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Ecology and Distribution of Neotropical Podocarpaceae

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ABSTRACT. Podocarps are a frequent, but rarely a dominant, component of neotropical wet forests extending from South America into central Mexico and the Greater Antilles. Although podocarps are often considered to be predominantly montane taxa, several species occur in lowland forest and are locally abundant on some Pacific and Atlantic coastal islands in Central America. Here we review literature on the origins and distribution of neotropical podocarps and highlight their apparent association with resource-poor environments. As a consequence of forest conversion and logging, many podocarps that were already habitat specialists are now further restricted to small and increasingly fragmented populations. Unfortunately, there is little information on the regeneration ecology of podocarps with which to assess the recruitment potential of these populations. An exception is the long-term studies of the dynamics of *Podocarpus urbanii*, a common species in montane forest in Jamaica. *Podocarpus urbanii* is moderately shade tolerant and successfully regenerates beneath undisturbed forest. The low juvenile mortality rate of *P. urbanii*, coupled with relatively high diameter growth, suggests that this species and possibly other podocarps may have greater utility for reforestation than is currently recognized.

DIVERSITY OF NEOTROPICAL PODOCARPACEAE

Central and South America harbor a large fraction of global podocarp diversity and are represented by five genera: *Podocarpus* (31 species), *Prumnopitys* (5 species), *Retrophyllum* (2 species), *Saxegothaea* (1 species), and *Lepidothamnus* (1 species). Most of these podocarps (excluding the last two genera) have a tropical distribution; the 29 neotropical *Podocarpus* species account for nearly a third of the species currently recognized in the genus (Farjon, 2001). Malesian podocarps show a diversity of forms, including parasitic, lianescent, and aquatic species on New Caledonia (Enright and Jaffré, this volume), whereas

neotropical taxa are all canopy trees of mature forest, although a few elfin forest species found on infertile soils (*P. tepuiensis*, *P. sprucei*, *P. buchholzi*) seldom grow more than a few meters tall.

PALEOHISTORY OF NEOTROPICAL PODOCARPACEAE

Podocarpaceae is a monophyletic group of Gondwanan origin with a fossil record dating back to the Early Cretaceous (Krassilov, 1974). Neotropical fossil evidence indicates the presence of podocarps in northern South America at least since the late Eocene to Oligocene (van der Hammen and Hooghiemstra, 2000). The modern distribution of podocarps, however, has been most affected by more recent events. The rise of the Andes from the south to north and west to east first created montane habitats 15 MYA, culminating in the rapid uplift of the Eastern Cordillera during the Pliocene 2–5 MYA (Gregory-Wodzicki, 2000; Antonelli et al., 2009; Graham, 2009). Although little is known about the flora and environment of tropical South America during the Pliocene, sediment records indicate that the principal species in northern Andes forests were the montane taxa *Weinmannia* (Cunoniaceae) and *Podocarpus* (van der Hammen, 1974).

Concurrent with Andean uplift, formation of the Panama land bridge allowed podocarp species to migrate north into Central America and potentially competing species to migrate south into the Andes. Analysis of continuous lake sediments from the plain of Bogota (Eastern Cordillera of the Andes, 2,580 m elevation), spanning the late Pliocene to the Holocene, indicate that podocarps were among the most important taxa in northern Andean forests during interglacial periods up to 330,000 years ago, before being replaced primarily by *Quercus* (oak) forests (van't Veer and Hooghiemstra, 2000). *Quercus* was one of the last immigrants to northern South America a million years ago (van der Hammen, 1989) and became dominant after the last glacial cycle at elevations of 2,000–3,000 m in the northern Andes and through Central America. *Quercus*, however, only extends as far south as the Colombia–Ecuador border (1°N; Hooghiemstra, 2006), so competitive exclusion by oaks cannot account for the rarity of podocarps in southern Andean forests.

Temperature fluctuations associated with glacial cycles may also have induced elevational shifts in podocarp populations. During the Pleistocene, podocarp pollen appears periodically at multiple low-elevation sites (Behling et al., 1999; Haberle and Maslin, 1999; Ledru et al., 2001;

Niemann and Behling, 2008). The occurrence of podocarps at lowland Amazonian sites has been interpreted as key evidence indicating glacial cooling (e.g., Liu and Colinvaux, 1985; Behling, 1998). Comparisons of the presumed extant elevational distribution of podocarps in Andean forests with paleorecords of podocarp pollen has led to an inferred climate cooling of 4.5°C–7.0°C during the Wisconsin glacial maximum (Liu and Colinvaux, 1985; Haberle and Maslin, 1999).

Although extensive pollen records exist for podocarps, glacial migration patterns of individual taxa cannot be corroborated using these data. Pollen identifications are limited to the generic level (Hooghiemstra et al., 2006), and interpretation of low-density pollen records are further affected by the potential for long-distance transport (e.g., Behling, 2001; but see van der Hammen and Hooghiemstra, 2000). However, palynological data, when combined with genetic analyses, provide a useful additional tool to infer the timing of podocarp migration patterns. Ledru et al. (2007) combined pollen records with molecular analysis of living material to infer relationships among 26 populations of three Brazilian endemic species (*P. sellowii*, *P. lambertii*, and *P. brasiliensis*) that occur in diverse forest types: along rivers in Cerrado, mid-elevational *Araucaria* forest, and Atlantic rainforest in southern and eastern Brazil. Clustering in the molecular data indicated that the three podocarps formed three groups: (1) a rather homogenous group consisting of *P. lambertii*, a species associated with *Araucaria* forest, suggesting recent population expansion in the last 3,000 years in southern Brazil; (2) a more heterogeneous northern group of *P. sellowii* (that also includes *P. brasiliensis*), associated with riverine forest that expanded earlier (~16,000 years ago); and (3) a montane and coastal group from eastern Brazil including both *P. sellowii* and *lambertii*, which are relicts from a population expansion over a short period during the cool and moist conditions of the last glaciations ~29,000 years ago. Combined genetic and palynological approaches now hold promise for understanding the distribution and timing of migration of northern and western Amazonian podocarps.

CURRENT RANGE DISTRIBUTION OF PODOCARPS

Neotropical podocarps have been collected extensively, with metadata available for >1,900 specimens accessible through the Global Biodiversity Information Facility (GBIF) (http://www.gbif.net, accessed 10 October

2009). Broad distributional patterns at the genus level are therefore generally well resolved. At the species level, however, taxon boundaries remain poorly differentiated, with some species based on very few specimens (Farjon, 2001). As a consequence, disjunct populations of some taxa continue to be discovered (Neill, 2008). Below, we describe distribution patterns for neotropical taxa recognized by Farjon (2001) based on plots of locality information for herbarium specimens.

The northern distributional limit of podocarps is delimited by *P. matudae*, with an outlying population in cloud forest in Tamaulipas, Mexico, at 23°N (Figure 3.1a). Two other Central American species with broad distributional patterns also extend into Mexico: *P. guatemalensis* occurs at 300 m elevation at the transition between lowland and mesophilic montane forest in Oaxaca and may also extend into the more-mesic forests in the southern Yucatan Peninsula, whereas *P. oleifolius* occurs in lower montane forest at 1,000 m in Veracruz. Elsewhere in Central America podocarp taxa mostly have broad geographic ranges: *P. oleifolius* occurs through to Panama and the Andes as far as Venezuela and northern Peru, *P. guatemalensis* extends to Colombia, and *P. costaricensis* has a narrower range restricted to central Costa Rica and eastern Panama. Two remaining Central American *Podocarpus* taxa recognized by Farjon (2001) are taxonomically more doubtful. *Podocarpus magnifolius* occurs in Bolivia, Peru, and Venezuela, but several additional collections have been made in eastern and central Panama. *Podocarpus monteverdeensis*, which occurs only in central Costa Rica, has been considered a synonym of *P. oleifolius* (Merello, 2003). A single endemic species of *Prumnopitys*, *P. standleyi*, occurs in Costa Rica in high-elevation oak forests.

