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Species composition, diversity and structure of novel forests of *Castilla elastica* in Puerto Rico

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Abstract: Attributes of novel forests (secondary forests containing introduced species) were compared with those of native secondary forests of similar age. The study area was the biological reserve called El Tallonal, in Puerto Rico. Species composition, tree density, basal area and soil bulk density were characterized; Importance value index (IVI), Shannon's diversity index *(H')* and total aboveground biomass (TAGB) were calculated for stands of novel forests for *Castilla elastica*, an introduced naturalized tree. The IVI of *C. elastica* was 37 percent; that for *Guarea guidonia*, a native species, was 14 percent. Compared to native secondary forests, *C. elastica* forests had similar species richness (27 species in an area of 0.3 ha), low diversity (H' = 0.63) and tree density (1039 trees ha^{-1}), moderate basal area (42 m^2 ha^{-1}) and TAGB (216 Mg ha^{-1}), and low soil bulk density (0.5 to 0.7 g cm^{-3}). The structural features of novel forests of *C. elastica* are in the normal range of variation for those of native secondary forests in the tropics.

Resumen: Los atributos de bosques novedosos (bosques secundarios que contienen especies introducidas) fueron comparados con los de bosques secundarios de edad similar. El área de estudio fue la reserva biológica El Tallonal, Puerto Rico. Se caracterizaron la composición de especies, la densidad de árboles, el área basal y la densidad aparente del suelo; se calcularon índices de valor de importancia (IVI), índices de diversidad de Shannon (H') y la biomasa aérea total para rodales de bosques novedosos de *Castilla elastica*, un árbol introducido y naturalizado. El IVI de *C. elastica* fue 37 por ciento; el de *Guarea guidonia*, una especie nativa, fue14 porciento. En comparación con los bosques nativos secundarios, los bosques de *C. elastica* tuvieron una riqueza de especies similar (27 especies en un área de 0.3 ha), una baja diversidad (H' = 0.63) y una baja densidad de árboles (1039 árboles ha^{-1}), un área basal (42 m^2 ha^{-1}) y una biomasa aérea total (216 Mg ha^{-1}) moderadas, y una baja densidad del suelo aparente (0.5 a 0.7 g cm^{-3}). Los rasgos estructurales de los bosques novedosos de *C. elastica* se encuentran dentro del intervalo normal de variación de losobservados en bosques secundarios nativos en los trópicos.

Resumo: Os atributos de florestas novas (florestas secundárias contendo espécies introduzidas) foram comparados com os de florestas secundárias nativas de idade similar. A área de estudo foi a reserva biológica chamada El Tallonal, em Porto Rico. A composição de espécies, a densidade de árvores, a área basal e a densidade aparente do solo foram caracterizadas. O índice de importância (IVI), o índice de diversidade de Shannon (H') e a biomassa total acima do solo (TAGB), sigla em inglês foram calculados para parcelas de florestas novas de *Castilla elastica*, uma árvore introduzida e naturalizada. O IVI de *C. elastica* foi de 37 porcento; jã para *Guarea guidonia*, uma espécie nativa, foi de 14 porcento. Comparadas com as florestas secundárias nativas, as florestas de *C. elastica* apresentaram uma riqueza de espécies similar (27 espécies numa área de 0,3 ha), baixa diversidade (H'= 0,63) e densidade de árvores

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(1.039 árvores ha^{-1}), uma área basal (42 m2 ha^{-1}), e uma TAGB (216 Mg ha^{-1}), e uma baixa densidade aparente do solo (0,5 a 0,7 g cm^{-3}) moderadas. As características estruturais de florestas novas de *C. elastica* situam-se na gama normal de variação de florestas secundárias nativas nos trópicos.

Key words: Basal area, Importance Value Index, native secondary forests, novel forests of *Castilla elastica*, total aboveground biomass, tree density, species richness, soil bulk density.

Introduction

Ecologists and the general public are concerned by the effects of biological invasions and species losses resulting from deforestation events, fast rates of land cover changes, and high rates of species introductions (Chapin *et al.* 2000; D'Antonio & Vitousek 1992; Robinson 1992). Moreover, a large percentage of the world's forest lands are already secondary forests, many of which contain large proportions of introduced species.

About 57 % of Puerto Rico's land area is covered by secondary forests that established themselves on abandoned agriculture lands (Brandeis *et al.* 2003). These secondary forests contain many introduced species, reflecting historical anthropogenic activity (Birdsey & Weaver 1982), and show novel plant species composition (Lugo 2009) - that is, combinations of native and introduced species, which now constitute what are referred to as novel forests (Hobbs *et al.* 2006; Lugo & Helmer 2004). Specifically, forests which have regenerated naturally after land abandonment, and have species composition differing from that of the surrounding landscape, have been defined as novel forests.

Novel forests in Puerto Rico are usually young, structurally simple (low basal area and low species richness), and contain few large trees (Lugo & Helmer 2004). Nevertheless, novel forests can be structurally similar to native secondary forests of the same age, especially when mature - that is, after 40 years of regeneration (Lugo 2004).

Micro-environmental factors also influence plant species composition and diversity. For example, the high bulk density of soil surface in secondary forests (higher than 0.95 g cm^{-3} [Birdsey & Weaver 1982]) reflects soil compaction by past anthropogenic use, while low to moderate soil bulk density (0.2 to 0.85 g cm^{-3}) is typical of native forests (Lugo & Scatena 1995). The regeneration process slowly restores soil physical conditions as the soil biota and organic matter recover. Soil bulk density can be an indicator of forest rehabilitation, because lower density means better soil conditions that can support a higher number of plant species, including slow-growing plant species typical of more complex forests.

