

Invasion by native tree species prevents biotic homogenization in novel forests of Puerto Rico

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Abstract There is concern that secondary forests dominated by introduced species, known as novel forests, increase taxonomical similarity between localities and lead to biotic homogenization in human-dominated landscapes. In Puerto Rico, agricultural abandonment has given way to novel forests dominated by the introduced African tulip tree *Spathodea campanulata* Beauv. (Bignoniaceae). In this study, I characterized the tree species composition of *S. campanulata* forests in Puerto Rico as means to evaluate if biotic homogenization is occurring. Non-metric multidimensional scaling was used to examine what variables were related to the large (≥ 10 cm diameter at breast height [DBH]), small (≥ 2.5 to < 10 cm DBH), and juvenile (< 2.5 cm DBH) tree species composition of 20 sites. Species composition was strongly related to substrate properties, less related to land use history, and unrelated to spatial attributes. The introduced species component was low (mean = 17%, S.E. = 1.8) and compositional differences were mostly due to native tree species of

secondary to old growth forests on equivalent substrates. Animals appear to disperse most species (86%) into these forests yet because of this some introduced species will persist. Although uncommon species were largely absent, recent species establishment is shaped by substrate properties making biotic homogenization in these forests unlikely. The *S. campanulata* forests of Puerto Rico facilitate native tree species establishment in lands where poor management practices extirpated the original forest. These results highlight the importance of remnant old growth forests or trees that act as seed dispersal sources and facilitate native species recovery in novel forests.

Keywords *Spathodea campanulata* · Introduced invasive species · Tropical secondary forests · Land cover change · Agricultural landscape

Introduction

Anthropogenic land cover change, species transport, and land abandonment can result in secondary forests dominated by introduced species and these are known as novel forests (Hobbs et al. 2006; Mascaro et al. 2008). Novel forests offer an opportunity to study the natural response of species to changes caused by humans in a relatively short time span. There is

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concern that biotic homogenization, which can be defined as increased taxonomical similarity between localities due to the spread of introduced species and the displacement of uncommon or localized species, is occurring in novel forests (Grau et al. 2003; Olden and Rooney 2006). Indeed, some studies suggest this process can occur at continental and regional scales (McKinney and Lockwood 1999; Winter et al. 2009).

The island of Puerto Rico was densely forested in pre-Hispanic times but was heavily deforested by human activity up to the mid twentieth century when less than 5% of the original forest remained (Birdsey and Weaver 1982). Since then, socio-economic changes caused the abandonment of agriculture and allowed the spontaneous reforestation of almost half the land area (Rudel et al. 2000). Prior to this trend, the African tulip tree, *Spathodea campanulata* Beauv. (Bignoniaceae), was introduced as an ornamental tree and was used as fencepost by farmers (Little and Wadsworth 1964). These circumstances allowed this wind-dispersed and light-demanding species to dominate many secondary forests in the moist regions of Puerto Rico (China and Helmer 2003).

Novel *S. campanulata* forests are now found in tropical islands through the globe (Haysom and Murphy 2003; Novotny et al. 2004). In Hawaii, these forests have very limited regeneration of native tree species possibly due to the loss of native avian seed dispersers and competitive exclusion caused by introduced tree species with adaptations new to this isolated island flora (Foster and Robinson 2007; Mascaro et al. 2008). In contrast, the tree species regenerating in *S. campanulata* forests in Puerto Rico are mostly native (Aide et al. 2000), and effective seed dispersal and diverse adaptations of native tree species, combined with heterogeneous environments and land use legacies, could lead to different compositional outcomes across sites.

This study describes the tree species composition of *S. campanulata* forests in Puerto Rico focusing on their origin status (introduced or native) and seed dispersal mode, and examines what variables (substrate, historic, or spatial) relate to composition as means to assess whether biotic homogenization is occurring at a regional scale. Land use legacies have lasting effects on tree species composition yet natural processes can shape recent tree species establishment according to substrate properties (García Montiel and Scatena 1994; Zimmerman et al. 2008). Thus, I

hypothesized that the species composition of older trees in *S. campanulata* forests is determined by land use history and that the composition of juvenile trees is determined by substrate properties. The results presented here increase our knowledge of the mechanisms influencing the development of novel forests and the possibility of biotic homogenization due to anthropogenic pressures.

Study region

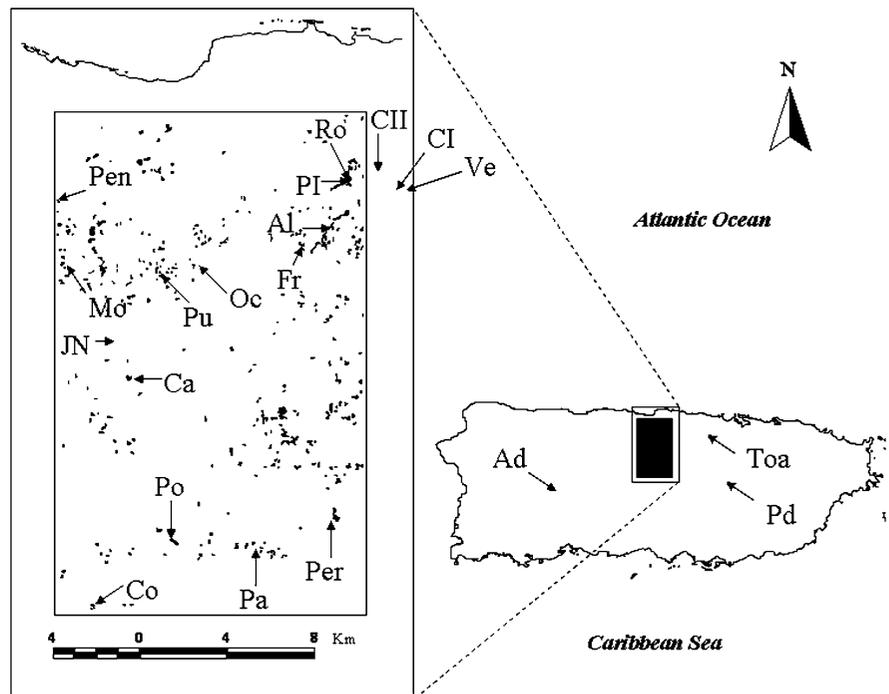
Northcentral Puerto Rico lies in the subtropical moist to wet life zones (18°N, 66–67°W; Fig. 1; Table 1; Ewel and Whitmore 1973). Through the region, mean annual precipitation and temperature ranged from 1,443 to 1,905 mm and from 22 to 25°C, respectively, during the period of 1971 through 2000 (NOAA 2002). The region is underlain by alluvial, karst, and volcanic geological substrates (Bawiec et al. 2001). Historically, alluvial floodplains were mostly used for sugar cane plantations, and karst depressions and volcanic slopes were used for coffee, tobacco, plantains, and subsistence agriculture (Table 1; Picó 1988). Agriculture was at times alternated with grazing, which also followed crop abandonment frequently.

