3) Some tree species show strong topographic preferences such as *Dacryodes excelsa* on ridges in tabonuco forest, *Cyrilla racemiflora* and *Micropholis garciniifolia* for ridges and upper slopes in most forest types, and *Prestoea montana* for ravines and lower slopes in all forest types. *Henriettea squamulosa*, the best distributed species in the LEF, is common on all topographies in all forest types, including palm brake. 4) Although *Cordia borinquensis*, *Croton poecilanthus*, and *Psychotria berteriana* were found on ridges and slopes at lower elevations they were not recorded on ridges in dwarf forest. 5) Secondary tree species such as *Cecropia schreberiana* and *Psychotria berteriana* have a cosmopoli-

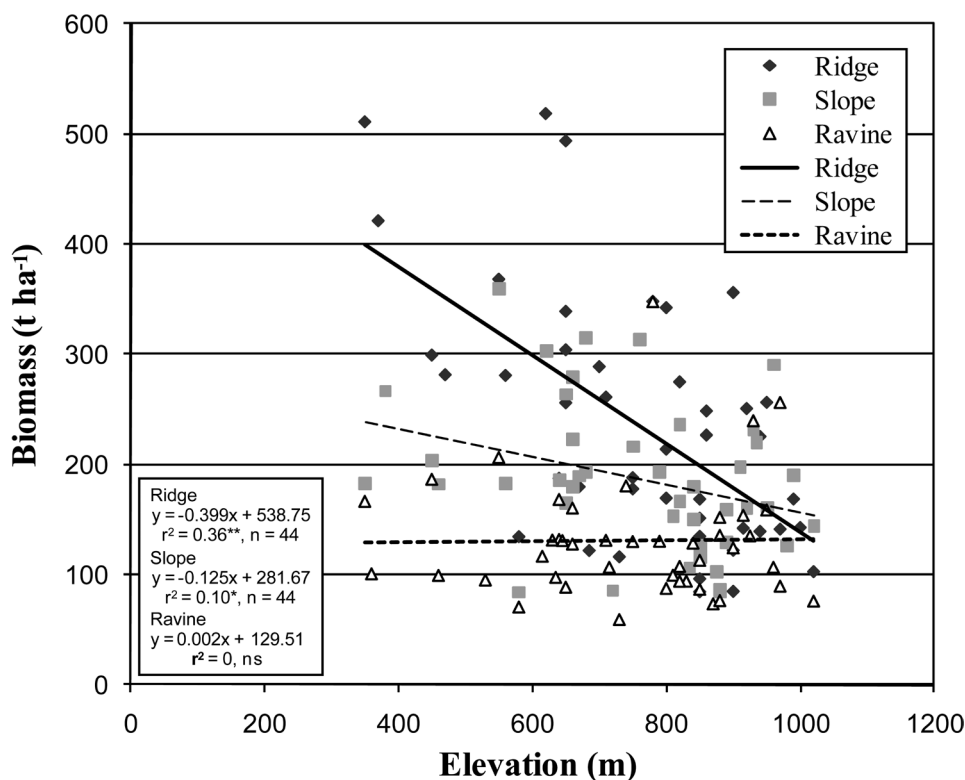


Figure 10. Regression of biomass per plot vs elevation, by topography, within the Luquillo Experimental Forest.