Castilla elastica (Moraceae)[1], an introduced tree from Central and South America (Sakai 2001), is an example of a naturalized species that forms novel forests in Puerto Rico. This species was possibly first introduced along roads for shade and ornamental purposes in northern karst of the country (Little *et al.* 2001).

The hypothesis underlying this study was that tree species composition, dominance and diversity of novel forests of *C. elastica* differed from those in native secondary forests and other novel forests of the same age. However, the vegetation structure and total aboveground biomass were expected to be similar. The objectives of this study were, therefore, to: (a) characterize species composition, diversity and structure of novel forests of *C. elastica*; and (b) measure the soil bulk density of two stands of *C. elastica* to see if past uses had compacted the soil and to provide a measure of soil rehabilitation.

Materials and methods

Study area

The study was conducted at El Tallonal (Fig. 1), a private natural reserve of 114 ha. The place is located in the municipality of Arecibo (18º 24 '27 " N and 66º 43 '53 " W), in the humid karst region of Puerto Rico. The study site is a subtropical moist forest (Ewel & Whitmore 1973), according to the Holdridge life zones system (Holdridge 1967). The

Footnote: [1] A full list of species mentioned , with authorities, will be found in the Appendix Table 1.

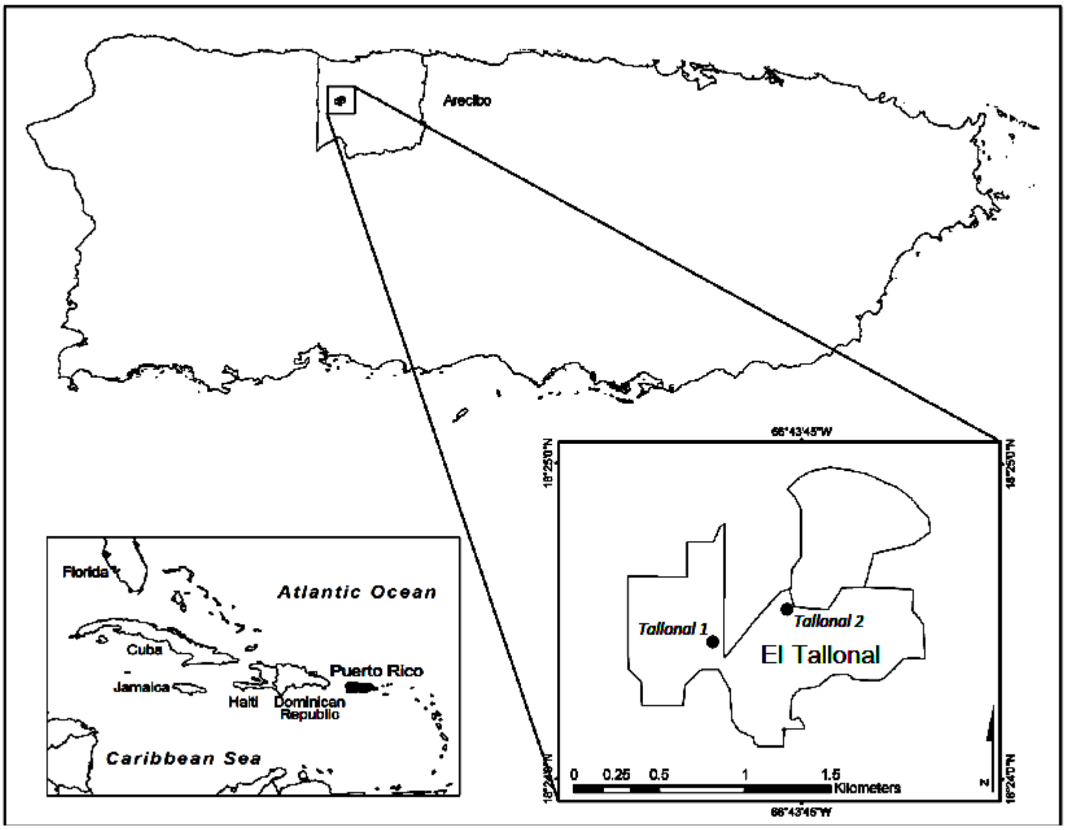

Fig. 1. Map of El Tallonal.

average annual temperature is 25.5 °C, and annual precipitation is 1295 mm.

Until the 1950's, the study area was used for agriculture and cattle grazing. After the abandonment of these activities, forest regeneration occurred naturally. Historical analyses of aerial photographs from 1936, 1963, 1977, 1983, 1995, and 2005 show that stands where *C. elastica* is dominant at El Tallonal have been recovering from cultivation for 40 to 50 years.

The karst terrain where the study area is located dates from early Cretaceous to Quaternary geological periods, and is composed of soils derived from dissolution of limestone rock (Monroe 1976). The Aymamón and Aguada karst formations, in the northern karst belt, date from the Oligocene and Miocene epochs (Behrensmeyer *et al.*1992). Karst geologic formations are chains of short, steeply sloping hills, called *mogotes*, with sinkholes interspersed among them, which characterize this type of karst formation. According to the soil classification for the area, the predominant soil type in the sinkholes of El Tallonal is the Almirante arcilloso (clayey, deep, moderate drainage [Báez Jiménez *et al.* unpublished]).

Within El Tallonal, two depressions (sinkholes) were identified and named Tallonal 1 and Tallonal 2 They measured 0.9 and 0.5 hectares respectively. In each a central point was established, the coordinates of which were:

	Tallonal 1	Tallonal 2
Longitude	66° 45' 33" W	66° 45' 01" W
Latitude	18° 24' 51" N	18° 25' 33" N
Altitude (m a.s.l)	122	116
Estimated age (y) since forest establishment	50	40

In what follows, Tallonal 1 and Tallonal 2 are referred to as "plots".