Materials and methods

Forest sampling

Tree structure and species composition was sampled in 20 randomly chosen *S. campanulata* forest sites between 2005 and 2007 (Fig. 1; Table 1). The point quarter method as described by Cottam and Curtis (1956) was used to sample structure and species composition of large (≥ 10 cm diameter at breast height [DBH]) and small (≥ 2.5 to < 10 cm DBH) tree size classes. At each site, 10 points were randomly selected in a haphazardly placed line transect. At each point, the species and DBH of four trees per size class were determined for a total of 40 trees per size class per transect. An additional transect was used at nine of the sites (Abelleira-Martínez 2009). At each site, all juvenile size class (< 2.5 cm DBH) trees in four randomly placed 5×5 m plots were counted and identified. Only species that grow ≥ 2.5 cm DBH were considered as juvenile trees.

Fig. 1 Map of Puerto Rico with inset of *Spathodea campanulata* forests in the northcentral region (spots; Abelleira-Martínez 2009) and the location of study sites (arrows) identified by the following codes; Ad Adjuntas, Al Almirante, CI Cibuco I, CII Cibuco II, Ca Caserío, Co Collores, Fr Fránquez, JN Juan Nieves, Mo Montebello, OC Ollas y Calderas, PI Paso del Indio, PD Pozo Dulce, Pa Pastos, Pen Penitente, Per Perchas, Po Pozas, Pu Pugnado, Ro Roseta, Toa Toa, Ve Vega



Tree density (trees/ha), basal area (m^2/ha), sampled area (ha), and species importance values (IV) were calculated for the large and small tree size classes following Cottam and Curtis (1956), and Ashby (1972). The point occurrence frequency, number of trees, and basal area of each species per transect were converted into percent of all species and these percents were averaged to calculate species IV's per size class per site. Juvenile tree size class density (trees/ha) was determined and species IV's were calculated as the average of the density and plot occurrence frequency of each species expressed in percentage of all species. The following attributes were determined for each species according to Little and Wadsworth (1964) and Little et al. (1974): natural geographical origin, fruit size and morphology, and maximum DBH and height. I determined seed dispersal syndrome (sensu van der Pijl 1969) based on fruit size and morphology.

Site variables

The geological substrate, elevation, and soil series and order of each site were determined from maps (Acevedo 1982; Bawiec et al. 2001; Table 1). The elevation of each site was classed as being <100,

≥ 100 to <200, or ≥ 200 m above sea level. Slope (%) was determined with a clinometer, estimated as the mid-point of the range, and classed as 0, >0 to <20, ≥ 20 to <50, and $\geq 50\%$.

Age since abandonment (ASA) was estimated from aerial photography of 1963–1964, 1971, 1977–1978, and 1985 as the mid-point of years showing use and abandonment, and was classed as ≥ 0 or <30 years (Table 1). Previous use was determined from conversations with landowners and neighbors, aerial photography, and a land cover map of 1977–1978 (Ramos and Lugo 1994). Three schemes were used to classify previous use. The previous land use (PLU) scheme separated sites used exclusively for growing crops from those used for cattle pastures. The previous agricultural use (PAU) scheme classed sites by the crop grown and cattle pastures was a class when it was the only previous use but was ignored at sites used for crops. The land use intensity (LUI) scheme assigned quantitative classes to the following land uses in order of increasing intensity: shade coffee (1), sun crops (i.e., subsistence agriculture, coffee, tobacco); (2), sun crops and cattle pasture (3), and sugar cane or cattle pasture (4). The rationale behind this scheme is that shade coffee is the least intensive use that allows for more remnant trees and

Table 1 Description of *Spathodea campanulata* forest study sites

Site	Substrate properties					Land use history		Spatial attributes					
	Geological substrate	Elevation (m)	Slope (%)	Soil series	Soil order	Age since abandonment (years)	Previous use	Forest patch area (ha)	Exposed edge (%)	Perimeter/area (m/m ²)	Latitude (°)	Longitude (°)	Landscape proximity group
Almirante	A	15	0	Toa	M	39	SC, P	2.0	0	0.055	18.41	66.38	NE
Cibuco I	A	10	0	Coloso	I	24	SC	16.7	45	0.020	18.42	66.35	NE
Cibuco II	A	10	0	Toa	M	38	SC	1.1	61	0.038	18.43	66.36	NE
Paso del Indio	A	10	0	Toa	M	24	SC, P	4.0	69	0.031	18.43	66.38	NE
Penitente	A	10	0	Toa	M	39	P	0.6	61	0.070	18.42	66.51	NW
Toa	A	5	0	Toa	M	26	P	1.0	100	0.039	18.42	66.26	Out
Vega	A	15	0	Coloso	I	25	SC	1.9	59	0.043	18.42	66.34	NE
Caserio	K	110	8–15	San Germán	E	39	T	1.4	0	0.052	18.35	66.48	NW
Fránquez	K	95	20–45	San Sebastián	M	36	SA, P	0.9	0	0.041	18.40	66.40	NE
Juan Nieves	K	30	8–15	San Germán	E	38	SA, P	4.2	5	0.022	18.37	66.49	NW
Montebello	K	150	8–15	San Sebastián	M	32	P	0.9	0	0.052	18.39	66.51	NW
Ollas y Calderas	K	140	25–50	San Sebastián	M	31	SA, P	0.8	18	0.041	18.39	66.45	NW
Pugnado	K	170	7–15	San Sebastián	M	24	SA, P	0.9	50	0.040	18.39	66.46	NW
Roseta	K	25	45	Tanamá Rock	RO	36	P	1.7	14	0.056	18.43	66.38	NE
Adjuntas	V	500	50–70	Maragüéz	I	25	SHC	11.3	71	0.013	18.17	66.73	Out
Collores	V	260	55	Consumo	U	36	C	1.2	0	0.040	18.25	66.49	S
Pastos	V	320	50–70	Múcara	I	32	C, P	1.0	10	0.054	18.28	66.42	S
Perchas	V	200	50–70	Múcara	I	39	C, P	9.0	36	0.015	18.29	66.39	S
Pozas	V	180	50–70	Múcara	I	39	T, P	3.6	0	0.027	18.28	66.46	S
Pozo Dulce	V	140	20–45	Múcara	I	37	C, P	0.4	18	0.072	18.23	66.08	Out

Letters for geology correspond to alluvial (A), karst (K), and volcanic extrusive (V) substrates. Letters for soil order correspond to mollisols (M), inceptisols (I), entisols (E), rock outcrop (RO) and ultisols (U). Letters for previous land use correspond to sugar cane (SC), pasture (P), tobacco (T), subsistence agriculture (SA), shade coffee (SHC), and sun coffee (C). Subsistence agriculture includes fruit and vegetable crops such as plantains, citrics, and horticulture. Landscape proximity groups are northeast (NE), northwest (NW) or south (S), and sites outside the main study region (Out) do not correspond to any group

soil protection. Sun crops sometimes include fruit trees that serve a similar purpose but the cattle grazing associated to some sun crops is a more intensive use. The LUI of sugar cane and cattle pastures were considered the most intense yet equivalent as both uses imply herbaceous vegetation, excludes remnant trees, and involves soil trampling by cattle as cattle carts were used in cane harvesting (Picó 1988).