Two species, *Podocarpus angustifolius* and *P. aristulatus,* occur in Cuba at 20°N–21°N, whereas *P. aristulatus* and *P. hispaniolensis* occur in Hispaniola and *P. purdieanus* and *P. urbanii* occur in Jamaica at 18°N. In contrast to the island endemics of the Greater Antilles, only a single species, *P. coriaceus*, is recognized to occur across the Lesser Antillean islands of Dominica, Guadeloupe, Martinique, Montserrat, and St. Kitts and Nevis, as well as Puerto Rico. An additional endemic species, *P. trinitensis*, occurs on Trinidad.

In South America, most tropical podocarps are distributed along the northern and western Andes or centered on the Guyana Shield of southern Venezuela (Figure 3.1b). Although some taxa have extensive distributions within the Andes (notably *P. parlatorei* in the southern Andes extending north into Bolivia and *P. oleifolius* through Peru, Ecuador, and Colombia), most species are more restricted

in their ranges and exhibit multiple disjunct populations suggestive of habitat specialization or refugial distributions. Three species, *P. magnifolius*, *P. celatus*, and *P. tepuiensis*, maintain populations in both the Guyana Shield and the western Andes. In addition to *Podocarpus*, three species of *Prumnopitys* and one species of *Retrophyllum* are associated with mid-elevation (*P. harmsiana*) and high-elevation (*P. montana, P. exigua,* and *R. rospigliosii*) tropical Andean forests.

ELEVATIONAL RANGE DISTRIBUTION OF PODOCARPS

Paleoclimate reconstructions for the neotropics based on podocarp pollen data hinge on the assumption that podocarps are restricted to montane forests. This assumption is clearly violated for Central American taxa, where *Podocarpus guatemalensis*, the most widespread species, has a primarily lowland distribution (Figure 3.2a). *Podocarpus guatemalensis* illustrates that under current climate conditions podocarps are capable of persisting at sea level; GBIF herbarium collection data indicate that *P. guatemalensis* occurs in Caribbean coastal habitat from Belize to Panama and along the Pacific coast from Costa Rica south to Isla Gorgona and the Chocó of Colombia. Elsewhere in South America, *P. guatemalensis* occurs primarily at <1,000 m elevation, with a few collections at 2,600 m in Zamora-Chinchipe, southern Ecuador, representing distributional outliers for this species. No occurrences of this species have been reported east of the Andes.

South American podocarp taxa do have a primarily montane or lower montane distribution, with a few exceptions (Figure 3.2b). Most notably, *P. celatus* occurs in lower montane and lowland forest across the western Amazon of Ecuador and Peru and the northern Amazon of Venezuela. The lowest elevation occurrence of this taxon is at 130 m in Loreto, Peru, where it occurs on infertile lateritic and white sand soils.

In the Greater Antilles, *Podocarpus urbanii* extends to the highest point of Jamaica (2,256 m; Asprey and Robbins, 1953), whereas on Hispaniola *P. aristulatus* scarcely occurs above 1,800 m in the Cordillera Central. *Podocarpus aristulatus* is restricted to cloud forests (1,550–1,800 m), where it is the third commonest tree; above 1,800 m forests are dominated by *Pinus occidentalis* (Martin et al., 2007). The absence of *Podocarpus aristulatus* at higher elevations may be related to fire. Above 1,800 m fires are associated with El Niño droughts, occurring, on average, every seven years (Martin and Fahey,
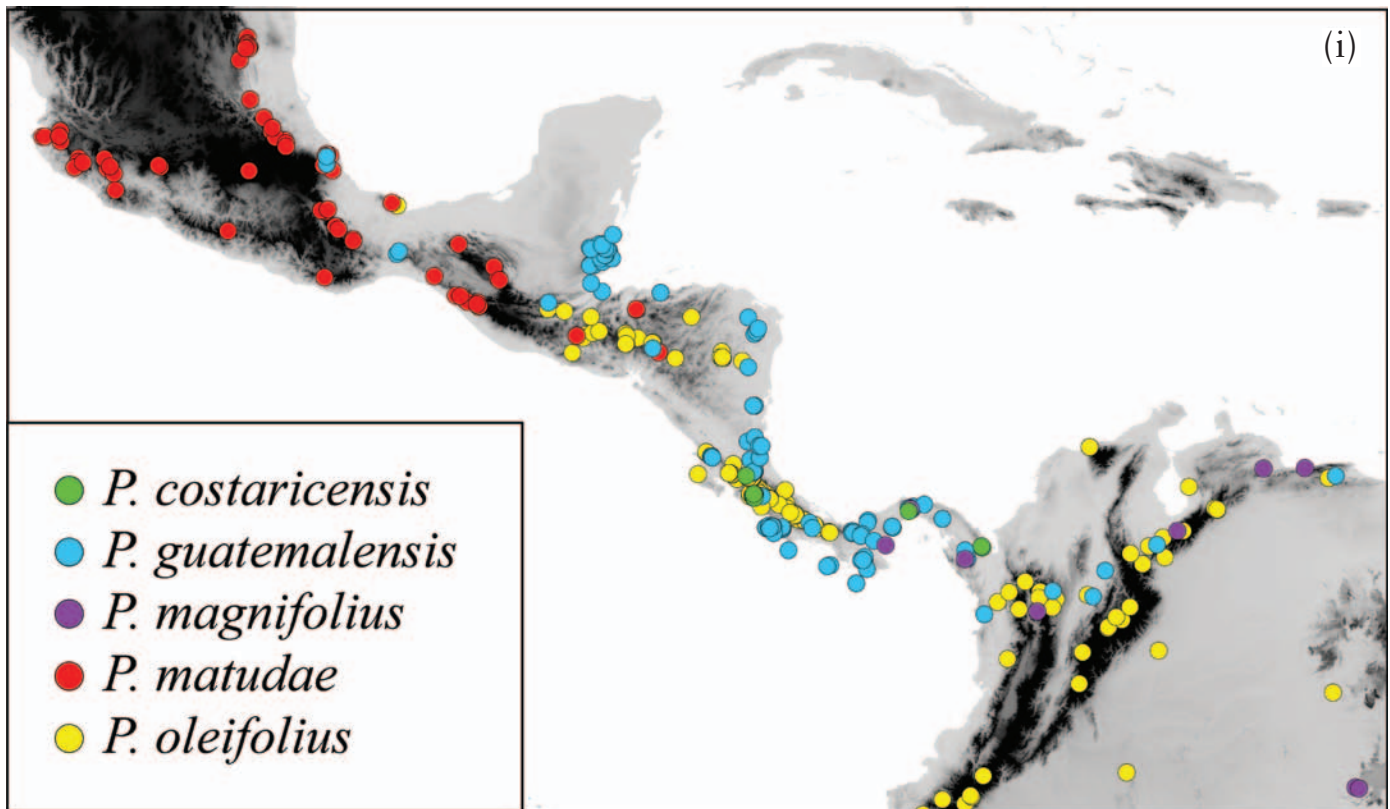
2006). In contrast, lower-elevation cloud forests do not support fire (Martin et al., 2007). On Hispaniola, a constraint on the distribution of *P. aristulatus* imposed by fire is consistent with the great majority of podocarps being intolerant of fire (Coomes and Bellingham, this volume).