Vegetation and soil sampling

The Point Quarter Method (PQM) was used to characterize the vegetation structure (Cottam & Curtis 1956), and trees were identified to species using a guide for trees in Puerto Rico (Little *et al.* 2001 and USDA – Natural Resources Conservation Center database).

In each of the two plots, two 100 m transects were established, one North-South, the other East-West, crossing at the central point of the plot, and observations on vegetation and soil were made along these transects. Ten points chosen at random along each transect were the centre points for tree selection. At each, the nearest large tree (≥10 cm dbh) and small tree (2.5 - 9.9 cm) in each quadrant was recorded, making a total of eighty trees in each size class for the plot. To make density calculations possible, the distance from the centre point to the tree was corrected for its radius, so that the distance used for density was from the centre – point on the transect to the centre of the tree. Individuals less than 2.5 cm in diameter at breast height (1.3 m) were ignored. In each size class, the frequency of each species was simply the proportion of points at which the species in question was recorded as the closest in at least one of the quadrants.

Soil samples were taken at the northern or western end of each transect, and again at 30 m and 60 m along the transect, giving a total of six soil sample positions in each of the two plots An 85 cm cylindrical sampler was used; at each sample position, samples covering two depth ranges, 0 - 15 cm and 16 - 30 cm, were collected.

Data analysis

Throughout this study, data for large trees, small trees, and both sizes combined ("all trees"), were analysed separately.

In each size class, the frequency (F_i) of species i was simply the proportion of points at which species i was recorded as the closest in at least one of the quadrants.

Tree density (D_i) and basal area (A_i) were calculated using DBH measurements and the mean distance (corrected for girth), from each tree to the central point from which it was identified (Cottam & Curtis 1956); these figures were totalled, over the whole plot, for each size class. The values for each species were converted into relative values by dividing by the total for all species in that size category:

Frequency: $F'_i = F_i / \Sigma_i F_i$
Density: $D'_i = D_i / \Sigma_i D_i$
Basal Area: $A'_i = A_i / \Sigma_i A_i$

Based on Balslev *et al.* (1987) with slight modification, these three values multiplied by 100 were averaged to give the importance value index (IVI, in percentage) for large, small and all trees of that species.

$IVI = 100 [F'_i + D'_i + A'_i] / 3.$

The species richness per sampled area and the Shannon's diversity index (*H'* [Shannon & Weaver 1949]) were calculated to assess tree diversity of stands. The following equation was used to calculate the total sampled area S_t:

$$S_t = (MCD)^2 * T;$$

Where, *MCD* is the mean distance from the tree to central point corrected for tree radius, and *T* is the total number of sampled trees (Cottam & Curtis 1956).

To characterize tree demography six size classes for DBH were distinguished as follows:

Class 1: 2.5 - 2.9 cm
Class 2: 3.0 - 5.9 cm
Class 3: 6.0 - 9.9 cm
Class 4: 10.0 - 19.9 cm
Class 5: 20.0 - 49.9 cm
Class 6: ≥ 50.0 cm

For tree height, on each plot, six large trees and ten small trees of the most important species were selected for clinometer measurements, and the results were compared with an estimate based on DBH derived from Brown *et al.* (1989), covering tropical moist forest in various countries. The equation used was :

$$H = \exp \{1.0710 + 0.5677 \ln (D)\}$$

Where, H is the height in metres and D the DBH in centimeters.

These estimates were found to agree satisfactorily with the actual measurements, subject to an error of 0.0 ± 0.9 (mean ± S. E.) m, so the estimated heights were used to calculate biomass, using the actual measurements of DBH.

Stem density for each DBH size class was expressed in stems ha^{-1}. Tree height and the total aboveground biomass (TAGB) were estimated using non-linear regressions for tropical moist forests (Brown *et al.* 1989). Height (H) of each tree was estimated from its DBH (D, in cm) using the following equation: $H = \exp \{1.0710 + 0.5677 \ln (D)\}$.

The weighted average wood density was determined directly from wood samples obtained from randomly chosen tree populations at El Tallonal. Ten wood cores were obtained from the most common species at each study site. Cores were cut using a borer 2.5 cm in diameter, to a depth of 15 cm, oven-dried at 105 ºC, and weighed. Literature data were used for those species that had not been obtained directly from El Tallonal (Francis 1995, 2000; Wittmann *et al.* 2008). Further, the IVI was used to weight the wood density in each stand.

Biomass was estimated using the equation: $TAGB = \exp \{-2.409 + 0.9522 \ln (D^2 H W)\}$ from Brown *et al.* 1989; this equation was applied to each tree using the DBH (D), estimated height (H), and weighted average wood density (W), to obtain the TAGB in kg tree^{-1}. The average total aboveground biomass was expressed in mega grams (Mg), and multiplied by the total tree density (for large, small and all trees) to arrive at a biomass per unit area (Mg ha^{-1}). Palms were not considered in the biomass calculations because available biomass equations for palms are for species other than that present at El Tallonal (*Roystonea borinquena*). Moreover, palms were not common at El Tallonal (IVI of 8 percent).

A t-test was used to test the soil bulk density variation between depths. Analysis of variance (ANOVA) and Tukey test were used to assess the soil differences among positions (along the transects). The mean DBH (cm) in each diameter class also were compared using ANOVA and Tukey test. All statistical analyses were done using JMP statistical program, 8.0.1., at a *P*-value ≤ 0.05.