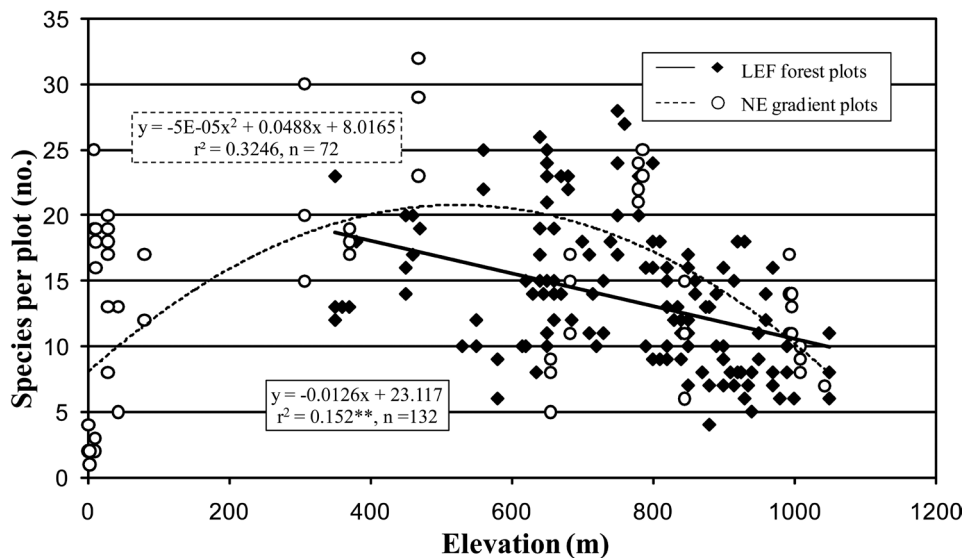


Figure 11. Regressions of mean number of species per plot vs elevation for two separate data sets in northeastern Puerto Rico: unimodal relationship of individual plot values in northeastern gradient sampling; and linear relationships for individual plot values within the Luquillo Experimental Forest.

tan distribution occupying disturbed sites within mature forests. *Cecropia* survives best in ravines within tabonuco, colorado, and palm forests, but is poorly represented in dwarf forest (Brokaw and Gear 1991).

Other relationships

Specific gravities for 86 LEF tree species ranged from 0.26 to 0.90 with nearly 75% between 0.50 and 0.79 g cm⁻³ (Reyes et al. 1992). Estimates of mean specific gravity by forest types within the LEF ranged from 0.49 to 0.63 for all sampled species, including palm, and from 0.60 to 0.66 for broadleaf species alone (i.e. excluding palm) (Weaver this study). Specific gravity tends to increase from tabonuco forest to dwarf forest. Palm brakes, the exception, are dominated by *Prestoea montana* and *Cecropia schreberiana*, woods that are much lighter in weight than other species.

Other studies in the LEF showed that tree taper, the amount of branch wood, and organic matter increase with elevation whereas typical dbh range, total timber volumes, aboveground biomass, leaf biomass, leaf area index, and specific leaf area are greater at lower elevations (Wadsworth 1949, Weaver and Murphy 1990). Also, tree biomass equations derived for tabonuco, colorado, and dwarf forests differ by forest type (Weaver and Gillespie 1992). Surveys along the LEF's elevational gradient also showed a decreasing trend in stem respiration due to changes in tree species composition, a decrease in the surface area of trees, and lower temperatures (Harris et al. 2008). Gould et al. (2006) show the relative amount of non native vas-

cular plant species greatest in lowland moist and dry forest communities, and the absolute and relative amount of endemic vascular plant species increasing with elevation. With regard to forest dynamics, litterfall, loose litter, litterfall/loose litter, herbivory rates, growth rates (i.e. dbh and woody biomass increment), and total aboveground net primary productivity decrease with elevation (Weaver and Murphy 1990). The notable exception in some instances is palm brake. Palms have large leaves, comparatively low biomass, and grow in less dense stands.

Conclusions

The change in major forest types by elevation from sea level to the Luquillo Mountain summits in northeastern Puerto Rico has been recognized by island residents for centuries. After the mid-1800s, researchers began to document this information, including variations in forest structure and species composition by elevation, landscape features, and past disturbance.

Sampling and disturbance

1) Sampling carried out in northeastern Puerto Rico has been limited in area and biased as to site selection. Within hilly or mountainous terrain, forest structure and species composition are heavily influenced by spatial (i.e. elevation and landscape features) and temporal (i.e. pre- and post-disturbance) factors. 2) Hurricanes have numerous im-