HABITAT ASSOCIATIONS OF NEOTROPICAL PODOCARPS

The global distribution of conifers suggests a competitive advantage over angiosperms at high latitude and in arid or nutrient-poor environments (Ellenberg, 1988). In tropical and mesic temperate forests, Bond (1989) suggested that conifers have been excluded by their relatively low seedling growth rates, compared with angiosperm competitors. Low-productivity environments may eliminate this competitive disadvantage; inherently slow growth and tissue turnover rates can result in greater use efficiency of nutrients for conifers than angiosperms (Grime, 1979). Recently, Coomes et al. (2005) highlighted an additional mechanism that might account for temperate-forest podocarp distributions. On the South Island of New Zealand,

fertile alluvial terraces are dominated by angiosperms, whereas nearby older, phosphorus-impoverished terraces are dominated by podocarps. However, rather than nutrient availability, Coomes et al. (2005) argued that a dense understory fern layer leading to a thick, slowly decomposing litter layer effectively prevents seedling recruitment of podocarps, whereas smaller-seeded angiosperms are able to establish on less-shaded elevated recruitment sites formed by fallen logs.

Herbarium metadata unfortunately provide little information on the habitat associations of neotropical podocarps, although notes on specimens of *P. celatus*, *P. coriaceus*, *P. ingensis*, and *P. oleifolius* comment on the presence of sandy or quartzite soils, whereas the Cuban endemic species *P. angustifolius* occurs on serpentine soils (identified as *P. ekmannii*) or on lateritic soils that are more organic-rich than those dominated by pine (*Pinus cubensis*) forest (Smith, 1954; Borhidi, 1991). Ideally, evidence for habitat associations could be provided by plot-based ecological studies, but podocarps seldom seem to occur in plots. Almost all neotropical permanent plots are in the Amazonian lowlands, where podocarps are scarce. Podocarps have not been reported from any of the >250
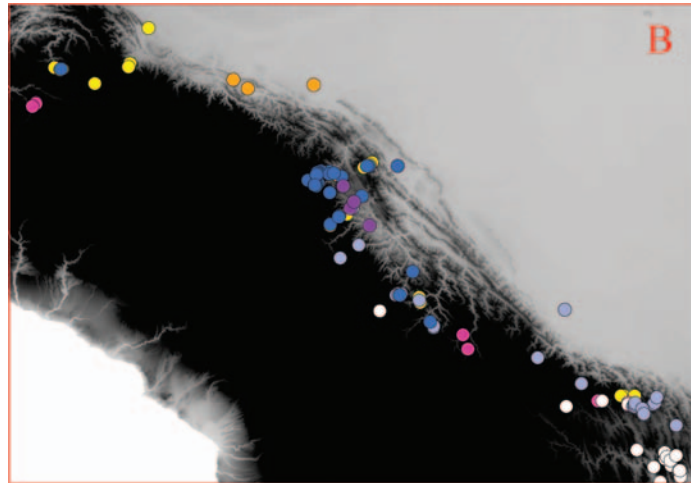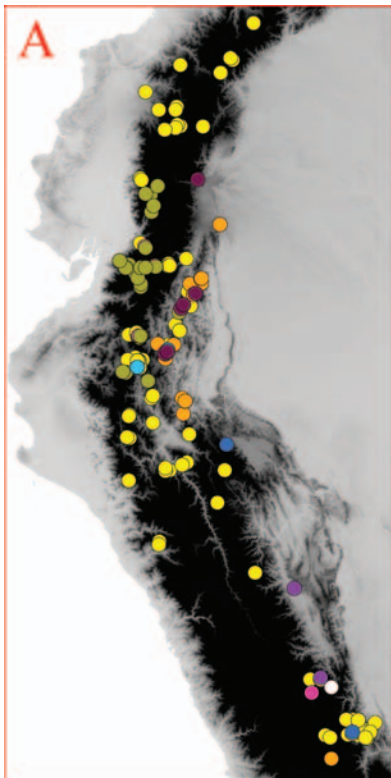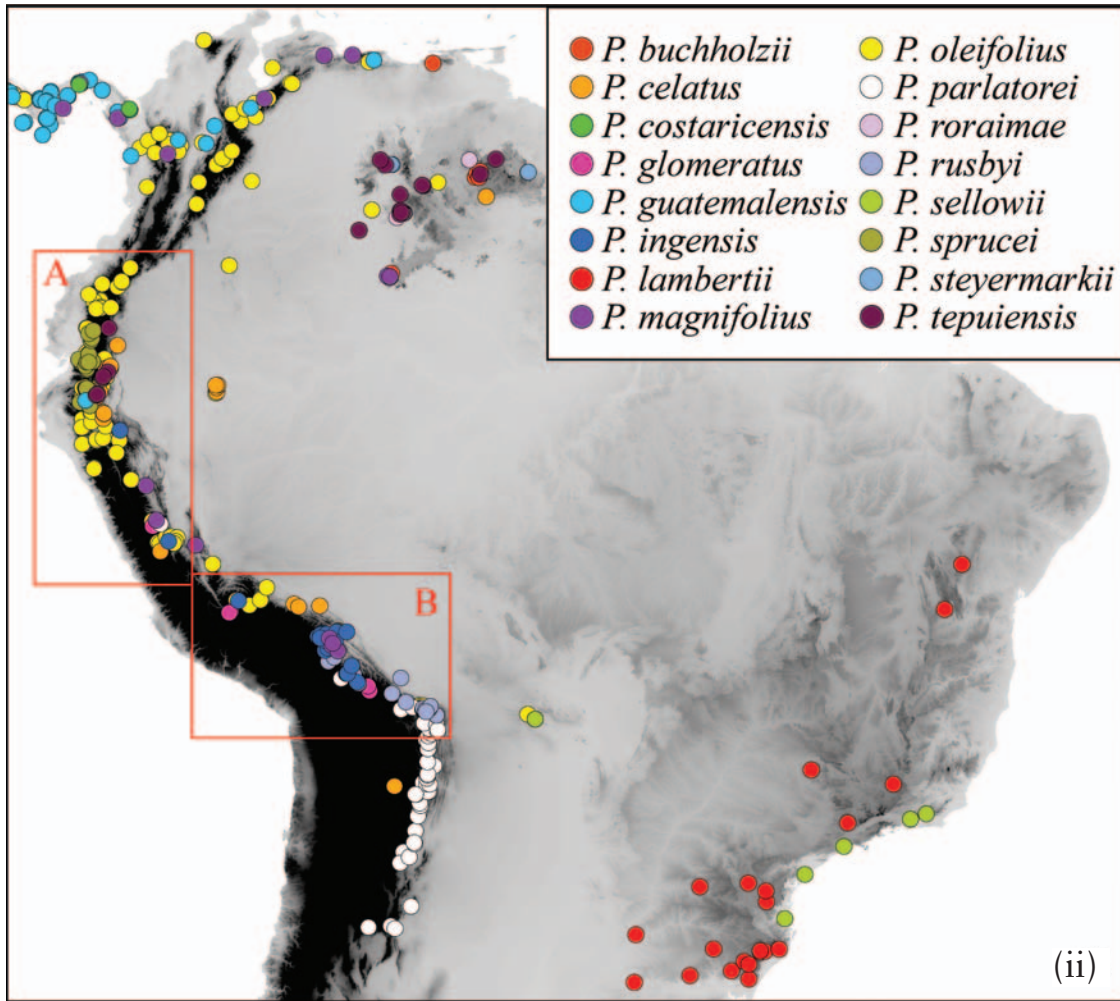
(i)

