# Structure and species composition of novel forests dominated by an introduced species in northcentral Puerto Rico

**Oscar J. Abelleira Martínez · Mariela A. Rodríguez · Ivonne Rosario · Nataly Soto · Armando López · Ariel E. Lugo**

**Abstract** The African tulip tree, *Spathodea campanulata* Beauv., is an introduced species forming novel forest types in Puerto Rico. These forests develop naturally after deforestation, agricultural use and land abandonment, and there are many questions as to their ecological characteristics. We sampled structure and species composition of large, small, and juvenile trees ($\geq$10, $\geq$2.5 to <10, and <2.5 cm diameter at breast height, respectively) in nine secondary forests dominated by *S. campanulata* on alluvial, karst, and volcanic substrates in northcentral Puerto Rico. No differences were found in *S. campanulata* forest structure between substrates. Of a total of 79 species found, 17 were introduced. Forests on karst and alluvium had the highest and lowest global species richness, respectively. Species richness increased from large to small to juvenile trees in most sites, but more so on karst. The percentage of introduced species was inversely related to species richness of tree size classes on all substrate types. The dominance of *S. campanulata* in the large tree size class was highest and lowest in alluvial and volcanic sites, respectively, and decreased from large to small to juvenile trees on all substrate types. Species richness of *S. campanulata* forests is lower than that of native forests on equivalent substrates. Although land use history affects composition, the juvenile tree species established in *S. campanulata* forests seems to correspond to the geological substrate were sites are found. This study shows *S. campanulata* restores forest structure and native tree species on abandoned agriculture and grazing lands in Puerto Rico. Management of these novel forests should consider them as resources were natural processes have the potential of making them more diverse.

O. J. Abelleira Martínez (✉) · A. E. Lugo
International Institute of Tropical Forestry, USDA Forest Service, Ceiba Street 1201
Jardín Botánico Sur, Río Piedras, PR 00926-1119, USA
e-mail: oabelleira@fs.fed.us

O. J. Abelleira Martínez · M. A. Rodríguez · I. Rosario · N. Soto · A. López
Alianza para el Aprendizaje de Ciencias y Matemáticas, Universidad de Puerto Rico,
Río Piedras, PR, USA

O. J. Abelleira Martínez
Departamento de Biología, Universidad de Puerto Rico, Río Piedras, PR, USA

## Introduction

Human activity is having significant effects on the environmental conditions that support
life in the planet. These effects include climate change, soil erosion, acid rain, deforestation, changed composition of atmospheric gasses, urbanization, and many others, which
lead some to declare this era as the era of human domination or the Homogeocene (McKinney and Lockwood 1999; Lockwood and McKinney 2001). A fundamental question
that emerges from these trends is: What is the response of the biota to anthropogenic
environmental change? Through time, the species composition of forests and other plant
communities have changed in response to natural environmental change, so that the forests
of today are different from those of the past (Behrensmeyer et al. 1992). Will anthropogenic effects cause similar changes in the species composition of modern forests? If so,
what will be their structure and species composition?

Given the high level of anthropogenic effects, some ecologists anticipate dire consequences for species diversity due to biotic homogenization, particularly in the tropics (see
Lockwood and McKinney 2001; Sodhi et al. 2007 for excellent reviews). Other ecologists
suggest that the biota will respond to novel environmental conditions with the natural
assembly of novel communities composed of a new combination and relative importance
of species (Hobbs et al. 2006; Williams and Jackson 2007). The emergence of novel forests
is considered a natural response to such anthropogenic effects as deforestation, land use
and degradation, and abandonment (Fig. 1 in Hobbs et al. 2006). Ecologists are now
documenting novel tropical forests in Hawaii (Mascaro et al. 2008), Puerto Rico (Lugo and
Helmer 2004), and elsewhere in the world (Hobbs et al. 2006) but there is insufficient
information on the structural variation and species composition of these forests. Moreover,
since these forests are usually dominated by introduced tree species, ecologists worry that
their establishment reduces local biodiversity by inhibiting the regeneration of native
species (Grau et al. 2003; Mascaro et al. 2008).

The Caribbean island of Puerto Rico is already exposed to the conditions of the Homogeocene due to its high population density (450 people/km²), large fraction of urban
development (15%), high proportion of introduced species in the flora (>20%), and long
history of land use involving deforestation, intensive agricultural use, degradation of lands,
and subsequent abandonment and forest regeneration (Rudel et al. 2000; Lugo 2004; Lugo
and Helmer 2004). This cycle of land use and abandonment is at an advanced stage. Over
the past 60 years, the island has experienced an unprecedented rate of land abandonment
and forest regeneration such that today, forest cover is over 50% after a low of 5% in the
1960s (Birdsey and Weaver 1982; Brandeis et al. 2007). The rapid rate of forest regeneration on degraded and abandoned agricultural lands allows for the study of closed canopy
novel forests to see if in fact dominance by introduced species inhibits the regeneration of
native species and suppresses plant biodiversity.

The structure and species composition of native forests in Puerto Rico is shaped by
climate and geological substrate type (Danserau 1966; Little et al. 1974; Lugo 2005).
Consequently, we studied the structure and composition of novel forest stands within a
humid climate on three different geological substrates (alluvial, karst, and volcanic) to
examine if they varied as native forests do. These novel forests are dominated by the

African tulip tree, *Spathodea campanulata* Beauv. (Bignoniaceae), an introduced species that has the potential to invade abandoned lands previously used for agriculture and grazing in many tropical islands (Aide et al. 2000; Haysom and Murphy 2003; Novotny et al. 2004). In Puerto Rico, it has been observed that the forest environment that naturally results from *S. campanulata*'s invasion is unfavorable for its own regeneration because of its intolerance to shade and allows for the regeneration of other tree species (Aide et al. 2000; Lugo 2004). However, how species composition changes from the older large trees to the recently established juvenile trees in these forests has not been studied properly. We hypothesized that (1) the structure and species composition of *S. campanulata* forests would vary as native forests on equivalent substrate types do and (2) species composition would change through tree size classes reflecting lower dominance of *S. campanulata* and higher species richness in juvenile compared to larger tree size classes. Our study contributes to the understanding of the role of introduced tree species in the response of the biota to anthropogenic disturbances, specifically natural regeneration processes on degraded and abandoned agricultural lands.