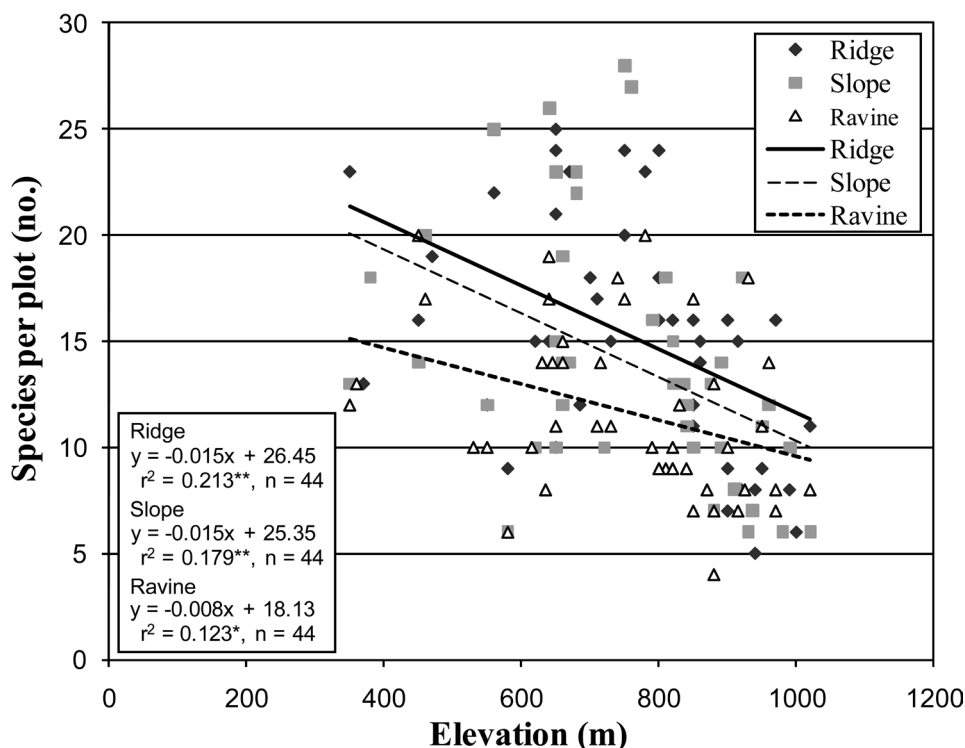


Figure 12. Regression of mean number of species per plot vs elevation, by topography, within the Luquillo Experimental Forest.

mediate and long-term impacts on forest structure (stem density, canopy height, biomass) and species composition (species richness). 3) Forests below 350 m in northeastern Puerto Rico have been heavily influenced by human activity, including about one-half of the LEF.

Forest structure

1) Within the LEF, stem density increases with elevation, most rapidly for ridges and slopes and less rapidly in ravines, with the greatest density on exposed, high elevation summits; alternatively, density increases with ascent by forest type: tabonuco < palm < colorado < dwarf; also, density differs by topography within forest types, usually with ridge > slope > ravine. 2) Within the LEF, canopy height decreases with elevation, most rapidly for ridges and least rapidly for ravines, with the tallest trees on protected ridges at low elevations; alternatively, height decreases with ascent by forest type: tabonuco > colorado ≥ palm > dwarf; also it varies by topography within forest types: tabonuco, ridge > slope > ravine; colorado and dwarf, ravine > slope > ridge; and palm brake, slope > ravine > ridge. 3) Forest biomass is greatest in coastal lowland, lower slope and tabonuco forests, declining at the extremes along the elevational gradient (i.e. coastal dry forest and dwarf forests). Also, standing biomass is least

immediately after hurricanes, increasing for ~50 yr during post-storm recovery. 4) Within the LEF, biomass declines with elevation, most rapidly for ridges, less so for slopes, but not in ravines; also, biomass declines with ascent by forest type, tabonuco > colorado > dwarf > palm; biomass also declines by topography within forest types: ridge > slope > ravine.

Species composition

1) Within the LEF, species richness declines with an increase in elevation, with the fewest species recorded on exposed, high elevation summits. Species richness is notably lower in both the palm brake and dwarf forests. The former is characterized by unstable soils and the latter by rigorous climate and saturated soils. 2) Within the LEF, at least 112 exotic tree species were introduced, mainly for timber trials. *Swietenia* hybrid occupies the largest area and *Syzygium jambos* is probably the best adapted to environmental conditions within the LEF.

Other factors

Forest dynamics show numerous trends associated with changes in elevation and forest types.