P. costaricensis
P. guatemalensis
P. magnifolius
P. matudae
P. oleifolius

Legend:
- P. buchholzii
- P. celatus
- P. costaricensis
- P. glomeratus
- P. guatemalensis
- P. ingensis
- P. lambertii
- P. magnifolius
- P. oleifolius
- P. parlatorei
- P. roraimae
- P. rusbyi
- P. sellowii
- P. sprucei
- P. steyermarkii
- P. tepuiensis

(ii)

FIGURE 3.1. Collection locations for neotropical *Podocarpus* species in (**i**, *facing page*) Central America and (**ii**) South America based on specimen metadata available through the Global Biodiversity Information Facility (http://www.gbif.net). Insets A and B provide enhanced regional detail. Antillean taxa and South American taxa with <10 georeferenced collections are omitted. Collections are plotted on the WorldClim gray-scale elevation surface for the neotropics (Hijmans et al., 2005). Darker shading indicates higher elevations.
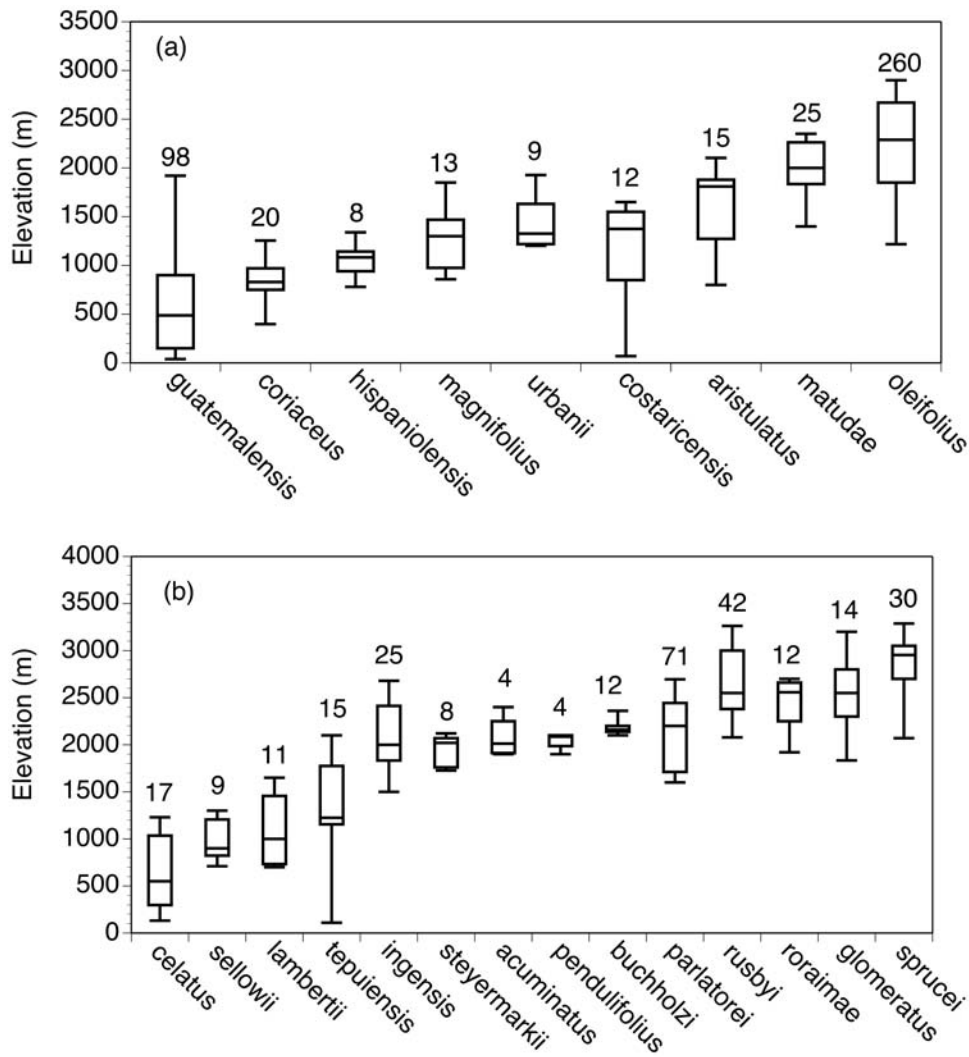
FIGURE 3.2. Box plots showing the median, 10th, 25th, 75th, and 90th percentiles for the elevation ranges of (a) Central American, Antillean, and widespread taxa and (b) South American *Podocarpus* species. Values above each box indicate the sample size for each species. Taxa with less than three elevational records are not included. Species are ordered by median elevation.

ha of the RAINFOR (Amazon Forest Inventory Network) 0.1–1 ha permanent plots arrayed across lowland Amazonia (O. Phillips, University of Leeds, personal communication), nor from lowland and montane 25–50 ha forest plots maintained by the Center for Tropical Forest Science (http://www.ctfs.si.edu). Because of their presumably patchy distribution, they are also absent from a network of 1 ha plots in the Colombian Andes (A. Duque, Universidad Nacional de Colombia, personal communication). When present in plots, they tend to occur at low relative density in species-rich forest. For nine *Podocarpus* species recorded in plot inventories, only in four cases did they account for >10% of either basal area or stem density (Table 3.1).

For four *Podocarpus* species, soils data accompanying plot inventories can be used to infer habitat specialization. *Podocarpus oleifolius* is a montane species distributed along the Continental Divide of Central America and the northern Andes. At the Fortuna Reserve in western Panama, *P. oleifolius* has a highly localized distribution: it is restricted to very wet sites with acidic humic soils underlain by a striking white soil developed from rhyolitic tuff (Table 3.1). It is absent from more fertile adjoining andesitic sites with similar elevation and rainfall (Andersen et al., 2010; J. Dalling, unpublished data). *Podocarpus oleifolius* also occurs on highly acidic soils in Venezuela (Kelly et al., 1994) and sandy acidic soils in northern Colombia

TABLE 3.1. Site information, stem density (density, individuals ha^{-1}), and basal area for neotropical permanent forest plots containing *Podocarpus* species. The table is sorted by latitude. See table footnotes for site, census information, and references. A dash (-) indicates that data are not available.

Species	Site	Elevation (m)	Rain (mm)	Soil pH	Basal area (m²ha⁻¹)	(%)	Density (ind ha⁻¹)	(%)	Fisher's alpha
P. matudae	Mexico [a]	800–1,400	2,500	-	1.1	3.5	83	7.1	-
P. matudae	Mexico [b]	1,800	1,000	-	4.1	5.5	120	5.7	15.1
P. aristulatus	Hispaniola [c]	1,100–2,500	2,000	-	4.2	18.0	32	4.0	8.5
P. hispaniolensis	Haiti [d]	1,280	-	-	14.9	21.0	222	6.3	11.7
P. urbanii	Jamaica [e]	1,580	3,000	4.1	10.1	29.1	420	10.3	10.2
P. urbanii	Jamaica [f]	1,580	3,000	3.6	12.0	26.6	840	15.7	8.5
P. urbanii	Jamaica [g]	1,580	3,000	4.3	8.5	18.0	156	3.9	7.4
P. urbanii	Jamaica [h]	1,580	3,000	3.0	0.7	1.1	117	1.5	3.4
P. urbanii	Jamaica [i]	1,760	3,000	3.7	5.5	9.9	225	3.0	-
P. urbanii	Jamaica [j]	1,620	3,000	5.0	2.0	4.6	113	2.5	-
P. urbanii	Jamaica [k]	1,660	3,000	4.1	4.4	6.4	80	1.4	-
Podocarpus spp.	Colombia [l]	2,940	1,500	-	35.9	45.0	120	3.8	12.5
P. oleifolius	Costa Rica [m]	2,300	3,300	-	-	-	20	3.5	11.1
P. oleifolius	Panama [n]	1,240	6,200	3.6	0.2	0.4	1	0.1	21.2
P. oleifolius	Panama [o]	1,100	4,300	3.9	2.5	7.8	6	0.6	12.6
P. oleifolius	Venezuela [p]	2,600	2,500	3.5	0.0	0.1	5	0.1	7.3
P. guatemalensis	Panama [q]	200	6,000	5.8	1.4	5.2	12	2.6	10.2
P. sprucei	Ecuador [r]	1,120	-	4.4	0.9	5.2	7	1.2	25.3
P. oleifolius	Ecuador [r]	1,120	-	4.4	0.3	1.9	4	0.7	20.1
P. tepuiensis	Ecuador [s]	1,620	-	4.6	0.9	7.0	9	1.7	21.6
P. selowii	Brazil [t]	10	1,875	-	0.1	0.4	3	0.4	30.3