## Study region and site selection

We selected three sites each on alluvial, karst, and volcanic geological substrates in the northcentral region of Puerto Rico (18°N, 65°W; Fig. 1). The region falls in subtropical moist to wet life zone climate and for the years 1971–2000, mean annual precipitation and temperature ranged from 1,443 to 1,905 mm and from 21.5 to 25°C, respectively
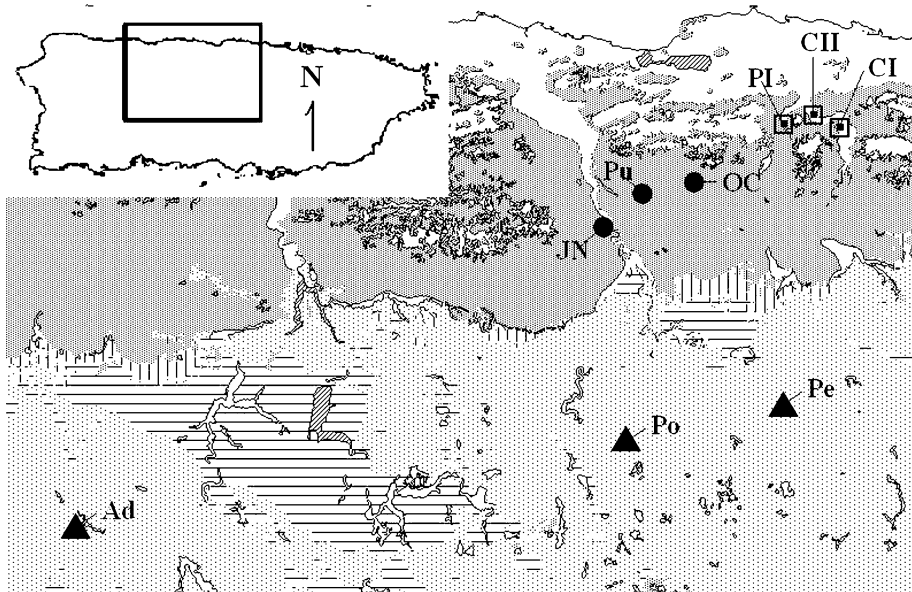


**Fig. 1** Study site locations on a map of geological substrate types (Bawiec et al. 2001). The inset delimits the location of the study region within mainland Puerto Rico. *Symbols* correspond to sites on the following substrates; *squares*: alluvial, *circles*: karst, *triangles*: volcanic. Site codes; *CI*: Cibuco I, *CII*: Cibuco II, *PI*: Paso del Indio, *JN*: Juan Nieves, *OC*: Ollas y Calderas, *Pu*: Pugnado, *Ad*: Adjuntas, *Pe*: Perchas, *Po*: Pozas. Site names correspond to the municipalities or neighborhoods were the sites were located

(Holdridge 1967; Ewel and Whitmore 1973; NOAA 2002). In Puerto Rico, *S. campanulata* is light demanding, evergreen to deciduous, and has intense orange-red annual mass flowering (Little and Wadsworth 1964; Francis 2000). Thus, we located and selected closed canopy forests that were orange-red during *S. campanulata*'s flowering using field observations and 1 m resolution aerial photography (CRIM 2004).

## Site descriptions

The elevation of all sites ranged from 10 to 200 m except for Adjuntas which is at 500 m above sea level. Alluvial sites are flat and slope ranges from 7 to 50% on karst sites and from 50 to 70% on volcanic sites. The soil on alluvial sites is derived from non-volca-niclastic sedimentary deposits from the Quaternary and on karst sites it is derived from similar deposits embedded in calcium carbonate rock from the Oligocene (Acevido 1982; Bawiec et al. 2001). The soil on volcanic sites is derived from weathering of extrusive volcaniclastic material from the Cretaceous. Alluvial sites are riparian and suffer periodic floods (Abelleira and Lugo 2008), karst sites are in closed depressions (Monroe 1976), and volcanic sites are near mountain bases.

The age since abandonment and land use history of each site was determined from interviews with local inhabitants and aerial photography from 1963, 1971, 1977–1978 (Ramos and Lugo 1994), and 1985. The age of each site, estimated as the mid-point between the most recent aerial photos showing use and the oldest showing abandonment, ranged from 24 to 39 years. This age range is suggestive of structural maturity for secondary forests in Puerto Rico (Aide et al. 2000; Chinea 2002).

The valleys where alluvial sites are located have been used for sugar cane plantations since the sixteenth century up to the twentieth century (Álvarez Nazario 1982; Picó 1988). A years' crop cycle consisted of cane growth, harvesting, burning and re-growth, sometimes interspersed with fallow years. The age of the sites suggests heavy machinery was not used but cattle plow lines are still evident. The depressions where karst sites are located might have been used for sugar cane as well but this crop was gradually abandoned in higher elevations during the first half of the twentieth century (Picó 1988). The crops planted immediately before abandonment in karst sites consisted of fruits such as citrus, avocado and plantains, and tubers such as cassava and yams. Agricultural activities were concentrated in lower ground were organic soil was available and the rather rocky upper slopes and ridges were used for firewood and pole harvesting. As a result, some marginal forest land remained on some ridges. Volcanic mountain slopes have been used for shade or sun coffee, tobacco, fruits, and cattle pastures (Picó 1988; Domínguez Cristóbal 2000). In shade coffee, remnant trees are left standing through coffee harvesting but the spacing between them may vary from closed to sparse cover. The only site previously used for shade coffee in this study, Adjuntas, appears to have had a sparse canopy since it was also used for growing citrus and plantains. At the other two volcanic sites the main crops were sun coffee and tobacco, respectively. Grazing was a common practice in fallow years between crops or after abandonment in all substrate types.

## Vegetation sampling

We sampled arboreal vegetation in large, small, and juvenile tree size classes ($\geq 10$, $\geq 2.5$ to $<10$, and $<2.5$ cm diameter at breast height [DBH], respectively). The large

and small tree size classes were sampled using the point quarter method as described by Cottam and Curtis (1956). At each site we selected 20 random points through haphazardly placed line transects. At each point we identified the species and measured the DBH of the nearest tree in each point-centered quarter for a total of 80 trees per size class per site. When individuals had more than one stem above ground all were measured. The juvenile tree size class was sampled by counting and identifying all juvenile trees with stems <2.5 cm DBH in four 5 × 5 m plots placed haphazardly. Only species that grow to ≥2.5 cm DBH were considered to be juvenile trees. We consulted Little and Wadsworth (1964) and Little et al. (1974) for identification and nomenclature.

## Data analysis

We calculated tree density (trees/ha), basal area (m$^2$/ha), sampled area (ha), and species importance values (IV) for the large and small tree size classes following Cottam and Curtis (1956), and Ashby (1972). The frequency of occurrence for each species included in the 20 point counts, the number of trees, and basal area were converted into percentage of all species and these percents were averaged to calculate species IVs per size class (Cottam and Curtis 1956). We calculated density of juveniles (trees/ha) and juvenile size class species IVs as the average of the density and plot occurrence frequency of each species expressed as percentage of all species. Species were classified as native, endemic or introduced and the percentage of introduced species for each size class per site was determined.