Forest patch area (FPA; ha) and perimeter to area ratio (P/A; m/m²) were determined from aerial photography of 1998 using Arc-View 3.2 (ESRI 1999; Table 1). FPA was classed into <1, ≥1 to <3, and ≥3 ha, and P/A as ≥ or <0.05 m/m². Most seed dispersal is limited to ~30 m away from forest edges (Zimmerman et al. 2000; Cubiña and Aide 2001). Thus, I considered an edge as exposed if no forest was found at <30 m perpendicular from the edge. The percentage of exposed edge (PEE) of each site was determined as the ratio of exposed edge length to the forest perimeter classed as 0, >0 to <50, and ≥50%. To examine if site location influenced species composition, sites were classed as > or ≤18.3° latitude, > or ≤66.4° longitude, and into three landscape proximity groups (LPG) where sites fell naturally except for isolated sites (Table 1; Fig. 1).

Data analysis

Multivariate analysis of variance (MANOVA) was used to compare mean tree density, basal area, species richness, and percentage of introduced species between sites. Geological substrate, elevation, slope, age since abandonment (ASA), previous land use (PLU), forest patch area (FPA), percentage of exposed edge (PEE), and perimeter to area ratio (P/A) per site were tested as independent variables (Table 1). Hotelling–Bonferroni tests were used to compare means. Normality and variance equality were tested with Shapiro–Wilks and *F*-max tests, respectively. All means were based on *n* = 20 sites except for species richness in the large and small tree size classes for which *n* = 29 transects. Infostat software (Di Rienzo et al. 2003) was used for all statistical tests.

Non-metric multidimensional scaling (NMS) of species IV's was used to analyze the variance in species composition across sites and was run on the slow and thorough autopilot mode in PC-Ord software using Sørensen's similarity index (McCune and

Mefford 1999). It was not possible to obtain stable NMS ordination solutions for the large and small tree size classes separately. Therefore, one ordination including large and small tree size classes was done using the arcsine square-root transformed mean IV of each species in both size classes. Species that occurred only at one site were excluded from NMS. Pearson correlations were used to relate the following quantitative variables to ordination axis scores: elevation, slope, ASA, land use intensity (LUI), FPA, PEE, P/A, latitude, and longitude (Table 1). Multi response permutation procedures (MRPP) were used to determine which of the following variables were related to the species composition of sites in NMS ordination space: geological substrate, elevation, slope, soil series and order, ASA, LUI, previous agricultural use (PAU), PLU, FPA, PEE, P/A, latitude, longitude, and landscape proximity group (LPG; Table 1). Variable classes with *n* < 2 were excluded from MRPP. Indicator species analysis (ISA; McCune and Mefford 1999) was used to determine what species drove compositional differences related to the most significant variable in MRPP.

Results

A total of 105 tree species were found of which 23 were introduced (22%) and five are endemic (5%; see Table 5 in Appendix). Most species are dispersed by animals (86%) and some by wind (11%). Most species (82%) grow to DBH of ≥10 cm and eight species (8%) grow to DBH ≥1 m. Most species (86%) grow ≥5 m tall and 29 species (27%) grow ≥20 m. There were 42, 54, and 90 species in the large, small, and juvenile tree size classes, respectively, and 27% of all species occurred in all size classes.

Large and small tree density ranged from 1,043 to 6,692 trees/ha (mean = 2,893, S.E. = 295), basal area ranged from 32 to 191 m²/ha (mean = 69, S.E. = 7.9), and neither was related to any variable (see Table 6 in Appendix). Juvenile tree density ranged from 4,200 to 74,100 trees/ha (mean = 29,332, S.E. = 4,269) and was lower at alluvial sites (mean = 10,986, S.E. = 2,435, *F* [2, 5] = 22.15, *P* = 0.003). Species richness ranged from 1 to 11 species per 40 trees per transect in the large (mean = 5, S.E. = 0.52; Table 6 in Appendix), 2 to 16 species

per 40 trees per transect in the small (mean = 9, S.E. = 0.62), and 8 to 35 species per 0.01 ha sampled per site in the juvenile (mean = 23, S.E. = 1.8) tree size classes, respectively. Species richness was lowest at alluvial sites in all size classes (mean = 3, S.E. = 0.43, $F [2, 14] = 12.15$, and $P = 0.0009$ for large; mean = 6, S.E. = 1.2, $F [2, 14] = 9.43$, and $P = 0.003$ for small; and mean = 17, S.E. = 2.18, $F [2, 5] = 5.02$, and $P = 0.06$ for juvenile tree size classes; respectively). The percentage of introduced species per site was 41, 21, and 15% (S.E. = 5.9, 2.4, and 1.8) in the large, small, and juvenile tree size classes respectively, and ranged from 8 to 35% for species in all size classes combined (mean = 17%, S.E. = 1.8; Table 6 in Appendix). In the large tree size class, there was a higher percentage of introduced species at sites with 0% slope (mean = 68%, S.E. = 9.3, $F [3, 5] = 6.11$, $P = 0.04$) which coincide with alluvial sites (Table 1), but no differences were found in the small and juvenile tree size classes.

Both large and small, and juvenile tree size class NMS ordinations of species composition produced valid solutions (Figs. 2 and 3; McCune and Mefford 1999). In the large and small tree size classes, slope, elevation, LUI, and latitude were significantly correlated to the main axis 1 which separated alluvial from karst and volcanic sites in ordination space (Table 2; Fig. 2). In the juvenile tree size class, slope, and latitude were the only variables significantly correlated to the main axis 1 which separated alluvial, karst, and volcanic sites from each other (Table 2; Fig. 3). No variables were significantly correlated to the secondary axis in either ordination (Table 2). According to MRPP, geological substrate grouped sites in a way that maximized compositional differences and similarities in both large and small, and juvenile tree size classes (Table 3; Figs. 2 and 3). Other variables significantly related ($P \leq 0.01$) to the variance in species composition across sites were, in order of significance, soil series, slope, LPG, PAU, elevation, longitude, LUI, and latitude in the large and small tree size classes, and slope, latitude, soil series, ASA, LPG, and PAU in the juvenile tree size class (Table 3).

One, five, and four species were indicators of the large and small tree, and two, eight, and six species were indicators of the juvenile tree size class composition of alluvial, karst, and volcanic sites, respectively

(Table 4). Only *S. campanulata* and *Andira inermis* were indicative of alluvial sites, the latter only in the juvenile tree size class. *Ardisia obovata*, *Casearia decandra*, *Ocotea coriacea*, and *Thouinia striata* were indicators of large and small, and juvenile tree size class composition at karst sites, and *Inga fagifolia* and *Ocotea leucoxydon* were as such at volcanic sites (Table 4).