[a] Puig et al. (1987), Gómez Farías, Tamaulipas, 23°3′N, 99°18′W, min dbh = 5 cm; means of nine 0.25 ha plots.
[b] Phillips and Miller (2002), Site 49, Sierra de Manantlan, Jalisco, 19°44′N, 104°15′W, min dbh = 2.5 cm; Gentry 0.1 ha transect plot.
[c] Martin et al. (2007), Cordillera Central, Dominican Republic, 19°1′N, 70°60′W, min dbh = 10 cm; means of twenty-five 0.05 ha plots.
[d] Senterre et al. (2006), Bois Cavalier, Macaya National Park, 18°19′N, 74°9′W, min dbh = 10 cm; 0.063 ha plot.
[e] Tanner and Bellingham (2006), wet slope forest, Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, 0.1 ha plot.
[f] Tanner and Bellingham (2006), mull ridge forest, Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, 0.1 ha plot.
[g] Tanner and Bellingham (2006), col forest ("gap" forest in Tanner, 1977), Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, 0.09 ha plot.
[h] Tanner and Bellingham (2006), mor ridge forest, Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, 0.06 ha plot.
[i] Bellingham (unpublished), ridge crest forest, Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, mean of six 0.02 ha plots.
[j] Bellingham (unpublished), windward slope forest, Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, mean of five 0.02 ha plots.
[k] Bellingham (unpublished), leeward slope forest, Blue Mountains National Park, 18°05′N, 76°39′W, min dbh = 3 cm, mean of five 0.02 ha plots.
[l] Phillips and Miller (2002), Site 119, Serranía de Perijá, Cesar, 10°30′N, 72°55′W, min dbh = 2.5 cm; Gentry 0.1 ha transect plot, three *Podocarpus* species occur in the plot.
[m] Lieberman et al. (1996), Volcan Barva elevational transect, 10°8′N, 84°6′W, min dbh = 10 cm, 1 ha plot.
[n] Dalling (unpublished), Quebrada Honda B, Fortuna Forest Reserve, 8°45′N, 82°14′W, min dbh = 10 cm, 1 ha plot.
[o] Dalling (unpublished), Quebrada Chorro, Fortuna Forest Reserve, 8°45′N, 82°14′W, min dbh = 10 cm, 1 ha plot.
[p] Kelly et al. (1994), Pico Bolivar, Sierra Nevada National Park, 8°35′N, 71°07′W, min dbh = 3.2 cm, 0.22 ha plot.
[q] Ibañez (unpublished) La Falla, Coiba Island, 7°30′N, 81°42′W, min dbh = 10 cm, 1 ha plot.
[r] Neill (2008), lower Nangaritza plot, Cordillera del Condor, 4°14′S, 78°39′W, min dbh = 10 cm, 1 ha plot.
[s] Neill (2008), upper Nangaritza plot, Cordillera del Condor, 4°14′S, 78°39′W, min dbh = 10 cm, 1 ha plot.
[t] Negrelle (2002), Volta Velha Reserve, Santa Catarina, 26°4′S, 48°38′W, min dbh = 5 cm, 1 ha plot.

(Marín, 1998) and reaches highest abundance in tannin-rich swamps at Monteverde, Costa Rica (Haber, 2000).

A striking parallel to *P. oleifolius* in Panama is the recent discovery of *P. tepuiensis* growing at 1,600 m along the Ecuador–Peru border (Neill, 2008). *Podocarpus tepuiensis* was previously thought to be endemic to the Guyana Shield of northwestern South America, where it occurs on sandstone mesas (tepuis). In Ecuador, *P. tepuiensis* is restricted to coarse quartzite outcrops dispersed along the Cordillera del Cóndor that consist of mid-Cretaceous

Hollin Formation sandstones. The Hollin Formation is similar to the Guyana Shield mesa sandstones >1,500 km away from which they are ultimately derived. Paired plots established on the Hollin Formation and adjacent granitic substrates showed that podocarps were restricted to sites underlain by sandstone (Neill, 2008).

Another widely distributed species, *P. guatemalensis*, occurs near sea level from Belize to Isla Gorgona on the Pacific coast of Colombia. In Panama, *P. guatemalensis* occurs on numerous Pacific and Atlantic coastal islands, including Coiba, Bastimentos, and Escudo de Veraguas, and occasionally in wet lowland forest on the mainland. On Coiba, *P. guatemalensis* occurs in one of seven 1 ha forest plots (A. Ibañez, Smithsonian Tropical Research Institute, unpublished data). The distribution of *P. guatemalensis* on Coiba appears to be constrained to mafic substrates on the southern side of a geological fault line (A. Ibañez, unpublished data). Although available evidence therefore suggests that podocarps are associated with acidic, infertile soils, this is not always the case. The Caribbean island species *P. aristulatus* and *P. purdieanus* occur in wet forest on karst limestone in central and western Cuba and western Jamaica, respectively (Borhidi, 1991; Bachman et al., 2007), where exposed rock outcrops and steep topography can result in a relatively open forest canopy.

HABITAT ASSOCIATIONS, FUNCTIONAL TRAITS, AND DEMOGRAPHY OF *PODOCARPUS URBANII* IN JAMAICAN MONTANE FOREST

Among the neotropical montane podocarps, our best understanding of relationships of distribution and abundance in relation to geology and soils is for *Podocarpus urbanii*, which is endemic to the Blue Mountains of eastern Jamaica, between 1,370 and 2,256 m (Buchholz and Gray, 1948). The Blue Mountains are composed of granodiorite, mudstones, sandstones, and conglomerates (Grubb and Tanner, 1976), and *P. urbanii* occurs on all of these rock types, although not on local outcrops of limestone (P. J. Bellingham, unpublished data). On the basis of stem density, *P. urbanii* is the fourth most abundant tree species in the upper slope and ridgetop forests of the Blue Mountains, accounting for 7% of stems >3 cm diameter at breast height (dbh) (Tanner and Bellingham, 2006), and the fourth highest basal area, behind three ericoid tree species (*Cyrilla racemiflora*, *Vaccinium meridionale*, and *Clethra occidentalis*; Bellingham et al., 2005).