Results

Species composition and dominance

A total of 27 tree species belonging to 26 genera and 20 families (Appendix Table 1) were identified from Tallonal 1 and Tallonal 2, of which 21 were native species and 6 introduced, considered naturalized (results for all trees with DBH ≥ 2.5 cm in Tallonal 1 and Tallonal 2 are presented in Table 1). The IVI for *C. elastica,* the commonest species, was 37 % (Table 1). The commonest native species was *Guarea guidonia* with an IVI of 14 %, followed by *Cecropia schreberian a*with 9 % (Table 1). The IVI of *C. elastica* was 33 % and 42 % in Tallonal 1 and Tallonal 2 respectively (Tables and 2). However, among smaller trees the IVI of *C. elastica* was similar for Tallonal 1 and Tallonal 2 (41 % and 42 % respectively; Appendix Table 1).

The dominance of *C. elastica* among both larger and smaller trees was higher than 30 percent. For all native trees combined. the IVI was 58 %, and for all naturalized species combined was 41 %. For larger trees (DBH ≥10 cm), these figures were 54 % and 46 % respectively (Table 2). On the other hand, for, smaller trees (DBH 2.5 - 9.9 cm) the combined importance values were 46 % for native species and 54 % naturalized species.

Tree richness and diversity

Combining the two plots, of the 27 species recorded, 10 were in both size categories, 5 occurred as larger trees only, 12 as smaller trees only. The species richness per sampled area had a positive linear relationship between 0.00 and 0.31 ha ($y = 1.17 + 80.3 x$, $r^2 = 0.93$). Moreover, the Shan-non's diversity *index* (*H'*) was 0.63.

Vegetation structure

At El Tallonal, the mean density of trees (> 2.5 cm DBH) was 1039 trees ha^{-1}, and the mean basal area was 42 m^2 ha^{-1}, (Table 1). *Castilla elastica* was reported at 38 out of 40 sample points, with a density of 700 trees ha^{-1}, and a basal area of 30 m^2 ha^{-1}.

The densest size class was the second (≥ 3 < 6 cm), with 390 stems ha^{-1} (Fig. 2.a). The mean DBH values differed between the size classes (f = 433, df = 5, $P < 0.0001$; Tukey test, q = 2.8, $P < 0.02$), except for classes 1 and 2 (Fig. 2.a). Introduced naturalized species constituted the majority of all stems measured in all DBH size class (Fig. 2b), ranging from 63 to 87 percent of stems.

Stand weighted wood density was 0.37 g cm^{-3}. in Tallonal 1 and 0.29 g cm^{-3} in Tallonal 2, giving an average of 0.33 g cm^{-3}. Large treess had a total aboveground biomass of 214 Mg ha^{-1} small trees 2 Mg ha^{-1} and 216 Mg ha^{-1} in total. (Table 3)

Soil bulk density

The average soil bulk density at El Tallonal was 0.5 ± 0.05 and 0.7 ± 0.06 g cm^{-3}, for the 0 to 15 and the 16 to 30 cm depths, respectively. The two depths differed in bulk density at $P < 0.05$ (t = 2.2, df = 10, $P = 0.04$). However, data did not differ between plots, or among spatial positions.

Discussion

Species composition and dominance

The species assemblage at El Tallonal (see Appendix Table 1, and Table 1) consists of a mixture of native and introduced naturalized trees. The tree community was comparable to other secondary forests in the karst region of Puerto Rico (Aukema *et al.* 2007; Marcano Vega *et al.* 2002). The species composition was also similar to that of novel foressts with *Spathodea campanulata* (Abe-lleira Martínez *et al.* 2010). All these places show the presence of remnants of commonly cultivated species, such as *Coffea arabica* and *Syzygium jambos*. Naturalized species such as *Spathodea campanulata* also often occur at these sites. Native species like *Cecropia schreberiana* and *Guarea guidonia* are typical of the region, and frequent found in secondary stands. However, the relative abundance

Table 1. Tree species composition, frequency (number), density (trees ha^{-1}), basal area (m^2 ha^{-1}), and Importance Value Index (IVI, %) for all trees with ≥ 2.5 cm DBH at Tallonal 1 (n = 160), Tallonal 2 (n = 160), and the average (n = 320).