Discussion

It is evident that animal seed dispersers are facilitating the invasion of native tree species into novel *S. campanulata* forests in Puerto Rico (see Table 5 in Appendix). Native birds that disperse seeds of species found abundantly as juvenile trees, such as *G. guidonia*, *Cupania americana*, and *O. coriacea*, are common in the region (see Table 5 in Appendix; Carlo et al. 2003). I observed some of these birds during my visits (i.e., *Loxigilla portorricensis*, *Margarops fuscatus*, *Spindalis portorricensis*, and *Vireo* spp.). I also observed the green tree lizard (*Anolis cuvieri*) which could be dispersing the small seeds of *Casearia guianensis*, *Coccoloba diversifolia*, and *Erythrolylon brevipes*, also found abundantly as juvenile trees (Vega-Castillo and Cuevas 2009). Seeds and juvenile trees of *A. inermis*, *Calophyllum calaba*, *Meliococcus bijugatus*, *Terminalia catappa*, *Thespesia grandiflora*, and *Syzygium jambos* were usually found in clumps on the ground and far from parent trees. These were probably dropped by roosting common fruit bats (*Artibeus jamaicensis*) which disperse some of these species locally (Rodríguez-Durán 2005). Thus, the presence and abundance of native seed dispersing fauna is a key factor that differentiates the patterns of species regenerating in novel *S. campanulata* forests in Puerto Rico and Hawaii, the latter being impoverished in native species of seed dispersers and regenerating trees.

The interrelated effects of substrate properties and land use history result in lower tree species richness at alluvial *S. campanulata* forests. Periodic floods in alluvial sites exclude intolerant species and this is illustrated by the specific example of two sites, Paso del Indio and Roseta (Table 1; Fig. 1). At Paso del Indio, an alluvial site that floods, juvenile tree density and species richness was 4,200 trees/ha and 14 species, and at Roseta, which is only a few meters

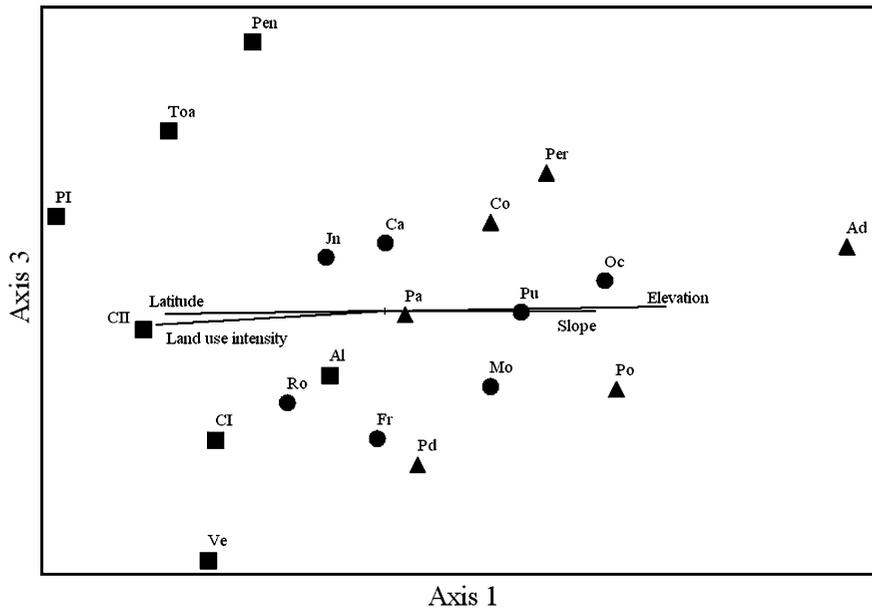


Fig. 2 Non-metric multidimensional scaling of species importance values per site in the large and small tree size classes. Final stress and instability for a tri-dimensional ordination solution were 10.6 and 10^{-5} , respectively. Most of the variance was explained by axes 1 and 3 which explained 58.5 and 14.8% of the variance, respectively, and these had 99.9% orthogonality.

Together, all three axes explained 87.9% of the variance. Only variables significant to $P < 0.05$ are included as correlation vectors (Table 2). Squares, circles, and triangles correspond to sites of alluvial, karst, and volcanic extrusive geological substrates, respectively. Codes for each site follow Fig. 1

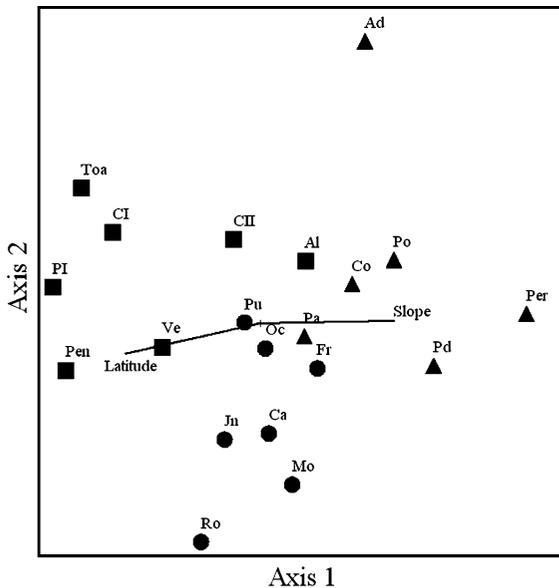


Fig. 3 Non-metric multidimensional scaling of species importance values per site in the juvenile tree size class. Final stress and instability for a bi-dimensional ordination solution were 13.4 and 10^{-5} , respectively. Axes 1 and 2 explained 44.4 and 41.4% of the variance, respectively, and had 99.8% orthogonality. Only variables significant to $P < 0.05$ are included as correlation vectors (Table 2). Codes and symbols follow Figs. 1 and 2

away on a contiguous karst slope, these values were 45,300 trees/ha and 33 species, respectively. Intensive agricultural use for sugar cane on alluvial valleys caused total deforestation and extirpated many native tree species adapted to flooding (Wadsworth 1950). Thus, remnant trees or forests in inaccessible places of low agricultural potential in karst and volcanic substrates served as better seed dispersal sources to *S. campanulata* forests on those substrates. Some common flood tolerant native tree species (i.e., *Bucida buceras* and *C. calaba*) are becoming established at alluvial sites possibly due to their natural occurrence in nearby karst and their traditional use as shade trees in rural areas (Little and Wadsworth 1964).