We used single factor ANOVA to compare forest structure, species richness, percentage of introduced species and dominant species IV in each tree size class segregated by substrate type ($n = 3$) and used a Tukey test ($\alpha \leq 0.05$) to compare means. Data were tested for normality and variance homogeneity and the Kruskal–Wallis test was used to compare non-normal data. Values reported for $F$ and $H$ statistics correspond to ANOVA and Kruskal–Wallis tests, respectively. Independent ad-hoc analysis was assumed when testing within size classes only and statistical analyses were done using Infostat statistical software (Di Rienzo et al. 2003).

Non-metric multidimensional scaling (NMS) ordination analysis was used on species IVs to determine compositional affinities between sites for each tree size class separately. Species that occurred only at one site were excluded and transformations were used to find valid solutions when necessary. We ran NMS on the slow and thorough autopilot mode in PC-Ord software using Sörensen's similarity index (McCune and Mefford 1999). Multi-response permutation procedures (MRPP) were used to examine if species composition of the sites was related to substrate type.

We consulted the literature to compare forest structure and species richness and dominance of *S. campanulata* forests with native undisturbed forests on equivalent substrate types. The extensive deforestation and agricultural use of the northcentral region precluded any opportunity to establish appropriate control plots in the study (Wadsworth 1950; Ewel and Whitmore 1973). Thus, comparisons to native forests types suffer from the use of different sampling methodologies and because of this our analysis contains an indeterminate source of error. We also compare our *S. campanulata* forests to other secondary forests studied in the area with the same caveats mentioned.

## Results

Forest structure

There were no significant differences in large and small tree density ($F[2, 6] = 0.17$, $P = 0.85$), basal area ($F[2, 6] = 2.38$, $P = 0.17$) or juvenile tree density ($F[2, 6] = 2.50$, $P = 0.16$) between substrate types (Table 1).

Species composition

We found a total of 79 tree species of which 17 were introduced and five are endemic ("Appendix"). There were on average seven species (SE = 1.1, $n = 9$, sampled area: 0.05–0.14 ha), 12 species (SE = 1.5, $n = 9$, sampled area: 0.03–0.10 ha) and 19 species (SE = 2.8, $n = 9$, sampled area: 0.01 ha) in the large, small, and juvenile tree size classes, respectively (Fig. 2). Species richness in the large tree size class was higher on volcanic sites and lower on alluvial sites (Fig. 2, $H[2, 6] = 5.76$, $P = 0.03$) but no significant differences were found in the small ($H[2, 6] = 5.07$, $P = 0.07$) and juvenile tree size classes ($F[2, 6] = 4.48$, $P = 0.06$). Post-hoc ANOVA on species richness of all size classes combined showed the highest and lowest values were on karst and alluvial sites, respectively ($F[2, 6] = 9.64$, $P = 0.01$). The percentage of introduced species in the large tree size class was about twice that in the small and juvenile size classes but it did not differ between substrates in any tree size class (Fig. 3; $H[2, 6] = 5.42$ and $P = 0.07$ for large, $H[2, 6] = 1.07$ and $P = 0.64$ for small, and $F[2, 6] = 1.53$ and $P = 0.29$ for juvenile tree size classes, respectively). Post-hoc ANOVA of percent introduced species in all size classes also showed no differences between substrates ($F[2, 6] = 1.58$, $P = 0.28$).

The IV of the first rank species was higher on alluvial sites and lower on volcanic sites in the large tree size class ($F[2, 6] = 5.95$, $P = 0.04$) but no difference was detected in the small ($F[2, 6] = 3.73$, $P = 0.09$) or juvenile ($F[2, 6] = 4.60$, $P = 0.06$) tree size classes ("Appendix"). In the large and small tree size classes, *S. campanulata* had the highest IV at all sites except Adjuntas. There, *S. campanulata* was second to *G. guidonia* by only three percent points (33 vs. 36%) in the large tree size class, but was considerably less important in the small and juvenile size classes. In the juvenile size class, *G. guidonia* had the highest IV at four sites, *A. inermis* and introduced *S. jambos* at two sites each, and *O. coriacea* at one site. On two volcanic sites, *S. campanulata* was absent in the juvenile tree size class. The endemic palm *Roystonea borinquena*, *Casearia sylvestris*, *Guarea guidonia*, and *S. campanulata* were the only species with an IV greater than five percent in the large and small tree size classes ("Appendix"). In addition to those just mentioned, species with such IV in the juvenile size class were *Andira inermis*, *Casearia guianensis*, *Calophyllum calaba*, *Ocotea coriacea*, *Ardisia obovata*, *Syzygium jambos*, and *Piper aduncum*.

Through all sites, the IV of *S. campanulata* was, on average, 75% in the large (SE = 6.3, $n = 9$), 45% in the small (SE = 9.3, $n = 9$) and 6% in the juvenile (SE = 1.9, $n = 9$) tree size classes (Fig. 4). The IV of *S. campanulata* was highest on alluvial sites and lowest on volcanic sites in the large (Fig. 4; $F[2, 6] = 5.49$, $P = 0.04$) and small ($F[2, 6] = 9.24$, $P = 0.01$) tree size classes but this was not significant in the juvenile size class ($H[2, 6] = 5.07$, $P = 0.08$). Post-hoc ANOVA for all size classes combined followed significantly the same pattern ($F[2, 6] = 13.61$, $P = 0.01$).

A valid NMS ordination solution was not found for the large and small tree size classes. The juvenile class NMS had a tri-dimensional solution with one axis explaining more than

**Table 1** Forest structure, and species richness and dominance of *Spathodea campanulata* forests and of native old growth and secondary forests of north-central Puerto Rico by geological substrate type