Podocarpus urbanii occurs across a range of soil types in the Blue Mountains. For example, it occurs in four forest types within 300 m of each other at 1,580–1,600 m that range considerably in soil pH and concentrations of carbon, nitrogen, and phosphorus (Tanner, 1977; Table 3.2). Forest stature declines from a canopy height of 18 to 7 m as soil pH decreases and soil C:N and N:P ratios increase across the sites (Table 3.2), and forest composition varies considerably (Tanner, 1977). *Podocarpus urbanii* is present in all forest types, with the highest proportion of total basal area and stem density occurring in slope forest and mull ridge forests (ridgetop forest lacking a deep litter layer), which have intermediate fertility (Table 3.2). *Podocarpus urbanii* is markedly less abundant in the short-stature mor ridge forest (which has highly acidic soils with high soil C:N and N:P; Table 3.2). The rarity of *P. urbanii* on the mor site is most likely a consequence of the high organic matter content of the mor soils (>47% carbon up to 30 cm soil depth; Tanner, 1977). Mor soils, in turn, derive from nutrient-poor recalcitrant litter produced by trees in the Ericales that dominate the site. A competitive advantage for the Ericales may arise from symbiotic association with ericoid mycorrhizas, which scavenge effectively for organic sources of nitrogen and phosphorus (Read et al., 2004). In the nearby mull ridge forest, bioassay experiments (Tanner, 1977; Healey, 1989), a field fertilization experiment (Tanner et al., 1990), and a root ingrowth experiment (Stewart, 2000) all indicate colimitation to plant growth by both nitrogen and phosphorus.

A more-extensive view of relationships between *P. urbanii* and site and soil variables is derived from 15 permanent plots within a 250 ha portion of the western part of the Blue Mountains centered on the axial range (plots 1,470–1,900 m, Bellingham et al., 2005; one plot at 1,300 m is below the lower altitudinal limit of *P. urbannii*). *Podocarpus urbanii* occurred in 12 of these plots, within which it comprised 1%–10% of stems ≥3 cm dbh (2004 census) and 1%–22% of stand basal area. The percentage of stems and basal area in the plots composed of *P. urbanii* was unrelated to altitude and slope ($r^2 < 0.18$, $p > 0.12$). The percentage of stems and basal area had a unimodal response to soil pH (most frequent in plots with soil pH 3.5–4.2 and not found in plots with soil pH > 5.0; range across plots: 3.1–5.7). The percentage of stems was positively related to soil C:N ratio ($r^2 = 0.30$, $p = 0.03$), but the percentage of basal area was not ($r^2 = 0.16$, $p = 0.14$), and both were unrelated to soil N:P ratio or total phosphorus concentration ($r^2 < 0.09$, $p > 0.28$).

In the Jamaican montane forests, *P. urbanii* has a specific leaf area 55 cm^2 g^{-1}, which is 32% less than the

TABLE 3.2. Percentage of total basal area and total stem density of *Podocarpus urbanii* (stems ≥3 cm diameter at 1.3 m) in four montane rainforest types within 300 m of each other in the Blue Mountains, Jamaica (1580–1600 m elevation; 2004 census), and canopy height and soil characteristics of each forest type. Data are from Grubb and Tanner (1976), Tanner (1977), and Tanner and Bellingham (2006).

Characteristic	Col	Slope	Mull	Mor
Total basal area (m² ha⁻¹)	58 ± 5.2	57 ± 3.7	45 ± 2.7	62 ± 6.7
P. urbanii basal area (%)	17 ± 5.3	22 ± 2.3	23 ± 3.1	2 ± 1.3
Total stem density (stems ha⁻¹)	4320 ± 277	4490 ± 318	6220 ± 313	8180 ± 512
P. urbanii stem density (%)	4 ± 1	13 ± 1.1	9 ± 1	2 ± 1
Canopy height (m)	12–18	8–13	8–13	(4–)5–7
Soil pH	4.3	4.1	3.6	3.0
Soil total carbon (%)	11.0 ± 1.4	9.1 ± 1.5	11.6 ± 1.5	49.0 ± 1.2
Soil total nitrogen (%)	1.1 ± 0.12	0.68 ± 0.08	0.88 ± 0.10	2.0 ± 0.03
Soil total phosphorus (%)	0.07 ± 0.01	0.04 ± 0.01	0.04 ± 0.01	0.05 ± 0.00
Soil C:N ratio	10 ± 0.3	13 ± 0.8	13 ± 0.4	24 ± 0.9
Soil N:P ratio	15.7 ± 1.3	20.4 ± 8.7	23.7 ± 5.5	43.8 ± 3.5
Foliar nitrogen (%), all species (*n*)	1.76 (8)	1.27 (9)	1.61 (14)	1.05 (13)
Foliar nitrogen (%), *P. urbanii*	0.86	0.71	0.71	0.69
Foliar phosphorus (%), all species (*n*)	0.10 (8)	0.08 (9)	0.07 (14)	0.05 (13)
Foliar phosphorus (%), *P. urbanii*	0.05	0.05	0.05	0.05

average (81 cm² g⁻¹) across 26 species in the forests, and a leaf thickness of 527 µm, which is more than double the average (237 µm) across 50 species in these forests (Tanner and Kapos, 1982). Across the four adjacent forest types described by Tanner (1977), the foliar nitrogen concentration of *P. urbanii* was consistently less than the average across co-occurring angiosperm species in each site (Table 3.2), whereas the foliar phosphorus concentration of *P. urbanii* was less than average in all but the very nutrient-poor mor ridge forest (Table 3.2). The lower foliar nitrogen concentration in a Jamaican montane podocarp compared to coexisting angiosperms is consistent with results from a temperate rainforest soil chronosequence (Richardson et al., 2005), although in that chronosequence foliar phosphorus concentrations of podocarps were generally not different from co-occurring angiosperms, in contrast to Jamaica.

The montane forests in which *P. urbanii* occurs are subject to frequent but irregular disturbance by hurricanes (with severe canopy damage, on average, every 25 years) and, locally, by landslides triggered by high-intensity rainfall and earthquakes. Comparative data for *P. urbanii* and coexisting angiosperms include a 30-year record of growth and survivorship in permanent plots (Tanner and Bellingham, 2006), seedling recruitment in experimental

tree fall gaps and undisturbed forest (Healey, 1990) and on a chronosequence of landslides (Dalling, 1994), and surveys of tree recovery from hurricane damage (Bellingham et al., 1994, 1995; Bellingham and Tanner, 2000).