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References

- Aide, T. M. et al. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. – *Biotropica* 28: 537–548.
- Aide, T. M. et al. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. – *Restor. Ecol.* 8: 328–338.
- Alvarez-Lopez, M. 1990. Ecology of *Pterocarpus officinalis* forested wetlands in Puerto Rico. – In: Lugo, A. E. et al. (eds), *Ecosystems of the World*, 15. Forested wetlands. Elsevier, pp. 251–265.
- Anonymous 1957. Seventeenth annual report. – *Caribb. For.* 18: 1–11.
- Bacon, P. R. 1990. Ecology and management of swamp forests in the Guianas and Caribbean region. – In: Lugo, A. E. et al. (eds), *Ecosystems of the World*, 15. Forested wetlands. Elsevier, pp. 213–250.
- Bannister, B. A. 1970. Ecological life cycle of *Euterpe globosa* Gaertn. – In: Odum, H. T. and Pigeon, R. F. (eds), *A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico*. U.S. Dept of Commerce, chapter B-18, pp. 299–314.
- Basnet, K. 1992. Effect of topography on the pattern of trees in tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. – *Biotropica* 24: 31–42.
- Basnet, K. et al. 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. – *Biotropica* 25: 28–35.
- Bates, C. Z. 1929. Efectos del huracán del 13 de septiembre de 1928 en distintos árboles. – *Rev. Agric. Puerto Rico* 23: 113–117.
- Baynton, H. W. 1968. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of Pico del Oeste. – *J. Arnold Arboretum* 49: 419–430.
- Baynton, H. W. 1969. The ecology of an elfin forest in Puerto Rico, 3. Hilltop and forest influences on the microclimate of Pico del Oeste. – *J. Arnold Arboretum* 50: 80–92.
- Beard, J. S. 1949. Natural vegetation of the Windward and Leeward Islands. – *Oxf. For. Mem.* 21: 1–192.
- Briscoe, C. B. 1966. Weather in the Luquillo Mountains of Puerto Rico. – Research Paper ITF-3, Inst. of Tropical Forestry, Río Piedras, PR.
- Briscoe, C. B. and Wadsworth, F. H. 1970. Stand structure and yield in the tabonuco forest of Puerto Rico. – In: Odum, H. T. and Pigeon, R. F. (eds), *A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico*. U.S. Dept of Commerce, chapter B-6, pp. 79–89.
- Brokaw, N. and Grear, J. S. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. – *Biotropica* 23: 386–392.
- Brown, K. A. et al. 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. – *For. Ecol. Manage.* 222: 145–152.
- Byer, M. D. and Weaver, P. L. 1977. Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. – *Biotropica* 9: 35–47.
- Calvesbert, R. J. 1970. Climate of Puerto Rico and the U.S. Virgin Islands. – U.S. Dept of Commerce, Environmental Services Administration, Environmental Data Service, Silver Spring, MD.
- Cintrón, B. B. 1983. Coastal freshwater swamp forests: Puerto Rico's most endangered ecosystem. – In: Lugo, A. E. (ed.), *Los bosques de Puerto Rico*. Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR, pp. 249–282.
- Cox, D. P. and Briggs, R. P. 1973. Metallogenic map of Puerto Rico. Map I-721. – U.S. Dept of Interior, U. S. Geological Survey, San Juan, PR.
- Crow, T. R. 1980. A rain forest chronicle: a thirty year record of change in structure and composition at El Verde, Puerto Rico. – *Biotropica* 12: 42–55.
- Crow, T. R. and Weaver, P. L. 1977. Tree growth in a moist tropical forest of Puerto Rico. – Research Paper ITF-22, Inst. of Tropical Forestry, Río Piedras, PR.
- Crow, T. R. and Grigal, D. F. 1979. A numerical analysis of arborescent communities in the rain forest of the Luquillo Mountains, Puerto Rico. – *Vegetatio* 40: 135–146.
- Eusse, A. M. and Aide, T. M. 2005. Patterns of litter production across a salinity gradient in a *Pterocarpus officinalis* tropical wetland. – *Plant Ecol.* 145: 307–315.
- Ewel, J. J. and Whitmore, J. L. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. – Research Paper ITF-18, Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR.
- Figuerola Colón, J. C. 1996. Phytogeographical trends, centers of high species richness and endemism, and the question of extinctions in the native flora of Puerto Rico. – *Ann. N. Y. Acad. Sci.* 776: 89–102.
- Francis, J. K. 1987. Performance of exotic tree species in Puerto Rico. – In: Figuerola, J. C. et al. (eds), *Management of the forests of tropical America: prospects and technologies*. Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR, pp. 377–388.
- Francis, J. K. 1989. The Luquillo Experimental Forest Arboretum. – Research note SO-358, Inst. of Tropical Forestry, Southern Forest Experiment Station, USDA Forest Service, New Orleans, LA.
- Francis, J. K. 1995. Forest plantations in Puerto Rico. – In: Lugo, A. E. and Lowe, C. (eds), *A century of tropical forestry research: results from the first half, themes for the second*. Springer, pp. 210–223.
- Francis, J. K. and Weaver, P. L. 1988. Performance of *Hibiscus elatus* in Puerto Rico. – *Commonwealth For. Rev.* 67: 327–338.
- Francis, J. K. and Liogier, H. A. 1991. Naturalized exotic tree species in Puerto Rico. – Gen. Tech. Rep. SO-82, International Inst. of Tropical Forestry, USDA Forest Service, New Orleans, LA.
- Francis, J. K. and Lowe, C. A. 2000. Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. –