Species	Tallonal 1				Tallonal 2				Mean			
	Frequency	Density	Basal area	IVI	Frequency	Density	Basal area	IVI	Frequency	Density	Basal area	IVI
Castilla elastica	18	723.08	28.92	33.7	20	661.1	34.294	42.2	38	700.6	30.8	37.1
Guarea guidonia	14	261.54	19.76	22.5	6	33.3	0.180	5.4	18	131.6	7.870	14.2
Cecropia schreberiana					3	16.7	1.647	12.6	3	9.9	0.975	9.0
Roystonea borinquena	1	7.69	0.82	11.5	8	55.6	2.795	12.1	9	29.6	1.640	8.0
Cordia sulcata					1	5.6	0.211	4.7	1	3.3	0.125	3.4
Spondias mombin					1	5.6	0.166	3.9	1	3.3	0.098	2.8
Chrysophyllum argenteum	6	53.85	0.15	5.1					6	23.0	0.066	2.7
Casearia guianensis	4	38.46	0.19	3.8					5	16.4	0.083	2.4
Citrus reticulata	1	7.69	0.16	2.8					1	3.3	0.066	2.0
Cinnamomum elongatum	2	15.38	0.17	2.7	1	5.6	0.014	1.1	3	9.9	0.082	1.9
Inga vera	1	7.69	0.08	1.8	2	11.1	0.076	2.3	3	9.9	0.080	1.8
Andira inermis	1	7.69	0.19	3.3	1	11.1	0.097	1.9	2	9.9	0.091	1.6
Spathodea campanulata	2	23.08	0.18	2.5	1	5.6	0.039	1	2	13.1	0.092	1.6
Zanthoxylum martinicense					1	5.6	0.078	2.3	1	3.3	0.046	1.5
Casearia sylvestris	2	15.38	0.09	2.2	1	5.6	0.007	0.9	3	9.9	0.013	1.3
Quararibea turbinata	1	7.69	0.01	0.9	2	11.1	0.013	1.7	3	9.9	0.013	1.3
Coffea arabica	1	7.69	0.01	0.9	1	5.6	0.005	0.9	2	6.6	0.008	0.9
Musa sapientum	1	7.69	0.05	1.4					1	3.3	0.020	0.9
Guapira fragans					2	11.1	0.011	1.7	2	6.6	0.007	0.9
Nectandra turbacensis					2	11.1	0.010	1.7	2	6.6	0.006	0.9
Faramea occidentalis	2	15.38	0.01	1.6					2	6.6	0.005	0.9
Cupania americana	1	7.69	0.03	1.1					1	3.3	0.012	0.7
Trichilia pallida					1	11.1	0.014	1.1	1	6.6	0.009	0.6
Syzygium jambos					1	5.6	0.008	1.0	1	3.3	0.005	0.5
Dendropanax arboreus	1	7.69	0.01	0.9					1	3.3	0.004	0.5
Myrcia splendens	1	7.69	0.05	1.4					1	3.3	0.002	0.4
Sloanea amygdalina					1	5.6	0.003	0.9	1	3.3	0.002	0.4
Total	20	1223	50.9	100.0	20	883	39.7	100.0	40	1039	42.3	100

Species are listed according to their average IVI.

Table 2. Tree species composition, frequency (number), density (trees ha^{-1}), basal area (m^2 ha^{-1}), and Importance Value Index (IVI, %) for large (≥ 10 cm DBH) and small trees (≥ 2.5 < 10 cm DBH) in Tallonal 1 and Tallonal 2 (n = 80).

Species	Tallonal 1 Frequency	Tallonal 1 Density	Tallonal 1 Basal area	Tallonal 1 IVI	Tallonal 2 Frequency	Tallonal 2 Density	Tallonal 2 Basal area	Tallonal 2 IVI
Large trees								
Castilla elastica	15	284.6	28.22	37.0	19	338.8	33.62	52.4
Guarea guidonia	14	253.8	19.83	32.7	1	5.6	0.14	3.5
Roystonea borinquena	1	7.7	0.82	10.1	7	50.0	2.76	15.2
Citrus reticulata	1	7.7	0.16	3.0				
Casearia guianensis	1	7.7	0.16	3.0				
Spathodea campanulata	1	7.7	0.15	2.9				
Cinnamomum elongatum	1	7.7	0.14	2.8				
Chrysophyllum argenteum	1	7.7	0.10	2.3				
Inga vera	1	7.7	0.08	2.2	1	5.6	0.05	2.2
Andira inermis	1	7.7	0.08	2.1	1	5.6	0.09	2.8
Casearia sylvestris	1	7.7	0.06	2.0				
Cecropia schreberiana					3	16.6	1.65	12.7
Cordia sulcata					1	5.6	0.21	4.7
Spondias mombin					1	5.6	0.17	4.0
Zanthoxylum martinicense					1	5.6	0.08	2.6
Total	20	608	49.8	100	20	439	38.8	100
Small trees								
Castilla elastica	18	438.5	0.727	41.0	20	322.22	0.68	42.56
Chrysophyllum argenteum	5	46.2	0.058	8.2				
Musa sapientum	1	7.7	0.047	8.0				
Cinnamomum elongatum	1	7.7	0.037	6.6	1	5.56	0.01	3.82
Casearia guianensis	4	30.8	0.038	6.5				
Casearia sylvestris	1	7.7	0.031	5.7	1	5.56	0.01	2.51
Cupania americana	1	7.7	0.029	5.4				
Faramea occidentalis	2	15.4	0.012	3.4				
Coffea arabica	1	7.7	0.012	3.0	1	5.56	0.01	2.19
Quararibea turbinata	1	7.7	0.012	3.0	2	11.11	0.01	3.69
Spathodea campanulata	1	15.4	0.015	2.8	1	5.56	0.04	8.44
Dendropanax arboreous	1	7.7	0.008	2.5				
Guarea guidonia	1	7.7	0.005	2.0	5	27.78	0.04	7.74
Myrcia splendens	1	7.7	0.005	2.0				
Roystonea borinquena					1	5.56	0.03	7.42
Inga vera					1	5.56	0.02	5.77
Guapira fragans					2	11.11	0.01	3.50
Nectandra turbacensis					2	11.11	0.01	3.35
Syzygium jambos					1	5.56	0.01	2.71
Andira inermis					1	5.56	0.01	2.35
Trichilia pallida					1	11.11	0.01	2.19
Sloanea amygdalina					1	5.56	0.00	1.77
Total	20	615	1.0	100.0	20	444	0.9	100.0

Species are listed according to their IVI in Tallonal 1.

of the species varied among studies reported in the references. This suggests that each location has a unique succession pathway, even with similar species composition.

In most native secondary humid karst forests, the single most common species has an IVI of 30 to 40 %, which is similar to values recorded by Lugo for novel forests of *C. elastica* (Lugo 2005: Table 3). Undisturbed forests in Sri Lanka also have IVI of 40 percent or higher for the most dominant species (Gunatilleke & Gunatilleke 1985). This suggests that novel forests of *C. elastica* are in the normal range of comparable communities with respect to species dominance.