| Forest type, land use history and age (years) | Elevation (m) | Diameter at breast height (cm) | Area sampled (ha) | Tree density (trees/ha) | Basal area (m$^2$/ ha) | Juvenile density (trees/ha) | Species richness | Dominant species and importance value (%) |
|---|---|---|---|---|---|---|---|---|
| **Alluvial** | | | | | | | | |
| *Spathodea* forest, sugar cane and pasture (24–38) | 10 | ≥2.5 | 0.07 | 2,514 (*1,216*) | 84 | 9,233 | 10 | *Spathodea campanulata* (83) |
| *Clussia-Syzygium* secondary forest (~40) | <10 | ≥2.5[a] | 0.06 | 3,200 | 26 | – | 11 | *Clussia rosea* (55) |
| Young secondary (>50) | <10 | ≥2.5[a] | 0.06 | 1,833 | 29 | – | 19 | *Hymenaea courbaril* (34) |
| Old secondary (>100) | <10 | ≥2.5[a] | 0.05 | 1,880 | 42 | – | 32 | *Manilkara bidentata* (32) |
| Old growth *Pterocarpus* forest (>60) | 3 | >2[b] | 0.03 | 2,433 (*700*) | – | – | 1 | *Pterocarpus officinalis* (100) |
| Old growth *Pterocarpus* forest | <10 | ≥2.5[c] | 0.1 | 1,680 (*860*) | 45 | – | 7 | *Pterocarpus officinalis* (61) |
| Old growth *Pterocarpus* forest ecotone | <10 | ≥2.5[c] | – | 1,660 | 48 | – | 19 | – |
| **Karst** | | | | | | | | |
| *Spathodea* forest, sun crops and pasture (24–38) | 30–170 | ≥2.5 | 0.08 | 2,550 (*706*) | 54 | 32,533 | 19 | *Spathodea campanulata* (64) |
| Secondary forest, pasture (18–38) | 90–300 | ≥1[d] | 0.05 | 6,201 | 31 | – | 16 | *Spathodea campanulata* (40) |
| Shade coffee (~35) | 235–310 | ≥1[d] | 0.05 | 2,981 | 28 | – | 14 | *Guarea guidonia* (36) |
| Old growth mesic forest | – | [e] | – | – | 24 | – | 15 | *Cinnamonum elongatum* (36) |
| Old growth mesic forest | – | [e] | – | – | 15 | – | 23 | *Cordia sulcata* (32) |
| Old growth mesic forest | <50 | >10[f] | 0.05 | (*119*) | 22 | – | 37 | *Casearia guianensis* (13) |
| **Volcanic** | | | | | | | | |
| *Spathodea* forest, sun-shade crops, pasture (25–39) | 180–500 | ≥2.5 | 0.08 | 2,931 (*983*) | 58 | 44,933 | 15 | *Spathodea campanulata* (42) |
| Young secondary | 60 | ≥4.1[g] | 0.4 | 2,459 | 12 | – | 29 | *Inga laurina* (31) |

**Table 1** continued

| Forest type, land use history and age (years) | Elevation (m) | Diameter at breast height (cm) | Area sampled (ha) | Tree density (trees/ha) | Basal area (m²/ ha) | Juvenile density (trees/ha) | Species richness | Dominant species and importance value (%) |
|---|---|---|---|---|---|---|---|---|
| Pasture (20–35) | 160–340 | ≥1[h] | 0.1 | 6,274 | 25 | – | 19 | *Guarea guidonia* (21) |
| Shade coffee (>20) | 270–770 | ≥1[h] | 0.1 | 6,220 | 30 | – | 23 | *Guarea guidonia* (18) |
| Shade coffee (∼30) | 416 | ≥4[i] | 0.1 | 1,680 | 18 | – | 17 | *Miconia prasina* (24) |
| Shade coffee (∼40) | 660–680 | ≥4[i] | 0.25 | 1,124 | 40 | – | 24 | *Prestoea montana* (46) |
| Old growth *Ocotea-Manilkara* forest (>60) | 47 | >2[c] | 0.03 | 4,389 (*633*) | 50 | – | 38 | *Hymenaea courbaril* (13) |
| Old growth *Dacryodes-Manilkara* forest (>60) | 380 | >2[c] | 0.03 | 2,911 (*1,022*) | 58 | – | 40 | *Dacryodes excelsa* (30) |

All sites are in subtropical moist to wet life zones (Holdridge 1967). Empty cells mean data were not reported. The data are means that correspond to trees of the diameter at breast height (DBH) reported except for large tree (>10 cm DBH) density which is in italics and juvenile tree (<2.5 cm DBH) density. The latter was only reported in this study. For data from other studies, the letter next to DBH corresponds to the following

[a] Figueroa Colón et al. (1984)

[b] Gould et al. (2006)

[c] Álvarez López (1990)

[d] Rivera and Aide (1998)

[e] Chinea (1980)

[f] Serrano et al. (1983)

[g] Weaver (1979)

[h] Popper et al. (1999)
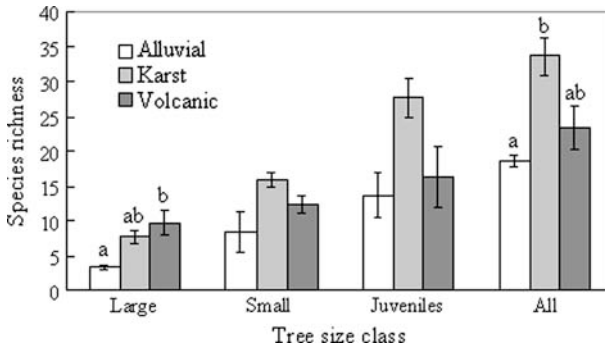
[i] Marcano Vega et al. (2002)

**Fig. 2** Mean and standard error of species richness in large, small, juvenile (trees >10, ≥2.5 to <10, and <2.5 cm diameter at breast height, respectively) and all tree size classes per site for each substrate type (*n* = 3). Letters denote different means by ANOVA–Tukey test (α ≤ 0.05). Sampled areas were 0.05–0.14, 0.03–0.10, and 0.01 ha for large, small, and juveniles tree size classes, respectively
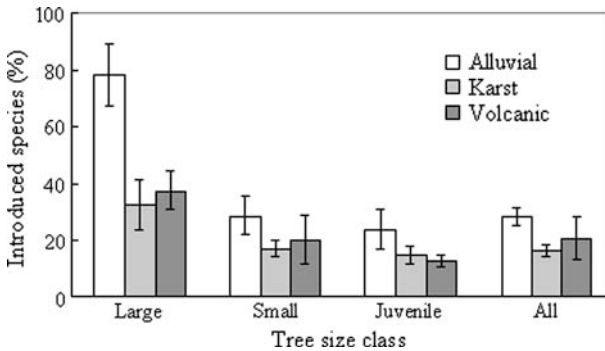


**Fig. 3** Mean and standard error of the percent of introduced species in large, small, juvenile (trees >10, ≥2.5 to <10, and <2.5 cm diameter at breast height, respectively) and all tree size classes per site for each substrate type (*n* = 3). *Letters* denote different means by ANOVA–Tukey test (α ≤ 0.05)
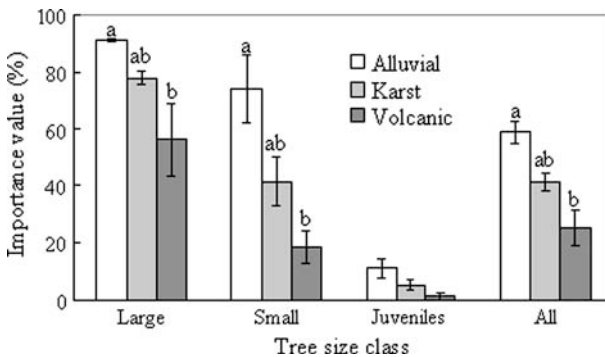