Introduced species compose a low percentage of the composition of *S. campanulata* forests, comparable to all the species in the flora (26%, Liogier and Martorel 2000) and in secondary forests (15%, China and Helmer 2003) of Puerto Rico. The higher percentage of introduced species in the large tree size class on flat alluvial sites is possibly due to the intensive land use history which extirpated many native tree species and facilitated the invasion of

Table 2 Pearson correlation coefficient (r) and proportion of variance explained (R^2) by quantitative variables correlated to ordination axes for large and small, and juvenile tree size classes

Variable	Large and small trees				Juvenile trees			
	Axis 1		Axis 3		Axis 1		Axis 2	
	r	R^2	r	R^2	r	R^2	r	R^2
Age since abandonment (years)	0.083	0.007	0.116	0.013	0.468	0.219	-0.395	0.156
Elevation (m)	0.842	0.709	0.124	0.015	0.621	0.386	0.384	0.147
Forest patch area (ha)	0.162	0.026	-0.027	0.001	0.041	0.002	0.472	0.223
Exposed edge (%)	-0.322	0.104	0.345	0.119	-0.528	0.279	0.555	0.308
Land use intensity (scale of 1–4)	-0.758	0.574	-0.199	0.040	-0.567	0.321	-0.301	0.090
Latitude (°)	-0.744	0.553	-0.096	0.009	-0.733	0.538	-0.348	0.121
Longitude (°)	0.543	0.294	0.366	0.134	0.061	0.004	0.191	0.037
Perimeter/area (m/m ²)	-0.263	0.069	-0.105	0.011	-0.138	0.019	-0.518	0.268
Slope (%)	0.729	0.532	0.037	0.001	0.730	0.533	0.094	0.009

Values in bold are statistically significant ($P < 0.05$)

Table 3 Multi response permutation procedures (McCune and Mefford 1999) within-group agreement statistic (A) and statistical significance (P) of the separation of the tree species composition in large and small, and juvenile tree size classes of sites based on each variable

Variable	Large and small trees		Juvenile trees	
	A	P	A	P
Geological substrate (3)	0.103	0.00001	0.120	0.000001
Soil series (5)	0.170	0.0001	0.133	0.0007
Slope (4)	0.099	0.0002	0.122	0.00001
Landscape proximity group (3)	0.082	0.0005	0.061	0.005
Previous agricultural use (5)	0.096	0.002	0.072	0.01
Elevation (3)	0.065	0.002	0.038	0.03
Longitude (2)	0.043	0.002	0.003	0.3
Land use intensity (3)	0.061	0.007	0.034	0.06
Latitude (2)	0.036	0.008	0.062	0.0002
Soil order (3)	0.014	0.02	0.048	0.02
Exposed edge (3)	0.019	0.1	0.040	0.02
Age since abandonment (2)	0.000	0.4	0.044	0.003
Forest patch area (3)	0.001	0.4	-0.013	0.8
Perimeter/area (2)	-0.004	0.6	0.014	0.1
Previous land use (2)	-0.004	0.6	-0.007	0.7

The number of classes is in parenthesis next to each variable. Variables are rank ordered according to P values in the large and small tree size classes

introduced species typically planted on roadsides (i.e., *Albizia procera* and *T. catappa*). As all alluvial valleys have historically been subject to intensive land use in Puerto Rico due to their agricultural potential, the effects of land use history and substrate

properties cannot be completely separated (Table 1). The recent incursion of native species dissolves any differences in the percentage of introduced species in the juvenile tree size class across sites yet seed dispersal by animals favors the perpetuation of some

Table 4 Statistical significance (P) of the tree species indicative of the composition of sites on different geological substrate types ($P < 0.05$) based on a 1,000 permutation Monte Carlo test on species importance values from indicator species analysis (McCune and Mefford 1999)

Species	Large and small trees	Juvenile trees
Alluvial		
<i>Spathodea campanulata</i> *	0.019	0.008
<i>Andira inermis</i>	–	0.001
Karst		
<i>Ocotea coriacea</i>	0.016	0.018
<i>Ardisia obovata</i>	0.021	0.004
<i>Thouinia striata</i> **	0.028	0.001
<i>Casearia decandra</i>	0.032	0.005
<i>Roystonea borinquena</i> **	0.045	–
<i>Randia aculeata</i>	–	0.002
<i>Exothea paniculata</i>	–	0.004
<i>Tabebuia heterophylla</i>	–	0.011
<i>Coccoloba diversifolia</i>	–	0.018
Volcanic		
<i>Cecropia scheberiana</i>	0.010	–
<i>Inga fagifolia</i>	0.019	0.018
<i>Ocotea leucoxylon</i>	0.022	0.006
<i>Erythrina poeppigiana</i> *	0.047	–
<i>Coffea arabica</i> *	–	0.006
<i>Miconia prasina</i>	–	0.008
<i>Capparis baducca</i>	–	0.020
<i>Miconia impetiolaris</i>	–	0.049

Species are rank ordered by P values for the large and small tree size class, and then by P values for juvenile trees. Introduced species denoted by * and endemics by **

introduced species (i.e., *M. bijugatus*, *T. catappa*, and *S. jambos*). Thus, it is unlikely that the composition of these novel forests will revert entirely to that of the old growth forests present before large scale anthropogenic changes in land cover.

The hypothesis that large and small tree size class species composition is shaped by land use history was partially supported yet substrate properties best explained the variance in composition (Tables 2, 3; Fig. 2). The hypothesis that juvenile tree species composition of *S. campanulata* forests is shaped by substrate properties was supported since geological substrate, slope, and soil best explained the variance in composition (Tables 1, 2, 3; Fig. 3). ASA, latitude, LPG, and PAU were also related to juvenile tree

species composition, but to a lower degree than substrate properties. Again, the coincidence of flat alluvial sites with intensive agricultural use for sugar cane harvesting and grazing limits the interpretation of these findings (Table 1).

Land use history (i.e., PAU and LUI) had comparably higher statistical significance in explaining the variance in species composition of large and small trees compared to the juvenile tree size class (Table 3). This shows historical legacies are still evident in older trees yet less so in recent species establishment. Furthermore, the differences in species composition due to substrate properties were more evident in the juvenile compared to the large and small tree size classes which suggests compositional differences due to substrate are developing (Tables 3, 4; Figs 2, 3). In this sense, the relation of ASA to juvenile tree size class species composition can result from more seed disperser visits and time for species establishment at older sites (Table 3). In addition, the secondary axis 2 separated karst from alluvial and volcanic sites in the juvenile tree size class (Fig. 3). This suggests that, aside from the correlated effects of substrate properties and land use history that separate site species composition by the main axis 1, there are other substrate related factors involved. Thus, since substrate properties are at least as important as land use history in determining tree species establishment and composition, it is unlikely that these forests are causing biotic homogenization in abandoned agricultural lands in Puerto Rico.

The classification of sites by latitude had the effect of grouping all alluvial and karst sites in a group ($>18.3^\circ\text{N}$) and all volcanic sites in another (Table 1; Fig. 1). The statistical significance of substrate properties in explaining the variance in species composition is much higher than that found when these sites are grouped together by their location in the landscape by latitude or LPG (Table 3). This shows that substrate properties and land use history are shaping recent species establishment rather than the location of sites in the landscape. The lack of effects of other spatial attributes (i.e., FPA, PEE, and P/A) is similar to other secondary forests where species composition relates more to substrate properties or land use history (Table 3; Aragón and Morales 2003; Lichstein et al. 2004). Some studies find significant effects of FPA, PEE, or P/A on secondary forest tree species composition yet these include a larger FPA

range which could explain why such relationships were not significant in this study (i.e., Galanes and Thomlinson 2009; Tables 1, 2, 3).