- International Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR.
- Frangi, J. L. and Lugo, A. E. 1985. Ecosystem dynamics of a sub-tropical floodplain forest. – *Ecol. Monogr.* 55: 351–369.
- Frangi, J. L. and Lugo, A. E. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. – *Biotropica* 23: 324–335.
- Frangi, J. L. and Lugo, A. E. 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. – *Biotropica* 30: 339–348.
- Gill, A. M. 1969. The ecology of an elfin forest in Puerto Rico, 6. Aerial roots. – *J. Arnold Arboretum* 50: 197–209.
- Gill, T. 1931. Tropical forests of the Caribbean. – Tropical Plant Research Foundation, Charles Lathrop Pack Forestry Trust, Baltimore, MD.
- Gleason, H. A. and Cook, M. T. 1927. Scientific survey of Porto Rico and the Virgin Islands: plant ecology of Porto Rico. – *N. Y. Acad. Sci.* 7: 3–173.
- Gómez-Pompa, A. and Vázquez-Yanes, C. 1974. Studies of the secondary succession of tropical lowlands: life cycle of secondary species. – In: *Proceedings of the First International Congress of Ecology: structure, functioning and management of ecosystems*. Center for Agricultural Publishing and Documentation, Wageningen, Netherlands, pp. 336–342.
- Gould, W. A. et al. 2006. Structure and composition of vegetation along an elevational gradient in Puerto Rico. – *J. Veg. Sci.* 17: 653–664.
- Gould, W. A. et al. 2008. The Puerto Rico gap analysis project. Volume 1: land cover, vertebrate species distributions, and land stewardship. – Gen. Tech. Rep. IITF-GTR-39, International Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR.
- Grubb, P. J. 1971. Interpretation of the ‘Massenerhebung Effect’ on tropical mountains. – *Nature* 229: 44–45.
- Guariguata, M. R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. – *J. Ecol.* 78: 814–832.
- Harris, N. L. et al. 2008. Estimates of species- and ecosystem-level respiration of woody stems along an elevational gradient in the Luquillo Mountains, Puerto Rico. – *Ecol. Model.* 216: 253–264.
- Holdridge, L. R. 1940. The possibility of close cooperation for mutual benefit between agriculture and forestry in the American tropics. – *Caribb. For.* 1: 25–29.
- Holdridge, L. R. 1967. Life zone ecology, rev. ed. – Tropical Science Center, San José, Costa Rica.
- Howard, R. A. 1968. The ecology of an elfin forest in Puerto Rico, 1. Introduction and composition studies. – *J. Arnold Arboretum* 49: 381–418.
- Howard, R. A. 1969. The ecology of an elfin forest in Puerto Rico, 8. Studies of stem growth and form and of leaf structure. – *J. Arnold Arboretum* 50: 225–266.
- Liegel, L. H. et al. 1985. Honduras pine spacing trial results in Puerto Rico. – *South. J. Appl. For.* 9: 69–75.
- Liogier, H. A. 1985–1997. Descriptive flora of Puerto Rico and adjacent islands – Spermatophyta. Vol. I–V. – Editorial de la Univ. de Puerto Rico, San Juan, PR.
- Little, E. L. Jr 1970. Relationships of trees of the Luquillo Experimental Forest. – In: Odum, H. T. and Pigeon, R. F. (eds), *A tropical rain forest: a study of irradiation and ecology at El Verde*, Puerto Rico. U.S. Dept of Commerce, chapter B-3, pp. 47–58.