**Fig. 4** Mean and standard error of the importance value of *Spathodea campanulata* in large, small, juvenile (trees >10, ≥2.5 to <10, and <2.5 cm diameter at breast height, respectively) and all tree size classes per site for each substrate type (*n* = 3). *Letters* denote different means by ANOVA–Tukey test (α ≤ 0.05)
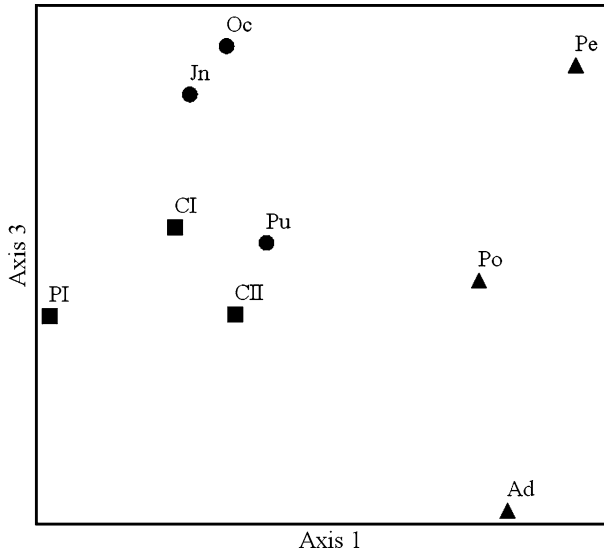
**Fig. 5** Non-metric multi-dimensional scaling ordination of juvenile tree (<2.5 cm diameter at breast height) size class species importance values by study site. The ordination had a tri-dimensional solution with a final stress of 1.8 and final instability of 0.00001 for 121 iterations. Axis 1 explained 54% and axis 3 explained 36% of the ordination with an orthogonality of 99%. *Squares*, *circles* and *triangles* correspond to alluvial, karst and volcanic sites, respectively. Site codes follow Fig. 1

half of the variance (Fig. 5). MRPP showed geological substrate was significantly related to the juvenile tree species composition of sites ($P = 0.002$).

## Discussion

The structure of *S. campanulata* forests was statistically uniform through substrate types, and this partially rejects our first hypothesis (Table 1). Species richness and composition did show differences between substrate types but differences in species richness were only evident in the large tree size class (Fig. 2). However, compositional differences between substrate types were most evident in the juvenile tree size class and this reflects recent establishment by native species (Fig. 5). This is discussed further below. The studies used in our comparison of *S. campanulata* forests to other forests in Puerto Rico did not always use the same DBH tree size classes as our study. Therefore, the comparison that follows is a generalization that mostly applies to the large and small (>2.5 cm DBH) tree size classes.

Comparison to native forests

The structure of *S. campanulata* forests resembles some native old growth and secondary forests on similar or different substrates in Puerto Rico (Table 1). Large tree density and basal area are in the high range of values reported for most other forests and probably result from rapid growth of *S. campanulata* stands invading abandoned fields. Native old growth forests dominated by *Pterocarpus officinalis* on alluvial swamps and *Dacryodes exelsa* on wet volcanic slopes have basal area comparable to *S. campanulata* forests (see also Eusse

and Aide 1999). Secondary forests on karst have high basal area in depressions where *S. campanulata* is found (Rivera and Aide 1998; Aukema et al. 2007).

Similar to secondary and old growth native forests, the tree species richness and dominance of *S. campanulata* forests showed differences according to the underlying geological substrate (Table 1). For example, native alluvial forests on riparian floodplains are characterized by lower tree species richness and high dominance by fewer species compared to karst and volcanic forests (Lugo 2005). Likewise, alluvial *S. campanulata* forests have lower species richness and higher dominant species IV compared to most other forests but are similar to native *Pterocarpus officinalis* floodplain forests (Table 1). Tree species richness and dominant species IV on karst and volcanic *S. campanulata* forests is comparable to other secondary forests on the same substrates, but species richness is lower and the dominant species IV is higher than in native old growth forests. Of all other forests used for this comparison (Table 1), alluvial forests had higher dominant tree species IV (mean = 56%, SE = 12, $n = 5$) compared to those on karst (mean = 31%, SE = 5, $n = 5$) and volcanic substrates (mean = 26%, SE = 4, $n = 7$). The *S. campanulata* forests in this study follow the same trend (Fig. 4; "Appendix").

Composition of tree size classes

Our hypothesis about the change in species composition through tree size classes is supported. When comparing large, small, and juvenile tree size class species richness and composition, it is evident species dispersed from elsewhere are becoming established in *S. campanulata* forests (Fig. 2; "Appendix"). It is also evident that native species are much more common than introduced ones in the small and juvenile tree size classes and that *S. campanulata* composes a minor part of the juvenile tree community (Figs. 3, 4). The degree to which this is true varied with substrate type. The lower species richness and high dominance of *S. campanulata* in the large tree size class of alluvial sites contrasts to their juvenile tree species richness which equaled that of forests on karst and volcanic substrates. This result highlights the role of seed sources and dispersal vectors. Higher species richness and lower dominance of *S. campanulata* in the large tree size class of karst and volcanic sites is related to the interaction of past land use with substrate type as discussed below. However, land use history has not impeded these sites from being invaded by native species that produce compositional differences akin to native forest types and this is clearly evident in the juvenile tree size class (Fig. 5).

Past land use and substrate

Although the volcanic region was used extensively for agriculture and grazing, remnant forest in places of difficult access (i.e., steep slopes, ridges) harbored and served as sources of native species (Figueroa Colón 1996; Helmer 2004). Likewise, studies of secondary forests on karst show most human disturbance occurred in depressions leaving the drier and inaccessible ridges and hilltops forested (Chinea 1980; Aukema et al. 2007). Higher species richness in the large tree size class of karst and volcanic sites results from remnant trees acting as perches for dispersers and nearby marginal vegetation serving as seed sources earlier during forest development compared to alluvial sites were intensive sugar cane harvesting eliminated such (Wadsworth 1950; McClanahan and Wolfe 1993).

Lower global species richness on alluvial sites can be of product of land use history and periodic flooding. Wood extraction and sugar cane harvesting extirpated the species native of alluvial old growth forests (Wadsworth 1950). Land use history limits species richness

in similar riparian alluvial secondary forests (Chinea 2002; Martin et al. 2004). Periodic flooding can also limit species richness on alluvial sites by mortality of flood intolerant species (Abelleira and Lugo 2008). For example, juvenile density on two floodable alluvial sites was lower than on other sites (6,300 and 4,200 trees/ha at Cibuco I and Paso del Indio, respectively; Fig. 1; Table 1).