Aside from the extirpation of flood tolerant native tree species, the strong relation of *S. campanulata* to alluvial sites is due to adaptations to periodical flooding (Pimenta et al. 1998), its fringe forest to savanna habitat in its native range (Hutchinson and Dalziel 1927), and full sun conditions in abandoned sugar cane and grazing fields. Besides *S. campanulata*, introduced species found by ISA are associated to coffee (*Coffea arabica*) farming at volcanic sites as *Erythrina poeppigiana* is typically used for coffee shade (Table 4). Except for introduced species, all species found by ISA are native and common in secondary to old growth forests on equivalent substrate types (Little and Wadsworth 1964; Little et al. 1974). Although these species are naturally present in other substrate types, it is their relative importance that drives compositional differences. For example, *A. inermis*, *Tabebuia heterophylla*, and *I. fagifolia* are found on all substrate types but had strong affinity for alluvial, karst, and volcanic sites, respectively (Table 4). Additionally, there were species with affinities to two substrates instead of one and thus were not detected by ISA. For example, *B. buceras*, *Bursera simaruba*, *C. calaba*, and *Cordia laevigata* on alluvial and karst sites, and *Chrysophyllum argenteum*, *Musa sapientum*, *Persea americana*, and *Quararibea turbinata* on karst and volcanic sites (see Table 5 in Appendix). Both *M. sapientum* (banana and plantain varieties) and *P. americana* (avocado) are introduced agricultural remnants that reflect similar land use history between karst and volcanic sites. At some karst and volcanic sites, some uncommon species were found (i.e., *Cedrela odorata* and *Prunus myrtifolia*) but these were represented by a single individual (see Table 5 in Appendix). Thus, the loss of uncommon species is an aspect of biotic homogenization that is mostly not prevented naturally in these forests.

Management implications

Natural processes, such as animal mediated seed dispersal and adaptations of native tree species to different growth environments, are enriching and shaping the tree species composition of novel *S. campanulata* forests in Puerto Rico. Recent species

establishment is largely shaped by substrate properties and this is preventing biotic homogenization in these forests at a regional scale. In addition, natural disturbances, such as hurricanes, speed up the succession and growth of native species in these forests (Aide et al. 2000; Flynn et al. 2009). Thus, it seems that novel forests that result from *S. campanulata*'s invasion of deforested and abandoned lands in Puerto Rico create conditions where modern biogeography and biodiversity theory suggests species richness and diversity will increase if dispersal and speciation are not limited (Hubbell 2001).

To further counteract biotic homogenization, the natural succession process started by *S. campanulata*'s invasion can be assisted by restoration planting of extirpated native tree species. This is more necessary at alluvial sites which offer an opportunity to restore some of the tree species found in the original forests that once occupied these valleys. Uncommon species with small populations and restricted geographical ranges, particularly those limited by the loss of dispersers, should be targeted by restoration efforts. Some native tree species that serve this purpose, depending on site, are *Coccoloba pubescens*, *Dacryodes excelsa*, *Diospyros ebenaster*, *Junglans jamaicensis*, *Manilkara bidentata*, *Prunus occidentalis*, and the palms *Acrocomia media* and *Aiphanes acanthophylla* (Wadsworth 1950; Little and Wadsworth 1964; Little et al. 1974). Restoration plantings of seedlings or juvenile trees should match canopy closure so that they are well established to take advantage of the higher light levels and leaf fall pulse that occurs during the deciduous canopy opening (Abelleira-Martínez 2009).

The example of Adjuntas illustrates how *S. campanulata*'s deciduous canopy can be favoring juvenile tree species establishment and growth (Table 1). This site had lower juvenile tree size class species richness compared to most sites in spite of high juvenile tree density (8 species and 74,100 trees/ha; Table 6 in Appendix). At this site, *G. guidonia*, an evergreen tree that was used for coffee shade (Table 1), co-dominated the canopy with *S. campanulata* which was absent in the juvenile tree size class. This suggests that lower light levels at Adjuntas can be limiting species establishment compared to forests where *S. campanulata*'s dominance is higher and more light penetrates to the forest floor during the deciduous period. The coincident leaf fall pulse can favor

juvenile tree growth by making nutrients more available in the soil (Lugo 2004). Alternatively, higher dominance by *S. campanulata* can be attracting more animal seed dispersers during the flowering period at the other sites and this can result in higher species richness. Other studies are needed to test these hypotheses.

The conservation of remnant old growth forest fragments and the wise use of living fences (i.e., spatial configuration and choice of species) to serve as seed dispersal sources and facilitate the recovery of native tree species after land abandonment are lessons learned from this and other agricultural landscapes (Helmer 2000; Starfinger et al. 2003; Guevara et al. 2005). The use of *S. campanulata* as fencepost in farms and its re-sprouting ability aided its invasion of abandoned lands in Puerto Rico. Other species were also used as fencepost or shade trees, and this aided their permanence in landscapes where farms were small and agricultural practices less intensive. Areas used for sugar cane on alluvial valleys were expansive, living fences were lacking, remnant forest fragments or trees were completely eliminated, and this is reflected by impoverished species richness and composition. Recently, some *S. campanulata* forests on former sugar cane fields on alluvial valleys have been cleared. This is unfortunate because these forests overcome the severe soil disturbance that results from

sugar cane harvesting and grazing, and create favorable conditions for invasion by native tree species that cannot invade abandoned pastures (i.e., *Cecropia scheberiana*, Silander 1979; Aide et al. 2000). In doing so, these forests restore and protect the soil of the best agricultural lands of Puerto Rico which are currently threatened by urban development (López et al. 2001; Helmer 2004). These lessons are critical in tropical islands where socio-economic changes can lead to agricultural abandonment and create favorable conditions for the growth of novel forests.

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Appendix

See Tables 5 and 6.

Table 5 Species found in this study and their descriptions according to Little and Wadsworth (1964) and Little et al. (1974)

Species	Size class	Importance value (%)			Origin	Dispersal mode	DBH (cm)	Height (m)
		A	K	V				
<i>Albizia procera</i> (Roxb.) Benth.	LSJ	1.03	–	–	I	A	61	18
<i>Andira inermis</i> (W. Wright) DC.	LSJ	9.70	3.95	5.18	N	Z	61	30
<i>Anona muricata</i> L.	J	–	–	0.09	I*	Z	15	6
<i>Ardisia obovata</i> Desv.	SJ	0.25	1.95	0.22	N	Z	15	17
<i>Bourreria succulenta</i> Jacq.	J	–	0.04	–	N	Z	30	15
<i>Buchenavia capitata</i> (Vahl) Eichl.	J	–	–	0.08	N	Z	183	27
<i>Bucida buceras</i> L.	SJ	0.42	0.64	–	N	Z	152	27
<i>Bursera simaruba</i> (L.) Sarg.	LJ	0.26	0.18	–	N	Z	91	21
<i>Calophyllum calaba</i> L.	LSJ	2.45	2.24	–	N	Z	91	20
<i>Capparis baduoca</i> L.	J	–	–	0.23	N	Z	5	5
<i>Capparis flexuosa</i> (L.) L.	J	0.10	0.04	–	N	Z	13	6
<i>Casearia decandra</i> Jacq.	SJ	0.36	1.45	0.17	N	Z	8	5
<i>Casearia guianensis</i> (Aubl.) Urban.	LSJ	2.84	4.24	3.23	N	Z	13	15
<i>Casearia sylvestris</i> Sw.	LSJ	1.31	0.07	0.18	N	Z	10	20
<i>Cassia siamea</i> Lam.	LSJ	0.90	5.51	5.60	I	Z	30	18