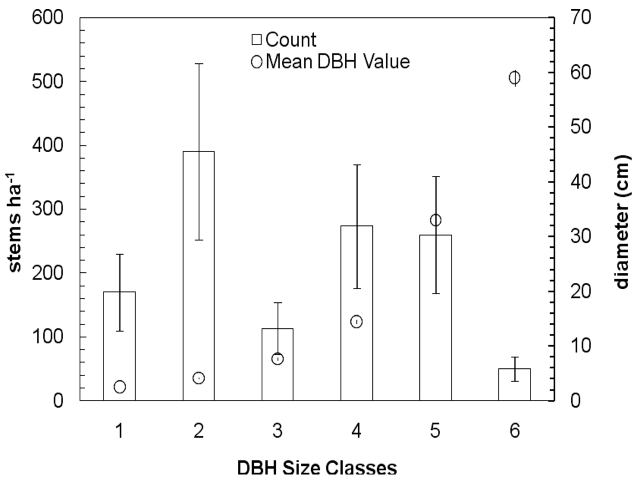

Fig. 2. (a) Stems per diameter at breast height (DBH) size class and average DBH.

Tree richness and diversity

Average species richness found in secondary forests in Puerto Rico is 39 ± 6.8 species in 0.1 hectare, for all trees with DBH more than 2.5 cm (Lugo 2005). However, El Tallonal had 27 species in 0.31 ha, which is similar to the number recorded in native secondary forests in China (23.2 ± 2.9 in 0.25 ha[Meng *et al.* 2011]). Nevertheless, the species/area curve at El Tallonal shows that 0.31 ha was not enough to report the real species richness contained in the area, because the species accumulation curve did not saturate. This suggests that there are more species in El Tallonal than have been recorded here.

According to Marcano Vega *et al.* (2002), abandoned coffee plantations in Puerto Rico had values for Shannon's index ranging from 2.0 to 3.5. However, stands showing high dominance were similar to novel forests of *C. elastica* in diversity (*H'* = 0.63), for example, forests dominated by *Spathodea campanulata* had *H'* = 0.7, by *Citharexylum fruticosum* L. (Verbenaceae) had *H'* = 0.8, and those dominated by *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) had *H'* = 0.4 (Brandeis 2006). Karst forests in Guatemala (Rey Benayas & Pope 1995) also had similar diversity to that in the present study (*H'* about 0.7).

Although the *H'* value for El Tallonal is low, it is within the range of variation for secondary forests around the tropics.

Vegetation structure

In karst sites in Puerto Rice, secondary forests following coffee plantations had a density of about 3000 trees ha^{-1} with DBH ≥ 1 cm (Rivera & Aide 1998; see Table 3). Similarly, in the Dominican Republic, a density of 3575 stems ha^{-1} was reported for abandoned cacao plantations (Rivera *et al.* 2000; see Table 3). Both these values were higher than in the novel forests of *C. elastica* reported here (1039 trees ha^{-1}). Secondary tropical forests in China also had higher tree density (2039 ± 478 [Meng *et al.* 2011]). However, the density of large trees in El Tallonal (513 trees ha^{-1}) was similar to those recorded for mature disturbed forests in French Guyana (507 trees ha$^{-1:}$ Brown *et al.* 1989).

In El Tallonal, the basal area (42 m^2 ha^{-1} for trees with DBH ≥ 2.5 cm) was similar to that in karst secondary forests in the same region (40 to 43 m^2 ha^{-1}: Chinea 1980; see Table 3). This is almost double the values reported for young secondary forests in Amazon (24.9 and 27.7 m^2 ha^{-1}: Feldpausch *et al.* 2005). Overall, basal area must be analyzed carefully because it is a structural forest feature influenced by the intensity of anthropogenic disturbances (Brandeis 2006), the age of the forest, and growth strategies of the dominant species.

The abundance of stems larger than 10 cm DBH was similar to values reported for urban forests in Puerto Rico (Lugo *et al.* 2005, Román Nunci *et al.* 2005). In Costa Rica, in a secon-dary forest, Cokeley *et al.* (unpublished) reported no trees of *Castilla elastica* between 10 and 29 cm in DBH However, trees of *C. elastica* in the same size range were very abundant at El Tallonal. Although introduced species were very abundant at El Tallonal (Fig. 2b), native species occurred in all DBH size classes, which shows that these species are regenerating below the canopy of *C. elastica* novel forests, and also have reached or maintained their space in the canopy.

The total aboveground biomass (216 Mg ha^{-1}) recorded here was higher than estimates for tropical moist secondary forests in Sri Lanka (124 Mg ha^{-1}) and disturbed forests in Malaysia (210 Mg ha^{-1}), but lower than in disturbed forests in French Guyana (277 Mg ha^{-1}: Brown *et al.* 1989, see Table 3). The moderate TAGB in *C. elastica* novel forests could be explained by the low wood density of *C. elastica*, which strongly influences the TAGB calculations of the forest because of its high dominance. Nonetheless, the values of biomass are within the range of variation of those for native secondary forests.

Soil bulk density

Soil bulk densities of El Tallonal (0.5 g cm^{-3} for

Table 3. Vegetation structure, total aboveground biomass (TAGB), species diversity (*H'*), and soil bulk density of El Tallonal and other native secondary tropical forests and novel forests. Blank spaces mean data unavailable.