The species composition of karst and volcanic sites reflects land use history through introduced trees planted by farmers. For example, *Citrus paradisi* (grapefruit), *Musa sapientum* (banana and plantain varieties), and *Persea americana* (avocado) on karst and volcanic sites, and *Coffea arabica* (coffee) on volcanic sites. The introduced tree species found on alluvial sites did not include any agricultural remnants because of complete clearing of vegetation during sugar cane harvesting and instead included trees planted for ornament or shade such as *Delonix regia* or *Terminalia catappa*, or other invaders of disturbed land such as *Albizia procera* and *Cassia siamea*. The legacy of previous land use practices upon species composition was most evident at Adjuntas (Fig. 1) were all species previously denoted as agricultural remnants were present and were both *S. campanulata* and *G. guidonia* co-dominated the large tree size class. Large *G. guidonia* trees were used for coffee shade which allowed the dominance of this species to remain throughout and after use. Other species associated to shade coffee on this site are *Inga vera*, *Inga laurina*, and *Erythrina poepiggiana*. Native species were also found in the large tree size class at this and the other volcanic and karst sites including *Cecropia schreberiana*, *Cinnamomum elongatum*, *R. borinquena*, *Tetragastris balsamifera*, *Thouinia striata*, and *Zanthoxylum martinicense*. Those and other native species were mostly absent in the large tree size class of alluvial sites.

We believe the higher IV of *S. campanulata* on alluvial sites is the product of a smaller number of species available for initial establishment due to historical factors combined with better growth conditions for *S. campanulata* (Fig. 4; Hall et al. 1992). The latter is also suggested by the positive, although non-significant, relationship of *S. campanulata* basal area to the number of trees per site ($r^2 = 0.30$, $P = 0.12$). Alluvial sites are at the high end of this relationship and volcanic sites at the low end. Lack of remnant trees due to sugar cane harvesting, a relatively constant water supply from river inputs and high soil fertility on alluvial sites can produce better growth conditions for light, water and nutrient demanding invasive trees such as *S. campanulata* (Funk and Vitousek 2007).

## Conclusion

The juvenile tree species community that is becoming established in the *S. campanulata* forests of northcentral Puerto Rico corresponds to geological substrate type (Fig. 5). An alternate explanation could be that species composition is responding to the location of sites in the landscape (Fig. 1). The relative effect of these and other variables is currently being investigated in another study. In any case, our results are strong evidence that these novel forests are not conducing to but rather deterring biotic homogenization by catalyzing the establishment of native tree species that can result in diverging successional trajectories in otherwise deforested lands. It appears that *S. campanulata*'s invasion process, although affected by substrate and land use history, results in forests of similar structure. However, the juvenile tree species composition of these novel forests shows differences strongly akin to those that occur in native forests mixed with some introduced species associated to previous land use.

We found that contrary to *S. campanulata*, native species dominate de juvenile tree communities of these novel forests. This contrasts to other studies that have found native species establishment to be inhibited in novel forest stands dominated by introduced species (Lichstein et al. 2004; Pratt et al. 2005; Mascaro et al. 2008). Our study shows that the ecological value of novel forests dominated by this introduced species in Puerto Rico is not less than that of other secondary forests when it comes to mitigating anthropogenic land cover change by native species restoration in abandoned agricultural and grazing lands. Since most native species are incapable of growing in degraded and abandoned lands, the ecological value of *S. campanulata* forests should not be overlooked (Aide et al. 2000). Planning and management decisions involving these novel forests should consider *S. campanulata*'s successional character and its value in restoring native species at deforested and degraded sites.

## Appendix

See Table 2.

**Table 2** Importance value (IV) of species in large and small (L and S, ≥10 and ≥2.5 <10 cm diameter at breast height [DBH], respectively), and juvenile (J, <2.5 cm DBH) tree size classes found in *Spathodea campanulata* forests of different geological substrate types

| Tree species | Size class | Alluvial IV (%) | Karst IV (%) | Volcanic IV (%) |
|---|---|---|---|---|
| *Spathodea campanulata** | LS | 82.8 | 64.1 | 41.6 |
| | J | 11.2 | 5.2 | 1.1 |
| *Terminalia catappa** | LS | 3.3 | – | – |
| | J | 2.3 | 0.4 | – |
| *Casearia guianensis* | LS | 3.1 | 1.0 | 2.2 |
| | J | 5.1 | 2.8 | 4.6 |
| *Guarea guidonia* | LS | 2.5 | 5.8 | 22.4 |
| | J | 14.1 | 12.9 | 24.9 |
| *Cassia siamea** | LS | 1.8 | 0.2 | – |
| *Albizia procera** | L | 1.6 | – | – |
| *Calophyllum calaba* | LS | 0.8 | 0.5 | – |
| | J | 10.4 | 7.2 | – |
| *Spondias mombin* | LS | 0.6 | – | 0.8 |
| | J | 1.1 | – | – |
| *Thespesia grandiflora*** | LS | 0.5 | 0.4 | – |
| | J | 1.1 | 1.9 | – |

**Table 2** continued

| Tree species | Size class | Alluvial IV (%) | Karst IV (%) | Volcanic IV (%) |
|---|---|---|---|---|
| *Casearia decandra* | S | 0.5 | 1.3 | – |
| | J | 1.1 | 1.8 | – |
| *Casearia sylvestris* | S | 0.5 | 5.4 | 3.2 |
| | J | 2.3 | 3.1 | 3.9 |
| *Zanthoxylum martinicense* | LS | 0.3 | 0.9 | 0.5 |
| | J | – | 0.2 | – |
| *Cordia laevigata* | S | 0.3 | – | – |
| | J | – | 0.7 | – |
| *Erythrina poeppigiana** | LS | 0.3 | – | 0.7 |
| *Bucida buceras* | S | 0.3 | – | – |
| | J | 1.1 | – | – |
| *Cupania americana* | S | 0.3 | 0.2 | 0.4 |
| | J | 1.6 | 4.1 | 3.4 |
| *Ocotea coriacea* | S | 0.3 | 0.7 | – |
| | J | 3.9 | 6.3 | 0.5 |
| *Eugenia biflora* | S | 0.3 | 0.4 | 0.9 |
| | J | 1.1 | 2.5 | 3.1 |
| *Roystonea borinquena*** | LS | – | 5.2 | 0.9 |
| | J | 3.2 | 2.0 | – |
| *Andira inermis* | LS | – | 3.0 | 4.0 |
| | J | 26.6 | 8.7 | 8.6 |
| *Cinamomum elongatum* | LS | – | 1.6 | 0.8 |
| | J | 0.6 | 3.4 | 1.1 |
| *Tetrazygia elaeagnoides* | LS | – | 1.5 | – |
| *Persea americana** | LS | – | 1.3 | 0.6 |
| *Musa sapientum** | LS | – | 0.8 | 1.6 |
| | J | – | 0.4 | – |
| *Thouinia striata*** | S | – | 0.7 | – |
| | J | – | 4.9 | – |
| *Guettarda scabra* | S | – | 0.6 | – |
| | J | 0.5 | 0.2 | – |
| *Ardisia obovata* | S | – | 0.6 | – |
| | J | – | 6.1 | – |
| *Citrus paradisi** | LS | – | 0.5 | 0.4 |
| *Tabebuia heterophylla* | S | – | 0.4 | – |
| | J | – | 2.6 | – |
| *Syzygium jambos** | LS | – | 0.4 | 2.1 |
| | J | 0.5 | 5.8 | 12.6 |
| *Dendropanax arboreus* | LS | – | 0.4 | 0.6 |
| | J | – | 0.3 | 0.5 |
| *Randia aculeata* | S | – | 0.4 | – |
| | J | – | 1.6 | – |