Pooling data from across four forests of contrasting soils and forest composition (Tanner, 1977), the tree size structure of *Podocarpus urbanii* shows a distribution skewed toward smaller sizes, with more small stems than two coexisting angiosperm canopy dominants, *Clethra occidentalis* and *Lyonia octandra*, but fewer small stems than *Hedyosmum arborescens* (Bellingham et al., 1995). The size structure of *P. urbanii* is similar to some podocarps in other tropical montane rainforests (e.g., *Falcatifolium falciforme*, Aiba et al., 2004) and warm temperate rainforests (e.g., *Nageia nagi*, Kohyama, 1986) and suggests that *P. urbanii* is at least moderately shade tolerant, which is consistent with its relatively high abundance as seedlings under intact canopies (Figure 3.3; Sugden et al., 1985; Healey, 1990). However, its size structure has not been constant in these permanent plots over 30 years. In 1974, at least 23 years after the forest had last been disturbed by a hurricane, small stems (<10 cm dbh) were common, and there were few large stems (>25 cm dbh; Figure 3.4). Hurricane Gilbert, the most powerful North Atlantic hurricane in the twentieth century, severely disturbed these
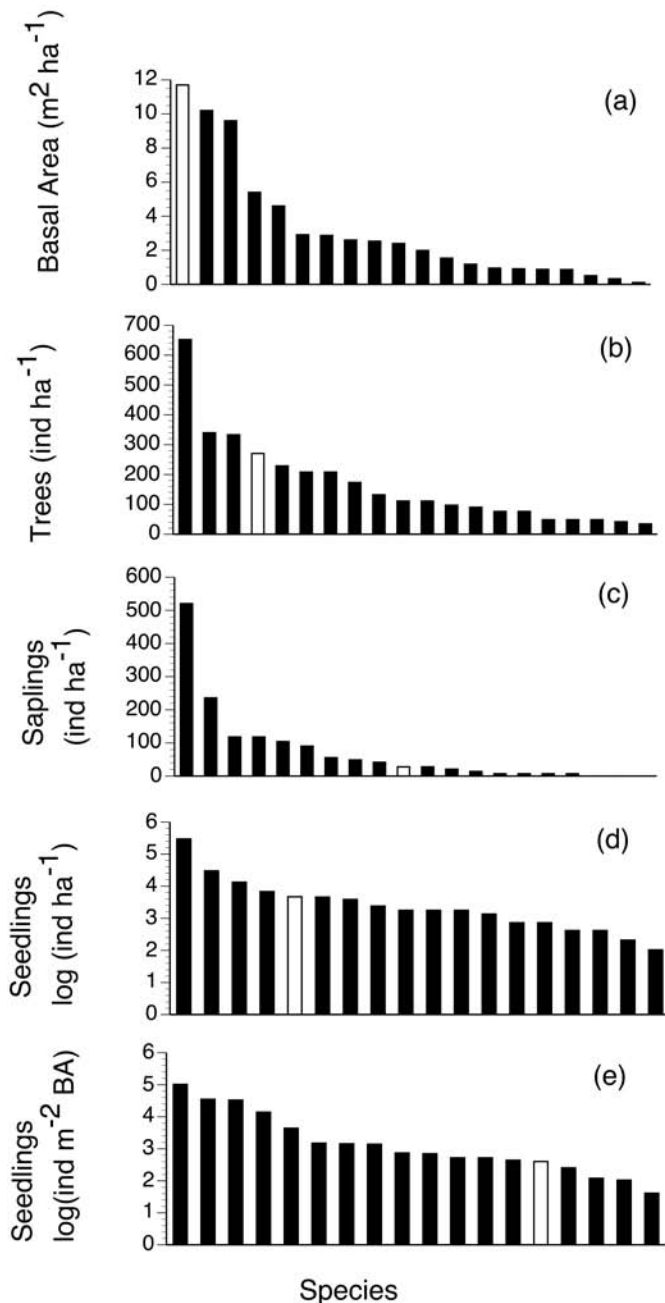
FIGURE 3.3. (a) Basal area, (b) stem density (individuals <3.2 cm diameter at 1.3 m height), (c) sapling density (individuals <3.2 cm diameter at breast height and >3 m height), (d) seedling density, (e) seedling number per unit basal area for all species (solid bars), and *P. urbanii* (open bars). Adult and sapling data are from six 0.024 ha plots; seedling data are from ninety-six 1 m² plots. Data are from Healey (1990).
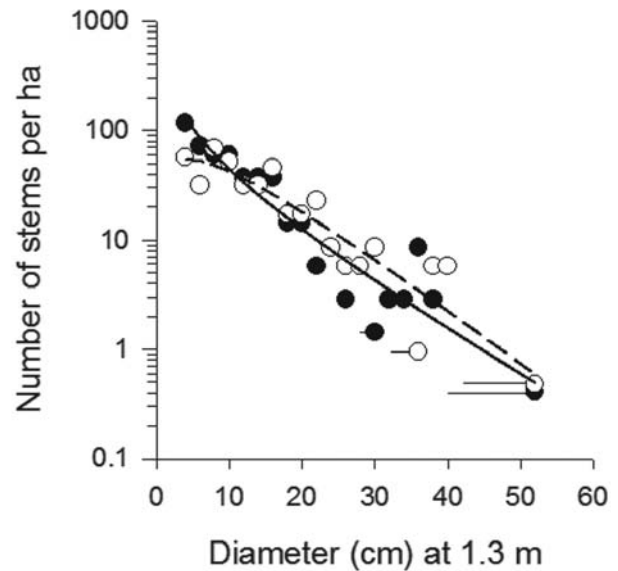

FIGURE 3.4. Frequency distribution of stems of *Podocarpus urbanii* ≥3 cm diameter at 1.3 m height, pooled across four forest types within 300 m of each other in the Blue Mountains, Jamaica (total area sampled = 0.35 ha) at two censuses of the same plots (1974, solid circles; and 2004, open circles). Data are in 2 cm interval classes, with averaged interval classes linked by a left-tailed horizontal bar. Curve fitting followed Kohyama (1986) and provided a better fit than the Weibull function (Bailey and Dell, 1973). Solid line (1974): $\ln(y) = 5.075 - 0.08148x - 0.6563\ln(x)$, $r^2 = 0.89$; dashed line (2004): $\ln(y) = 2.684 - 0.1226x + 0.5334\ln(x)$, $r^2 = 0.85$.

forests in 1988 (Bellingham et al., 1995). Sixteen years later, in 2004, there was a greater frequency of stems >20 cm dbh, but many fewer stems <10 cm dbh than in 1974 (Figure 3.4).

Over the past 30 years, mortality rates for *P. urbanii* were between two- and sevenfold lower than co-occurring species on slope, mull ridge, and col forests but similar to co-occurring species on the infertile mor ridge site (Figure 3.5a). Differences in mortality rates among sites probably reflect spatial heterogeneity in tree mortality resulting from Hurricane Gilbert in 1988 linked to ridge and slope topography (Bellingham, 1991). The low mortality of *P. urbanii* relative to co-occurring species does not appear to be a consequence of structural traits. *Podocarpus urbanii* has the fourth lowest wood density in the community (0.6 g cm⁻³; Tanner, 1977) and above-average diameter growth rates at all sites except the mor ridge (Figure 3.5b). Recruitment rates into the 3 cm dbh class, however, have been exceptionally low at all sites (Figure 3.5c), and there is little contribution of resprouting to population
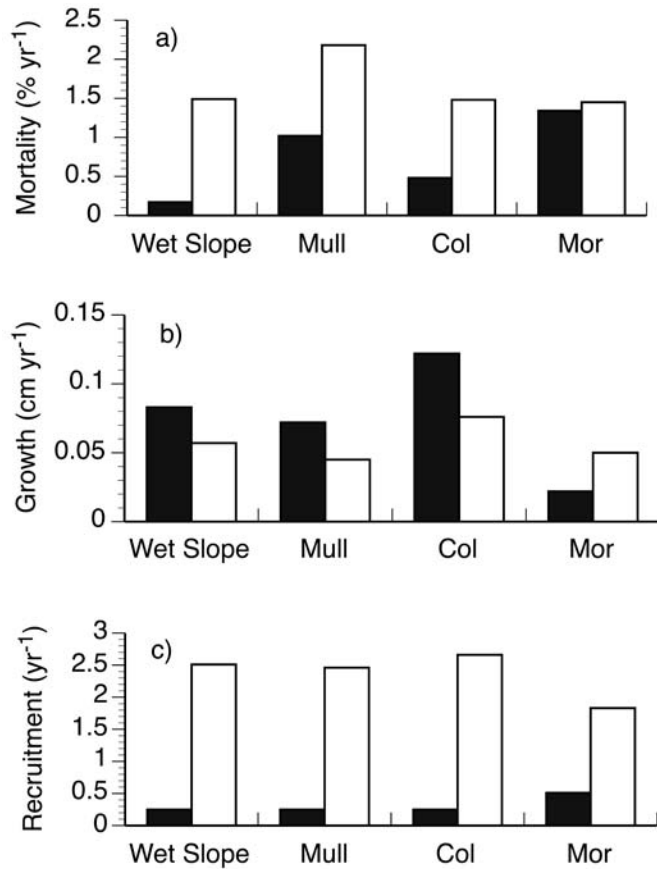
FIGURE 3.5. Annualized (a) mortality, (b) growth, and (c) recruitment rates of *Podocarpus urbanii* (solid bars) and all other species (open bars) from 1974 to 2004 for individuals >3 cm dbh at four forest types in the Blue Mountains, Jamaica (see Table 3.2). *Podocarpus*, all sites combined, mortality (calculated from a census of n = 136), recruitment (n = 11), growth (n = 136). Other species, all sites combined, mortality (n = 1417), recruitment (n = 904), growth (n = 822). Mortality and recruitment rate calculations follow Burslem et al. (2000).