Sites (diameter at breast height)	Forest type	Substrate/ soil type	Age (years)	Sampled area (ha)	IVI (%)	Basal area (m^2 ha^{-1})	TAGB (Mg ha^{-1})	*H'*	Soil bulk density (g cm^{-3})	Species richness (number)	Tree density (stems ha^{-1})	Source
El Tallonal in Puerto Rico (≥2.5 cm)	Subtropical moist	Limestone (karst)	>50	0.3	37	42	216	0.63	0.5-0.7	27	1039 (,513^L+ 526^S]	Present study
Abandoned cacao plantations in Dominican Republic (≥1 cm)	Subtropical moist	Limestone (karst)	>25	0.2	33	27				19	3575	Rivera *et al.* 2000
Abandoned coffee plantations, in Puerto Rico (≥1 cm)	Subtropical moist	Limestone (karst)	35	0.1	24	27 (9-50‡)				21	3000	Rivera & Aide 1998
Abandoned pastures in Puerto Rico (≥2.5 cm)	Subtropical moist	Limestone (karst)	35-40			15-45	200 - 300			18	2500 - 10000	Aide *et al.* 2000
Abandoned shade coffee plantations in Puerto Rico (≥1 cm)	Subtropical wet	Ultisols, inceptisols	10- >40	0.12	19-36	10-45		2.0 - 3.5†		64	4000 - 14000	Marcano Vega *et al.* 2002
Disturbed forests in Malaysia[a] (≥15 cm) and French Guyana[b] (≥10 cm)	Tropical moist			0.5^a;0.1^b		$15\text{-}18^a$; 28^b	156 - 210^a; 277^b			161^b	$176\text{-}177^a$; 507^b	Complied in Brown *et al.* 1989
Secondary forest in *Sabana*, Puerto Rico (≥4 cm)	Subtropical wet	clayey	15-30	0.2	15	28^L	109		0.54-0.6	24	1234^L	Lugo 1992
Secondary forest in El Verde, Puerto Rico (≥4 cm)	Subtropical wet	clayey	>50	0.2	15	33^L	80		0.57-0.91	37	1593^L	Lugo 1992
Secondary forests in Puerto Rico (≥2.5 cm)	Subtropical moist	karst				14-43				15 - 24		Chinea 1980

Contd...

Table 3. Continued.

Sites (diameter at breast height)	Forest type	Substrate/ soil type	Age (years)	Sampled area (ha)	IVI (%)	Basal area ($m2\ ha^{-1}$)	TAGB ($Mg\ ha^{-1}$)	H'	Soil bulk density ($g\ cm^{-3}$)	Species richness (number)	Tree density (stems ha^{-1})	Source
Secondary forests in northern Puerto Rico (≥2.5 cm)	Subtropical moist	Limestone (karst)		4.1	65 - 97[L]	27 ± 4	169 ± 31	0.9		152	3998 ± 672	Brandeis 2006
Secondary forests in Río Abajo, Puerto Rico (≥2.5 cm)	Subtropical moist	karst		0.1	30 - 40	22 ± 1		1.5 - 4.5		39±6.8	2753 ± 500	Complied in Lugo 2005
Spathodea campanulata novel forests in Puerto Rico (≥2.5 cm)	Subtropical moist	karst	30 - 50[c]; 24 - 38[d]	0.05[d]	64[d]	30[c]; 54[d]	130[c]			19[d]	2550 ± 706[d]	[c]Brandeis *et al.* 2009; [d]Abelleira Martínez *et al.* 2010
Tabonuco forests in Puerto Rico (≥2.5 cm)	Subtropical wet	volcanic		0.07 - 0.2		>30	86 - 272			11-42	891 - 2658	Compiled in Lugo 2005

*IVI of dominant species. L=large trees (≥10 cm of DBH); S=small trees (≥2.5< 10 cm of DBH). †= sites of 40 years old. ± S.E. a and b refer to the two El Tallonal plots; c and d refer to the respective sources. ‡=range.

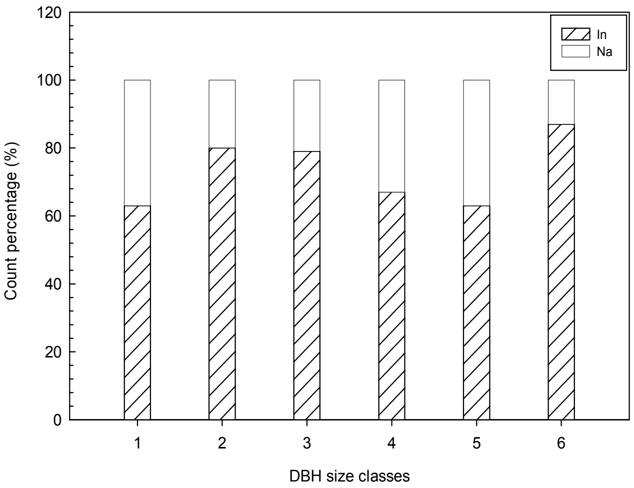

Fig. 2. (b) Percentage of stems of introduced (In) and native species (Na) for each diameter class.

the depth range 0 to 15 cm, and 0.7 g cm^{-3} for the range 15 to 30 cm) were lower than those reported for secondary wet forests in Costa Rica (0.7 g cm^{-3} for a depth of 0 to 15 cm [Reiners *et al.* 1994]), and for karstic sinkholes in Puerto Rico (0.9 g cm^{-3}, for a depth of 0 to 10 cm, and 1.0 g cm^{-3}, for 10 to 20 cm: Ruiz Jaén & Aide 2005). These results suggest that the soil below these forests has recovered its structural features, or that past agricultural activities did not cause significant damage to soil profiles. They also complement the observation that the current concentration of nutrients and other soil properties are adequate to support the high biodiversity found in those forests (Viera Martínez *et al.* 2008)

Conclusions (and recommendations)

Novel forests of *C. elastica* are one type of secondary forests emerging from human activities that have produced distinct plant communities after 40 to 50 years of regeneration. Actually, the presence of *C. elastica* has contributed to the regeneration process of the whole study area, and probably has promoted adequate micro-environmental conditions for the establishment of native species on previously deforested and farmed lands. So far, there is no evidence that *C. elastica* has replaced native species.