**Table 2** continued

| Tree species | Size class | Alluvial IV (%) | Karst IV (%) | Volcanic IV (%) |
|---|---|---|---|---|
| Vitex divaricata | L | – | 0.2 | – |
| Ceiba pentandra | L | – | 0.2 | – |
| Citharexylum fruticossum | L | – | 0.2 | – |
| Chrysophyllum argenteum | LS | – | 0.2 | 0.2 |
| | J | – | 1.2 | – |
| Piper amalago | S | – | 0.2 | – |
| | J | – | 0.2 | – |
| Inga vera | LS | – | 0.2 | 1.9 |
| | J | – | – | 2.2 |
| Guettarda ovalifolia | S | – | 0.2 | – |
| Ocotea leucoxylon | LS | – | – | 4.2 |
| | J | – | – | 2.9 |
| Tetragastris balsamifera | LS | – | – | 3.0 |
| | J | – | – | 4.7 |
| Inga laurina | LS | – | – | 2.1 |
| | J | 1.1 | – | 3.9 |
| Cecropia scheberiana | L | – | – | 1.6 |
| Urera baccifera | S | – | – | 1.2 |
| Coffea arabica* | S | – | – | 0.7 |
| | J | – | – | 5.0 |
| Guapira fragrans | S | – | – | 0.6 |
| Quararibea turbinata | S | – | – | 0.2 |
| | J | – | – | 1.1 |
| Trichilia pallida | S | – | – | 0.2 |
| | J | – | 0.9 | 1.0 |
| Sheflera morototoni | S | – | – | 0.2 |
| Piper aduncum | S | – | – | 0.2 |
| | J | – | – | 6.4 |
| Cordia sulcata | S | – | – | 0.2 |
| Meliococcus bijugatus* | J | 4.5 | 2.0 | – |
| Erythroxylon brevipes | J | 2.6 | 0.9 | 0.5 |
| Psidium guajava* | J | 1.1 | – | – |
| Delonix regia* | J | 1.0 | – | – |
| Eugenia monticola | J | 0.6 | 1.4 | – |
| Cochlospermum vitifolium* | J | 0.6 | – | – |
| Leucaena leucocephala* | J | 0.5 | 0.4 | – |
| Psychotria nervosa | J | – | 1.8 | – |
| Gesneria pedunculosa** | J | – | 0.8 | – |
| Tecoma stans* | J | – | 0.8 | – |
| Exothea paniculata | J | – | 0.7 | – |
| Comocladia glabra | J | – | 0.5 | – |
| Cestrum macrophyllum | J | – | 0.5 | – |

**Table 2** continued

| Tree species | Size class | Alluvial IV (%) | Karst IV (%) | Volcanic IV (%) |
|---|---|---|---|---|
| *Miconia tetrandra* | J | – | 0.4 | – |
| *Samyda dodecandra* | J | – | 0.4 | – |
| *Clusia rosea* | J | – | 0.4 | – |
| *Ficus citrifolia* | J | – | 0.4 | – |
| *Daphnopsis americana* | J | – | 0.3 | – |
| *Heterotrichum cymosum*** | J | – | 0.3 | – |
| *Coccoloba diversifolia* | J | – | 0.2 | – |
| *Parathesis crenulata* | J | – | 0.2 | – |
| *Miconia impetiolaris* | J | – | – | 2.3 |
| *Miconia prasina* | J | – | – | 1.8 |
| *Faramea occidentalis* | J | – | – | 1.6 |
| *Capparis baducca* | J | – | – | 1.0 |
| *Anona muricata** | J | – | – | 0.5 |
| *Buchenavia capitata* | J | – | – | 0.5 |
| *Drypetes glauca* | J | – | – | 0.5 |

The data are based on three sites per substrate, 20 point-quarters per site for each L and S tree size class, respectively, and four 25 m² plots per site for the J tree size class. Species IV's reported for the L and S tree size classes are based on data sets including both size classes combined but the size class reported corresponds to those in which the species was present (IV ≠ 0). Species are IV rank-ordered by substrate following those that occurred in the L and S tree size classes and then by those occurring only in the J tree size class

\* Introduced species

\*\* Endemic species

# References

Abelleira OJ, Lugo AE (2008) Post sugar cane succession in moist alluvial sites in Puerto Rico. In: Myster R (ed) Post-agricultural succession in the Neotropics. Springer, New York, pp 73–92

Acevido G (1982) Soil survey of Arecibo area of northern Puerto Rico. USDA Soil Conservation Service and UPR, Mayagüez

Aide TM, Zimmermann JK, Herrera L et al (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restor Ecol 8:328–338. doi:10.1046/j.1526-100x.2000.80048.x

Álvarez López M (1990) Ecology of *Pterocarpus officinalis* forested wetlands in Puerto Rico. In: Lugo A, Brinson M, Brown S (eds) Ecosystems of the world 15: forested wetlands. Elsevier, The Netherlands, p 251

Álvarez Nazario M (1982) Orígenes y desarrollo del español en Puerto Rico (Siglos XVI y XVII). Editorial Universidad de Puerto Rico

Ashby WC (1972) Distance measurements in vegetation study. Ecology 53:980–981. doi:10.2307/1934321

Aukema J, Carlo TA, Collazo JA (2007) Landscape assessment of tree communities in the northern karst region of Puerto Rico. Plant Ecol 189:101–115. doi:10.1007/s11258-006-9169-5

Bawiec WJ, Krushensky RD, Shellekens JH (2001) Geology of Puerto Rico. USGS Open File Report 98-34, USGS Caribbean District, San Juan

Behrensmeyer AK, Damuth JD, DiMichele WA (1992) Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. The University of Chicago Press, Chicago

Birdsey RA, Weaver PL (1982) The forest resources of Puerto Rico. Resource Bulletin SO-85, USDA Forest Service Southern Forest Experiment Station, New Orleans

Brandeis TJ, Helmer EH, Oswalt SN (2007) The status of Puerto Rico's forests, 2003. USDA Forest Service, Southern Research Station Resource Bulletin SRS-119, Asheville

Chinea JD (1980) Forest vegetation of the limestone hills of northern Puerto Rico. MS Thesis, Cornell University, New York

Chinea JD (2002) Tropical forest succession on abandoned farms in the Humacao municipality of eastern Puerto Rico. For Ecol Manag 167:195–207

Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. Ecology 37:451–460

CRIM (2004) Puerto Rico aerial photography by cuadrant. Estado Libre Asociado de Puerto Rico