Table 5 continued

Species	Size class	Importance value (%)			Origin	Dispersal mode	DBH (cm)	Height (m)
		A	K	V				
<i>Cecropia scheberiana</i> Miq.	L	–	–	0.61	N	Z	61	21
<i>Cedrela odorata</i> L.	J	–	–	0.06	N	A	152	30
<i>Ceiba pentandra</i> (L.) Gaertn.	L	–	0.08	–	N	A	244	24
<i>Cestrum diurnum</i> L.	J	–	0.05	–	I	Z	8	5
<i>Cestrum macrophyllum</i> Vent.	J	–	0.07	0.11	N	Z	8	6
<i>Chrysophyllum argenteum</i> Jacq.	LSJ	–	0.63	0.17	N	Z	20	8
<i>Cinnamomum elongatum</i> (Vahl.) Kostern	LSJ	0.68	1.80	1.29	N	Z	41	30
<i>Citharexylum fruticosum</i> L.	LJ	0.18	0.08	–	N	Z	30	12
<i>Citrus aurantifolia</i> (L.) Swingle	J	0.10	–	–	I	Z	–	6
<i>Citrus paradisi</i> Macfayden	LS	–	0.24	0.14	I*	Z	15	6
<i>Clusia rosea</i> Jacq.	J	–	0.05	–	N	Z	61	18
<i>Coccoloba diversifolia</i> Jacq.	SJ	–	0.59	–	N	Z	61	18
<i>Coccoloba venosa</i> L.	J	0.15	–	–	N	Z	20	9
<i>Cocos nucifera</i> L.	J	–	–	0.06	I	H	51*	18
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	J	0.09	–	–	I	A	30	8
<i>Coffea arabica</i> L.	SJ	–	–	1.33	I	Z	8	5
<i>Comocladia glabra</i> (Schultes) Spreng	J	0.10	0.29	–	N	Z	5	6
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken.	LSJ	–	–	0.69	N	A	46	20
<i>Cordia laevigata</i> Lam.	SJ	0.51	0.42	–	N	Z	30	20
<i>Cordia sulcata</i> DC.	S	–	–	0.23	N	Z	46	20
<i>Cupania americana</i> L.	LSJ	1.27	1.93	1.76	N	Z	36	27
<i>Daphnopsis americana</i> (Mill.) J.R. Johnst.	J	–	0.06	–	N*	Z	15	8
<i>Delonix regia</i> (Bojer) Raf.	SJ	0.64	–	–	I	Au	61	15
<i>Dendropanax arboreus</i> (L.) Decne. & Planch	LSJ	–	0.24	0.27	N	Z	30	18
<i>Dipholis salicifolia</i> (L.) DC.	J	–	0.08	–	N	Z	91	15
<i>Drypetes glauca</i> Vahl.	J	–	–	0.08	N	Z	15	9
<i>Erythrina poeppigiana</i> (Walp.) O.F. Cook	LS	0.85	0.59	0.13	I	A	122	21
<i>Erythroxylon brevipes</i> DC.	J	0.06	–	0.31	N	Z	10	8
<i>Eugenia axillaris</i> (Sw.) Willd.	J	–	0.12	–	N	Z	13	6
<i>Eugenia biflora</i> (L.) DC.	SJ	1.19	1.48	2.35	N	Z	20	9
<i>Eugenia monticola</i> (Sw.) DC.	J	0.41	0.46	0.17	N	Z	15	15
<i>Exothea paniculata</i> (Juss.) Radkl.	J	–	0.42	–	N	Z	51	20
<i>Faramea occidentalis</i> (L.) A. Rich.	J	0.19	–	0.26	N	Z	8	9
<i>Ficus citrifolia</i> Mill.	LSJ	0.13	0.22	0.14	N	Z	76	18
<i>Gesneria pedunculosa</i> (DC.) Fritsch	SJ	–	0.16	0.29	E	Z	3	5
<i>Guapira fragans</i> (Dum.-Cours.) Little	SJ	0.21	0.20	0.42	N	Z	51	24
<i>Guarea guidonia</i> (L.) Sleumer.	LSJ	6.70	7.19	16.0	N	Z	91	23
<i>Guettarda ovalifolia</i> Urban	S	–	0.06	–	N	Z	10	9
<i>Guettarda scabra</i> (L.) Vent.	SJ	0.07	0.24	–	N	Z	15	12
<i>Heterotrychum cymosum</i> (Wendl.) Urban	J	–	0.04	–	E	Z	8	5
<i>Hibiscus tileaceus</i> L.	LS	–	–	0.56	I*	Au	15	6
<i>Hymenaea courbaril</i> L.	L	–	–	0.17	N	Z	122	20
<i>Inga fagifolia</i> (L.) Willd.	LSJ	0.36	–	3.15	N	Z	46	21