FIGURE 3.6. Density of new seedling recruits per hectare of principal canopy species recorded in forty-eight 1 m^2 plots distributed across (a) three understory plots and (b) three forest gaps simulating hurricane damage, 18 months after an initial survey. (c) Seedling recruits recorded on four 14-year-old landslides triggered by road construction. Data are from Healey (1990) and Dalling (1992).

maintenance of *P. urbanii*, in contrast to many of the co-existing angiosperms (Bellingham et al., 1994).

Differences in adult growth and mortality rates among species in part reflect differences in susceptibility to hurricane damage. *Podocarpus urbanii* was significantly more resistant to hurricane damage than the community average when assessed up to four years after Hurricane Gilbert (Bellingham et al., 1995), but the decline in recruitment between 1974–1984 and 1994–2004 suggests that its comparative abundance may derive from periods of relatively less disturbance. Evidence to support this view derives from a study 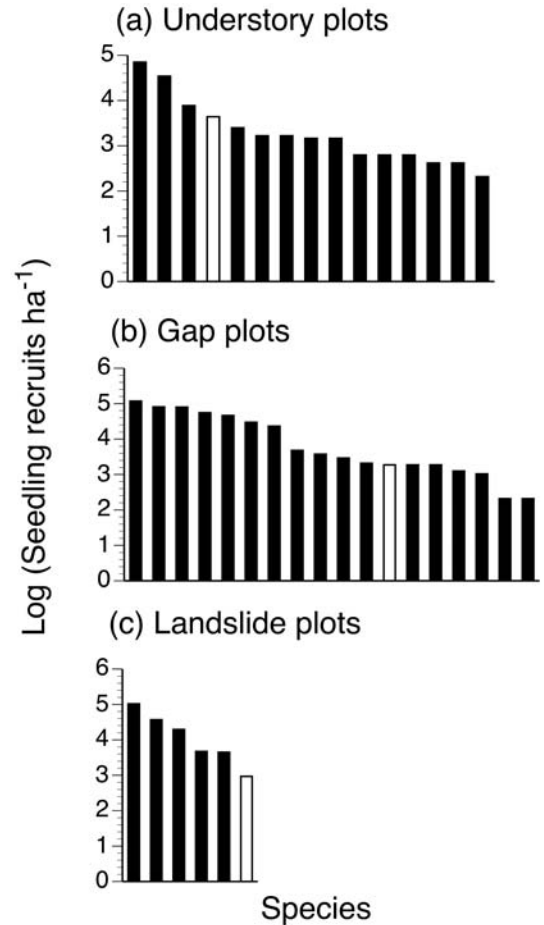of experimental canopy gaps, similar to those formed during Hurricane Gilbert, in which *P. urbanii* was the twelfth most abundant species as seedlings compared with being the fourth most abundant species as seedlings under adjacent closed canopies (Healey, 1990; Figure 3.6a,b). *Podocarpus urbanii* may also benefit from other more patchy and less frequent disturbances such as landslides (Dalling, 1994; Figure 3.6c), although observations of recruitment on older (>50 years old) landslides (Dalling, 1994) suggest that they are much more important recruitment sites for ericoid canopy trees.

In summary, *Podocarpus urbanii* is a moderately shade-tolerant tree species in Jamaican montane forest,

capable of regenerating from seed in undisturbed forest more frequently than many of the other principal canopy species. *Podocarpus urbanii* leaf traits and low adult mortality rates are also consistent with shade tolerance. However, *P. urbanii* maintains surprisingly high diameter growth rates, which is probably attributable to its relatively low wood density and may help explain the frequency of this species in hurricane-prone forest.

CONSERVATION AND MANAGEMENT OF NEOTROPICAL PODOCARPS

Of 31 neotropical podocarps, 11 are considered at risk (near-threatened to endangered), 13 are of "least concern," and 5 species lack sufficient data to be evaluated (International Union for Conservation of Nature [IUCN], 2009). Taxa of least concern either have widespread distributions, with populations within protected areas (e.g., *Podocarpus oleifolius*, *P. guatemalensis*), or are restricted to remote, undisturbed rainforests, principally in the Guyana Shield or western Andes. With the exception of *Podocarpus coriaceus*, which occurs on multiple Lesser Antillean islands, all podocarp taxa that occur in the insular Caribbean are of conservation concern. Most threatened are the three Greater Antilles endemics, *P. hispaniolensis*, *P. angustifolius*, and *P. purdieanus*, each of which has restricted distributions on Hispaniola, Cuba, and Jamaica, respectively. Species for which data are insufficient to make a status evaluation include the Trinidad endemic, *P. trinitensis*, and taxa whose distributions are either restricted or scattered or in localities where logging or forest conversion may threaten populations in the future.

In the absence of information on population size or growth, IUCN designation of threatened species must rely heavily on criteria based on observed range size. Our review, indicating that many podocarps are associated with infertile soils, suggests that the large observed geographic ranges (Figure 3.1) of many species may support only small, localized, and therefore unconnected populations. For example, the range distribution of *Prumnopitys harmsiana* includes portions of Venezuela, Colombia, Ecuador, Peru, and Bolivia. However, in Colombia the species is known from only five small populations 600 km apart (Cogollo, 2007). The predominantly mid-elevational distribution of many podocarp taxa (Figure 3.2) has also meant that many populations have been drastically reduced by forest clearance for coffee cultivation, pasture, and row crops (Cogollo, 2007).

In addition to land conversion, several podocarp species have been logged extensively in Colombia and probably elsewhere (Torres-Romero, 1988; Cogollo, 2007). Species that reportedly formed high-density stands, including *Retrophyllum rospigliosii* and *Podocarpus guatemalensis*, are now almost extinct in the Rio Magdalena valley (Torres-Romero, 1988). As yet, few efforts at ex situ conservation of neotropical podocarps have been attempted; however, several species in Antioquia, Colombia, including *R. rospigliosii*, have been promoted for watershed reforestation or have been established in arboreta (Velasquez-Rua, 2005).

Attempts at propagating podocarp seedlings for reforestation have met with limited success. Marín (1998) notes that germination and establishment success of *Podocarpus oleifolius* and *Prumnopitys harmsiana* seedlings are low, whereas propagation of cuttings using plant hormone treatments or removal of established seedlings from wild populations has been more effective. Poor seedling establishment success may also account for the relative paucity of *Podocarpus urbanii* in secondary forest when compared to nearby old-growth forest sites (McDonald and Healey, 2000). Growth and survival trials of seedling transplants, however, indicate that *P. urbanii* performs well above average relative to other Jamaican montane forest trees (McDonald et al., 2003), suggesting that podocarps may have unrealized potential for reforestation.

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