Danserau P (1966) Studies on the vegetation of Puerto Rico: description and integration of the plant-communities. UPRM Institute of Caribbean Science Special Publication No. 1

Di Rienzo JA, Balzarini M, Casanoves F et al (2003) Infostat statistical software. Universidad Nacional de Córdoba, Argentina

Domínguez Cristóbal CM (2000) Panorama histórico forestal de Puerto Rico. Editorial de la Universidad de Puerto Rico

Eusse AM, Aide TM (1999) Patterns of litter production across a salinity gradient in a *Pterocarpus officinalis* tropical wetland. Plant Ecol 145:307–315. doi:10.1023/A:1009832627166

Ewel JJ, Whitmore JL (1973) The ecological life zones of Puerto Rico and the US Virgin Islands. USDA Research Paper ITF-18

Figueroa Colón JC (1996) Phytogeographical trends, centers of high species richness and endemism, and the question of extinctions in the native flora of Puerto Rico. In: Figueroa Colón JC (ed) The annals of the New York academy of sciences: the scientific survey of Puerto Rico and the Virgin Islands, vol 776. The Academy, New York, pp 89–102

Figueroa Colón JC, Totti L, Lugo AE et al (1984) Structure and composition of moist coastal forests in Dorado, Puerto Rico. USDA Research Paper SO-202

Francis JK (2000) *Spathodea campanulata* Beauv., Bignoniaceae. In: Francis JK, Lowe CA (eds) Silvics of native and exotic trees of Puerto Rico and the Caribbean islands. USDA General Technical Report IITF–15, Río Piedras, Puerto Rico, pp 484–487

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low resource systems. Nature 26:1079–1081

Gould WA, González G, Carrero Rivera G (2006) Structure and composition of vegetation along an elevational gradient in Puerto Rico. J Veg Sci 17:563–574

Grau RH, Aide TM, Zimmerman JK et al (2003) The ecological consequences of socioeconomic and land-use changes in post agriculture Puerto Rico. Bioscience 53:1159–1168. doi:10.1641/0006-3568(2003)053[1159:TECOSA]2.0.CO;2

Hall CAS, Stanford JA, Hauer FR (1992) The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos 65:377–390. doi:10.2307/3545553

Haysom KA, Murphy ST (2003) The status of invasiveness of forest tree species outside their natural habitat: a global review and discussion paper. FAO UN Forestry Department Forest Health and Biosecurity Working Paper FBS-3E

Helmer EH (2004) Forest conservation and land development in Puerto Rico. Landsc Ecol 19:29–40. doi:10.1023/B:LAND.0000018364.68514.fb

Hobbs RJ, Arico S, Aronson J et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob Ecol Biogeogr 15:1–7. doi:10.1111/j.1466-822X.2006.00212.x

Holdridge LR (1967) Life zone ecology. Tropical Science Center, Costa Rica

Lichstein JW, Grau HR, Aragón R (2004) Recruitment limitation in secondary forests dominated by an exotic tree. J Veg Sci 15:721–728

Little EL, Wadsworth FH (1964) Common trees of Puerto Rico and the Virgin Islands. USDA Agriculture Handbook 249, Washington DC, USA

Little EL, Woodbury RO, Wadsworth FH (1974) Trees of Puerto Rico and the Virgin Islands. USDA Agriculture Handbook 449, Washington DC, USA

Lockwood JL, McKinney ML (2001) Biotic homogenization. Kluer Academic/Plenum Publishers, New York

Lugo AE (2004) The homogeocene in Puerto Rico. In: Zarin DJ, Alavalapati JRR, Putz FE, Schmink M (eds) Working forests in the Neotropics: conservation through sustainable management? Colombia University Press, New York, pp 366–375

Lugo AE (2005) Los bosques. In: Joglar R (ed) Biodiversidad de Puerto Rico: vertebrados y ecosistemas. Instituto de Cultura Puertorriqueña, Puerto Rico, pp 397–548

Lugo AE, Helmer E (2004) Emerging forests on abandoned land: Puerto Rico's new forests. For Ecol Manag 190:145–161

Marcano Vega H, Aide TM, Baez D (2002) Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. Plant Ecol 161:75–87. doi:10.1023/A:1020365507324

Martin PH, Sherman RE, Fahey TH (2004) Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old growth riparian forests in the Dominican Republic. Biotropica 36:297–317

Mascaro J, Becklund KK, Hughes RF et al (2008) Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. For Ecol Manag 256:593–606

McClanahan TR, Wolfe RW (1993) Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conserv Biol 7:279–288. doi:10.1046/j.1523-1739.1993.07020279.x

McCune B, Mefford MJ (1999) Multivariate analysis of ecological data (PC-Ord), version 4.25. MjM Software, Gleneden Beach, Oregon

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–452. doi:10.1016/S0169-5347(99)01679-1

Monroe WH (1976) The karst landforms of Puerto Rico. USGS Professional Paper 899

NOAA (2002) Monthly station normals of temperature, precipitation, and heating and cooling degree days, 1971–2000: Puerto Rico. Climatography of the United States No 81

Novotny V, Miller SE, Leps J et al (2004) No tree is an island: the plant-caterpillar food web of a secondary rain forest in New Guinea. Ecol Lett 7:1090–1100. doi:10.1111/j.1461-0248.2004.00666.x

Picó F (1988) Historia general de Puerto Rico. Ediciones Huracán, Puerto Rico

Popper N, Dominguez Cristóbal C, Santos A et al (1999) A comparison of two secondary forests in the coffee zone of central Puerto Rico. Acta Cient 13:27–41

Pratt PD, Quevedo V, Bernier L et al (2005) Invasions of Puerto Rican wetlands by the Australian tree Melaleuca quinquenervia. Caribb J Sci 41:42–54

Ramos OM, Lugo AE (1994) Mapa de la vegetación de Puerto Rico. Acta Cient 8:63–66

Rivera LW, Aide TM (1998) Forest recovery in the karst region of Puerto Rico. For Ecol Manag 108:63–75

Rudel TK, Pérez Lugo M, Zichal H (2000) When fields revert to forest: development and spontaneous reforestation in post-war Puerto Rico. Prof Geogr 52:386–397. doi:10.1111/0033-0124.00233

Serrano AE, Ortiz C, Aponte M (1983) Vegetación y factores edáficos en el bosque de Cambalache. In: Lugo AE (ed) Los bosques de Puerto Rico. Institute of Tropical Forestry USDA and Department of Natural Resources of Puerto Rico, pp 131–151

Sodhi NS, Brook BW, Bradshaw CJA (2007) Tropical conservation biology. Blackwell, Malden

Wadsworth FH (1950) Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. Caribb For 11:38–46

Weaver PL (1979) Tree growth in several tropical forests of Puerto Rico. USDA Research Paper SO-152, San Juan

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Front Ecol Environ 5:475–482. doi:10.1890/070037