Table 5 continued

Species	Size class	Importance value (%)			Origin	Dispersal mode	DBH (cm)	Height (m)
		A	K	V				
<i>Inga vera</i> Willd.	LSJ	0.10	0.48	1.24	N*	Z	91	18
<i>Leucaena leucocephala</i> (Lam.) deWit	J	0.22	0.06	–	I*	Z	10	8
<i>Lonchocarpus pentaphyllus</i> (Poir.) DC	J	–	0.15	0.06	N	A	30	21
<i>Mangifera indica</i> L.	L	–	–	0.23	I	Z	91	20
<i>Meliococcus bijugatus</i> Jacq.	J	0.82	0.39	–	I	Z	61	18
<i>Miconia impetolaris</i> (Sw.) D. Don.	J	–	0.08	0.68	N	Z	8	6
<i>Miconia prasina</i> (Sw.) DC.	J	–	0.23	0.72	N	Z	10	8
<i>Miconia tetrandra</i> (Sw.) D. Don	J	–	0.06	–	N	Z	30	18
<i>Musa sapientum</i> L.	LSJ	–	0.30	0.62	I	–	–	–
<i>Myrcia splendens</i> (Sw.) DC.	J	–	0.04	–	N	Z	20	18
<i>Ocotea coriacea</i> (Sw.) Britton	LSJ	1.64	3.30	0.23	N	Z	30	9
<i>Ocotea leucoxydon</i> (Sw.) Mez	LSJ	–	–	2.47	N	Z	25	15
<i>Palicourea riparia</i> Benth.	J	0.10	–	–	N	Z	8	5
<i>Parathesis crenulata</i> (Vent.) Hook. f.	J	0.10	0.16	0.06	N	Z	8	5
<i>Persea americana</i> Mill.	LS	–	0.39	0.14	I	Z	46	9
<i>Petitia dominguensis</i> Jacq.	L	–	0.43	–	N	Z	30	21
<i>Picramnia pentandra</i> Sw.	J	0.25	0.35	–	N	Z	10	6
<i>Pimenta racemosa</i> (Mill.) J.W. Moore	LJ	0.05	–	0.40	N	Z	36	17
<i>Piper aduncum</i> L.	SJ	0.12	–	1.13	N	Z	15	9
<i>Piper amalago</i> L.	SJ	–	0.10	0.17	N	Z	8	5
<i>Pithecellobium saman</i> (Jacq.) Benth.	J	0.10	–	–	I	Z	122	20
<i>Prunus myrtifolia</i> (L.) Urban	J	–	0.09	–	N	Z	10	8
<i>Psidium guajava</i> L.	J	0.16	0.05	–	I	Z	20	5
<i>Psychotria nervosa</i> Sw.	J	–	0.58	0.46	N	Z	8	3
<i>Quararibea turbinata</i> (Sw.) Poir	SJ	–	0.04	0.31	N	Z	25	12
<i>Randia aculeata</i> L.	SJ	–	0.90	0.11	N	Z	8	6
<i>Roystonea borinquena</i> O.F. Cook	LSJ	0.98	4.69	1.18	E	Z	61*	18
<i>Samyda dodecandra</i> Jacq.	J	–	0.10	–	N	Z	5	5
<i>Shaefferia frutescens</i> Jacq.	J	–	0.12	–	N	Z	13	9
<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyerl. & Prodin	S	–	–	0.07	N	Z	46	18
<i>Sideroxylon foetidissimum</i> Jacq.	J	–	0.04	–	N	Z	183	30
<i>Spathodea campanulata</i> Beauv.	LSJ	53.5	41.2	33.9	I	A	46	24
<i>Spondias mombin</i> L.	LSJ	0.60	–	0.57	N*	Z	76	18
<i>Syzygium jambos</i> (L.) Alst.	LSJ	0.44	1.40	4.27	I	Z	20	9
<i>Tabebuia heterophylla</i> (DC.) Britton	LSJ	–	0.12	–	N	A	46	18
<i>Tecoma stans</i> (L.) Juss. ex HBK	J	0.14	0.98	0.41	I*	A	8	8
<i>Terminalia catappa</i> L.	LSJ	1.78	0.09	–	I	Z	30	15
<i>Tetragastris balsamifera</i> (Sw.) Oken.	LSJ	–	–	1.95	N	Z	46	24
<i>Tetrazygia eleagnoides</i> (Sw.) DC.	LS	–	0.63	–	N	Z	15	9
<i>Thespesia grandiflora</i> DC.	LSJ	3.87	1.10	1.01	E	Z	46	15
<i>Thouinia striata</i> Radlk.	LSJ	0.05	1.98	0.06	E	A	20	15
<i>Thrinax morisii</i> H. Wendl.	J	–	0.04	–	N	Z	15*	5

Table 5 continued

Species	Size class	Importance value (%)			Origin	Dispersal mode	DBH (cm)	Height (m)
		A	K	V				
<i>Trichilia hirta</i> L.	SJ	0.50	0.19	–	N	Z	15	6
<i>Trichilia pallida</i> Sw.	SJ	0.43	0.39	0.50	N	Z	20	12
<i>Urera baccifera</i> (L.) Gaud.	S	0.23	–	0.50	N	Z	8	5
<i>Vitex divaricata</i> Sw.	L	–	0.08	–	N	Z	76	20
<i>Zanthoxylum martinicense</i> (Lam.) DC.	LSJ	0.30	0.62	0.77	N	Z	46	27

Size class denotes that the species was found in the large (L), small (S) or juvenile (J) tree size class. Importance values correspond to the average of all size classes per site combined by alluvial (A), karst (K), and volcanic extrusive (V) geological substrates. Origin denotes species as endemic (E), introduced (I), or native (N) to Puerto Rico. Dispersal mode corresponds to anemochoric (A), zoochoric (Z), hydrochoric (H) and autochoric (Au) dispersal syndromes (sensu van der Pijl 1969). Diameter at breast height (DBH) and height is the maximum reported. Blank IV's denote absence of species in substrate and blanks in other columns denote absence of data for that species. Asterisks next to origin denote it is disputed or uncertain and asterisks next to DBH denote palms

Table 6 Forest structure, species richness, and percentage of introduced species of *Spathodea campanulata* forests in this study

Site	Tree density (trees/ha)	Basal area (m ² /ha)	Juvenile density (trees/ha)	Species richness			Introduced species (%)		
				L	S	J	L	S	J
Adjuntas	1,367	51.9	74,100	12 (7, 10)	11 (7, 9)	8	42.0	36.4	12.5
Almirante	1,482	190.9	8,000	3	5	21	33.3	20.0	14.3
Caserío	6,692	56.8	42,300	5	7	32	20.0	14.3	9.4
Cibuco I	1,981	73.1	6,300	4 (2, 4)	14 (5, 14)	8	100.0	29.0	12.5
Cibuco II	2,441	98.5	17,200	3 (1, 3)	5 (3, 4)	19	67.0	40.0	36.8
Collores	3,671	45.3	51,000	8	8	24	25.0	37.5	12.5
Fránquez	2,699	69.0	25,900	4	9	27	25.0	11.1	11.1
Juan Nieves	2,566	36.6	48,933	8 (2, 7)	18 (7, 16)	33	25.0	11.0	9.1
Montebello	2,749	55.4	30,600	8	9	35	12.5	11.1	11.4
Ollas y Calderas	2,123	54.6	18,900	6 (5, 5)	15 (9, 11)	26	50.0	20.0	19.2
Pastos	4,157	43.8	48,600	6	11	24	33.3	18.2	8.3
Pozo Dulce	3,095	32.5	44,200	11	7	25	18.2	14.3	12.0
Paso del Indio	3,119	79.7	4,200	3 (1, 3)	6 (2, 5)	14	67.0	17.0	21.4
Penitente	1,043	56.3	10,800	2	10	15	50.0	20.0	13.0
Perchas	3,027	82.9	40,800	6 (2, 6)	11 (9, 10)	23	33.0	18.0	8.7
Pozas	4,399	40.2	19,900	11 (9, 9)	15 (11, 11)	18	18.0	7.0	16.7
Pugnado	2,960	71.6	19,200	9 (4, 6)	15 (11, 11)	24	22.0	20.0	16.7
Roseta	4,453	63.7	45,300	6	14	33	16.7	7.1	9.1
Toa	1,691	34.6	8,200	1	5	15	100.0	40.0	33.3
Vega	2,145	102.6	22,200	5	10	26	60.0	30.0	15.4

Tree density and basal area include large and small tree size classes (≥ 2.5 cm diameter at breast height [DBH]) and juvenile density includes trees < 2.5 cm DBH. Species richness and percent introduced species is given for each tree size class sampled: large (L), small (S), and juveniles (J). The number in parenthesis next to species richness in L and S tree size classes corresponds to the number of species found per 40 trees per transect at sites where two transects were sampled (see methods). Sampled areas ranged from 0.02 to 0.09 ha and from 0.01 to 0.08 ha per 40 trees per transect in the L and S tree size classes, respectively, and was 0.01 ha for the juvenile tree size class at all sites

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