- Little, E. L. Jr and Wadsworth, F. H. 1964. Common trees of Puerto Rico and the Virgin Islands. – *Agricultural Handbook No. 249*, USDA Forest Service, Washington, DC.
- Little, E. L. Jr and Woodbury, R. O. 1976. Trees of the Caribbean National Forest. – Res. Pap. ITF-20, Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR.
- Little, E. L. J. et al. 1974. Trees of Puerto Rico and the Virgin Islands. – *Agricultural Handbook No. 449*, U.S. Dept of Agriculture, Forest Service, Washington, DC.
- Lugo, A. E. and Snedaker, S. C. 1974. The ecology of mangroves. – *Annu. Rev. Ecol. Syst.* 5: 39–64.
- Lugo, A. E. and Figueroa, J. 1985. Performance of *Anthocephalis chinensis* in Puerto Rico. – *Can. J. For. Res.* 15: 577–585.
- Lyford, W. H. 1969. The ecology of an elfin forest in Puerto Rico, 7. Soil, root, and earthworm relationships. – *J. Arnold Arboretum* 50: 210–224.
- Marrero, J. 1948. Repoblación forestal en el Bosque Nacional del Caribe de Puerto Rico: experiencias en el pasado como guía para el futuro. – *Caribb. For.* 9: 148–213.
- Marrero, J. 1950. Reforestation of degraded lands in Puerto Rico. – *Caribb. For.* 11: 3–15.
- Martinuzzi, S. et al. 2009. Conversion and recovery of Puerto Rican mangroves: 200 years of change. – *For. Ecol. Manage.* 257: 75–84.
- Medina, E. et al. 2007. Nutrient and salt relations of *Pterocarpus officinalis* L. in coastal wetlands of the Caribbean: assessment through leaf and soil analyses. – *Trees Struct. Funct.* 21: 321–327.
- Nevling, L. I. Jr 1970. The ecology of an elfin forest in Puerto Rico, 5. Chromosome numbers of some flowering plants. – *J. Arnold Arboretum* 50: 99–103.
- Odum, H. T. et al. 1970. Climate at El Verde, 1963–1966. – In: Odum, H. T. and Pigeon, R. F. (eds), *A tropical rain forest: a study of irradiation and ecology at El Verde*, Puerto Rico. U.S. Dept of Commerce, chapter B-22, pp. 347–418.
- Reyes, G. et al. 1992. Wood densities of tropical tree species. – Gen. Tech. Rep. SO-88, Southern Forest Experiment Station, USDA Forest Service, New Orleans, LA.
- Salvia, L. A. 1972. Historia de los temporales de Puerto Rico y las Antillas, 1542 a 1970. – Editorial Edil, Univ. of Puerto Rico, Río Piedras, PR.
- Sastre-de Jesús, I. 1979. Ecological life cycle of *Buchenavia capitata* (Vahl.) Eichl., a late secondary successional species in the rain forest of Puerto Rico. – MS thesis, Univ. of Tennessee, Knoxville, TN.
- Scatena, F. N. and Lugo, A. E. 1995. Geomorphology, disturbance, and the soils and vegetation in two subtropical wet steep-land watersheds of Puerto Rico. – *Geomorphology* 13: 199–213.
- Shreve, F. 1914. A montane rain forest: a contribution to the physiological plant geography of Jamaica. – Publication no. 199, Carnegie Inst., Washington, DC.
- Simon, A. et al. 1990. The role of soil process in determining mechanisms of slope failure and hillslope development in a humid-tropical forest, eastern Puerto Rico. – *Geomorphology* 3: 263–286.
- USDA Natural Resources Conservation Service 2002. Soil survey of the Caribbean National Forest and Luquillo Experimental Forest, Commonwealth of Puerto Rico. – USDA Natural Resources Conservation Service, Washington DC.