Contrary to the initial hypothesis, the species composition, dominance and diversity of novel forests of *C. elastica* were quite similar to those of native secondary forests, differing only in the relative abundance of species. In fact, there are many complex pathways to regeneration, and the results show that, even with similar native species composition, many forest configurations are possible depending on the site history, ecology of the species present, and forest age (Ewel 1980).

Tree diversity in these novel forests is lower than the average reported for native forests in the region, but it is not out of the range of variation. Additionally, novel forests of *C. elastica* are as diverse as some native forests in the tropics.

The low tree density, moderate basal area and TAGB, and low soil bulk density are structural features of novel forests of *C. elastica* that are also in the normal range of variation of secondary forests and other novel forests in the tropics. These results support the hypothesis of similar structural attributes between novel and native forests of similar age.

Based on the above conclusions, I do not support the eradication of *C. elastica* from the study area. This would be a costly and ineffective management attempt. Additionally, once the ecosystem in focus provides adequate micro-environmental conditions for native species, changes caused by the removal of *C. elastica* could possibly affect the other species indirectly. Nevertheless, the transplantation of native species to the understory of these forests might be helpful to accelerate the regeneration of native species in the area. Moreover, long-term studies of novel forests in the tropics are necessary to establish patterns of changes in species composition and diversity, and their consequent effects on forest structural attributes.

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Appendix Table 1. List of species found at the study area, family, local vernacular name(s), growth form, and spatial distribution at study sites.

Species	Family	Local vernacular (Spanish [English])	Growth form	Spatial distribution	
				Tallonal 1	Tallonal 2
Andira inermis (W. Wright) Kunth ex DC.[Na]	Fabaceae – Papilionoideae	moca [cabbagebark tree]	Tree	x	x
Casearia guianensis (Aubl.) Urban[Na]	Flacourtiaceae	palo blanco [Guyanese wild coffee]	tree/shrub	x	
Casearia sylvestris Sw.[Na]	Flacourtiaceae	cafeíllo [wild coffee]	tree/shrub	x	x
Castilla elastica Sessé[In]	Moraceae	caucho [Panama rubber tree]	Tree	x	x
Cecropia schreberiana Miq.[Na]	Cecropiaceae	yagrumo [pumpwood]	Tree		x
Chrysophyllum argenteum Jacques[Na]	Sapotaceae	lechecillo [bastard redwood]	Tree	x	
Cinnamomum elongatum (Vahl ex Nees) Kosterm.[Na]	Lauraceae	laurel avispillo	Tree	x	x
Citrus reticulata Blanco[In]	Rutaceae	china mandarina [tangerine]	tree/shrub	x	
Coffea arabica (L.)[In]	Rubiaceae	café [Arabian coffee]	tree/shrub	x	x
Cordia sulcata DC.[Na]	Boraginaceae	moral [mucilage manjack]	tree/shrub		x
Cupania americana L.[Na]	Sapindaceae	guará [wild ackee]	Tree	x	
Dendropanax arboreus (L.) Decne & Planch. ex Britton[Na]	Araliaceae	polio [angelica tree]	tree/shrub	x	
Faramea occidentalis (L.) A. Rich.[Na]	Rubiaceae	cafeíllo [false coffee]	tree/shrub	x	
Guapira fragans (Dum.-Cours.) Little.[Na]	Nyctagenaceae	corcho [black mampoo]	Tree		x
Guarea guidonia (L.) Sleumer[Na]	Meliaceae	guaragua [American muskwood]	tree/shrub	x	x
Inga vera Willd.[Na]	Fabaceae - Mimosoideae	guaba [river koko]	Tree	x	x
Musa sapientum L.*[In]	Musaceae	guineo [banana]	tree/shrub/forb/herb	x	
Myrcia splendens (Sw.) DC.[Na]	Myrtaceae	hoja menuda [punchberry]	tree/shrub	x	
Nectandra turbacensis (Kunth) Nees[Na]	Lauraceae	laurel amarillo	Tree		x
Quararibea turbinata (Sw.) Poir.[Na]	Bombacaceae	garrocho [swizzlestick tree]	tree/shrub	x	x
Roystonea borinquena O.F. Cook[Na]	Arecaceae	palma real [Puerto Rico Royal palm]	Tree	x	x
Sloanea amygdalina Griseb.[Na]	Elaeocarpaceae	Motillo	Tree		x
Spathodea campanulata P. Beauv.[In]	Bignoniaceae	tulipán africano [African tulip tree]	Tree	x	x
Spondias mombin L.[Na]	Anacardiaceae	jobo [yellow mombin]	Tree		x
Syzygium jambos (L.) Alston[In]	Myrtaceae	pomarrosa [rose-apple]	Tree		x
Trichilia pallida Sw.[Na]	Meliaceae	gaeta [gaita]	tree/shrub		x
Zanthoxylum martinicense (Lam.) DC.[Na]	Rutaceae	espino rubial [white pricklyash]	Tree		x

In = Introduced naturalized; Na = native species. Source: Plants Home USDA database and Little *et al.* 2001.
* = Synonym of *Musa* × *paradisiaca* L. 9 pro sp.
[acuminata × balbisiana]