- Van Valen, L. 1975. Life, death, and energy of a tree. – *Biotropica* 7: 260–269.
- Wadsworth, F. H. 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. – PhD thesis, Univ. of Michigan, Ann Arbor, MI.
- Wadsworth, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. – *Caribb. For.* 11: 38–47.
- Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains, I. The setting. – *Caribb. For.* 12: 93–114.
- Wadsworth, F. H. 1952. Forest management in the Luquillo Mountains, III. Selection of products and silvicultural policies. – *Caribb. For.* 13: 93–119.
- Wadsworth, F. H. 1970. Review of past research in the Luquillo Mountains of Puerto Rico. – In: Odum, H. T. and Pigeon, R. F. (eds), *A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico*. U.S. Dept of Commerce, chapter B-2, pp. 33–46.
- Wadsworth, F. H. and Bonnet, J. A. 1951. Soil as a factor in the occurrence of two types of montane forest in Puerto Rico. – *Caribb. For.* 12: 67–70.
- Wadsworth, F. H. and Englerth, G. H. 1959. Effects of the 1956 hurricane on forests of Puerto Rico. – *Caribb. For.* 20: 38–51.
- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. – *Biotropica* 23: 379–385.
- Walker, L. R. et al. 1991. Ecosystem, plant, and animal responses to hurricanes in the Caribbean. – *Biotropica* 23: 313–521.
- Walker, L. R. et al. 1996. Long term responses of Caribbean ecosystems to disturbance. – *Biotropica* 28: 414–614.
- Weaver, P. L. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. – *Caribb. J. Sci.* 12: 129–144.
- Weaver, P. L. 1983. Tree growth and stand changes in the sub-tropical life zones of the Luquillo Mountains of Puerto Rico. – Res. Pap. SO-190, Southern Forest Experiment Station, USDA Forest Service, New Orleans, LA.
- Weaver, P. L. 1986. Growth and age of *Cyrilla racemiflora* L. in montane forests of Puerto Rico. – *Interciencia* 11: 221–228.
- Weaver, P. L. 1987. Ecological observations on *Magnolia splendens* Urban in the Luquillo Mountains of Puerto Rico. – *Caribb. J. Sci.* 23: 340–351.
- Weaver, P. L. 1989a. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. – *Interciencia* 14: 181–192.
- Weaver, P. L. 1989b. Taungya plantings in Puerto Rico. – *J. For.* 87: 37–41.
- Weaver, P. L. 1990. Succession in the elfin woodland of the Luquillo Mountains of Puerto Rico. – *Biotropica* 22: 83–89.
- Weaver, P. L. 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. – *Interciencia* 16: 142–151.
- Weaver, P. L. 1992. An ecological comparison of canopy trees in the montane rain forest of Puerto Rico's Luquillo Mountains. – *Caribb. J. Sci.* 28: 62–69.
- Weaver, P. L. 1994. Baño de Oro Natural Area, Luquillo Mountains, Puerto Rico. – Gen. Tech. Rep. GTR-SO-111, Inst. of Tropical Forestry, USDA Forest Service, New Orleans, LA.
- Weaver, P. L. 1999. Impacts of Hurricane Hugo on the dwarf cloud forest of Puerto Rico's Luquillo Mountains. – *Caribb. J. Sci.* 35: 101–111.
- Weaver, P. L. 2000. Environmental gradients affect forest structure in Puerto Rico's Luquillo Mountains. – *Interciencia* 25: 254–259.
- Weaver, P. L. 2001. Thinning and regeneration in Puerto Rico's colorado forest, with comments about their effect on the Puerto Rican parrot. – *Caribb. J. Sci.* 37: 252–258.
- Weaver, P. L. 2002. A chronology of hurricane induced changes in Puerto Rico's lower montane rain forest. – *Interciencia* 27: 252–258.
- Weaver, P. L. 2008. Dwarf forest recovery after disturbances in the Luquillo Mountains of Puerto Rico. – *Caribb. J. Sci.* 44: 150–163.
- Weaver, P. L. 2010. Forest structure and composition in the lower montane rain forest of the Luquillo Mountains in Puerto Rico. – *Interciencia* 35: 640–646.
- Weaver, P. L. 2011. Tree species distribution and forest structure along environmental gradients in the dwarf forest of the Luquillo Mountains. – *Bois For. Trop.* 306: 33–44.
- Weaver, P. L. and Bauer, G. P. 1986. Growth, survival and shoot borer damage in mahogany plantings in the Luquillo Forest in Puerto Rico. – *Turrialba* 36: 509–522.
- Weaver, P. L. and Francis, J. K. 1990. The performance of *Tectona grandis* in Puerto Rico. – *Common. For. Rev.* 69: 313–323.
- Weaver, P. L. and Murphy, P. G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. – *Biotropica* 22: 69–82.
- Weaver, P. L. and Gillespie, A. J. R. 1992. Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. – *Common. For. Rev.* 71: 35–39.
- Weaver, P. L. and Schwagerl, J. 2009. U.S. Fish and Wildlife Service refuges and other nearby reserves in southwestern Puerto Rico. – Gen. Tech. Rep. GTR-IITF-40, International Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR.
- Weaver, P. L. et al. 1999. Las Cabezas de San Juan Nature Reserve (El Faro). – Gen. Tech. Rep. GTR IITF-5, International Inst. of Tropical Forestry, USDA Forest Service, Río Piedras, PR.
- White, H. H. Jr 1963. Variation of stand structure correlated with altitude in the Luquillo Mountains. – *Caribb. For.* 24: 46–52.
- Zou, X. et al. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. – *For. Ecol. Manage.* 78: 147–157.