Seed dispersal turns an experimental plantation on degraded land into a novel forest in urban northern Puerto Rico

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ABSTRACT

Planting tree species with desirable traits may catalyze forest regeneration in increasingly common degraded lands by restoring soil properties and attracting seed dispersers. We sampled forest regeneration in an experimental plantation of *Albizia lebbek*, an introduced N-fixing species, on a degraded pasture in northern Puerto Rico, 27 years after its establishment. We hypothesized that the abundance of animal-dispersed tree species within this unmanaged plantation would be (1) greater than in adjacent pastures; (2) higher at distances closer to secondary forest; and (3) increased over the 20 years since floristic surveys were last conducted in the site. We sampled forest structure and tree species composition, and compared the abundance of animal-dispersed tree species on plots located within the adjacent pasture and the *A. lebbek* plantation, within the plantation in plots distanced at 10, 35, and 60 m from secondary forest, and within the plantation at 7 vs. 27 years after plantation establishment. We found higher abundance of animal-dispersed tree species in the *A. lebbek* plantation than in the pasture. Distance from secondary forest had no effect on the abundance of animal-dispersed species. The abundance of animal-dispersed species increased by 14% between 7 and 27 years after plantation establishment. In all, these results indicate that *A. lebbek* trees facilitated the establishment of native animal-dispersed species by shading out tall grasses and acting as perches for animals throughout the plantation. We found that *A. lebbek* lost its dominance in the site to another introduced N-fixing species, *Leucaena leucocephala*, possibly due to unfavorable traits such as susceptibility to pathogens. Our findings document a transition from an experimental plantation to a novel urban forest that harbors an array of native tree species, largely due to the dispersal of seeds by animals. A noteworthy example is the presence of *Guaiacum officinale*, an animal-dispersed and endangered tree species native to the dry forests of southern Puerto Rico. Our results highlight how monocultures of introduced tree species with desirable traits can catalyze the regeneration of native tree species in chronically degraded lands.

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1. Introduction

The reforestation of degraded post-agricultural lands can improve landscape attributes that ensure species persistence, functional diversity, and ecological resilience (Lugo and Helmer, 2004; Chazdon, 2008). Although unassisted natural forest regeneration may be viable for ecological restoration in some cases, this may not be possible when chronic (i.e., continued and recurring) land use and disturbances, such as grazing and fire, result in the dominance of tall grasses, soil compaction, decreased soil fertility, and loss of rootstocks and seed banks (Holl et al., 2000; Zimmerman et al., 2000; Chinea, 2002; Lamb et al., 2005). Under such conditions, jump-starting or catalyzing forest regeneration by tree planting may be necessary (Parrotta, 1993; Parrotta et al., 1997). Planting monocultures of tree species that can cope with such degraded environments has been suggested as a cost-effective and efficient means to reach restoration goals by shading out tall grasses, improving soil structure and fertility, and acting as perches for seed dispersal agents in chronically degraded lands (Lugo, 1997; Parrotta et al., 1997; Wunderle, 1997).

In northern Puerto Rico, vast areas of coastal alluvial flats were deforested and used chiefly for sugar cane plantations between the 16th and 20th centuries (Picó, 1937, 1988; Wadsworth, 1950). Many of these lands where subsequently converted to grazing

lands, aided by the introduction of tall grasses that were more productive for livestock fodder production. A reforestation project undertaken by Parrotta (1987) in 1984 on a site that was abandoned after intensive sugarcane cultivation and grazing was used to assess whether monocultures of an introduced and fast growing N-fixing tree, *Albizia lebbek*, were able to catalyze native forest tree regeneration. After seven years, in 1991, this experimental plantation was being colonized by an array of introduced and native tree species (Parrotta, 1993). In this study, we returned to this *A. lebbek* plantation 27 years after its establishment and sampled forest structure, tree species composition, and the abundance of animal-dispersed and native tree species present at the site. Our aim was to assess the success of the planting of introduced *A. lebbek* in restoring forest structure and native tree species on chronically degraded post-agricultural lands that are becoming increasingly common due to agricultural intensification, land degradation and abandonment.

Dominance of tall grasses and soil compaction brought about by grazing often act to prevent tree species establishment and arrest succession (Zahawi and Augspurger, 1999; Holl et al., 2000). The distance to seed sources also limit the seed rain that gets dispersed to such sites and therefore the array of tree species that can get successfully established (Holl, 1999; Zimmerman et al., 2000). Planting monocultures of trees with desirable traits, such as fast growth and the capacity to cope with nutrient-depleted and compacted soils, may overcome these barriers to forest regeneration (Lugo, 1997; Parrotta et al., 1997; Wunderle, 1997; Lamb et al., 2005; Brockerhoff et al., 2008). We expected that the *A. lebbek* experimental plantation would have developed significant forest structure, estimated by tree density and basal area, compared to adjacent unplanted and unmanaged pastures. More specifically, we expected that the abundance of animal-dispersed tree species would be higher in the *A. lebbek* plantation than in adjacent pastures due to planted trees acting as perches for animal seed dispersers (McClanahan and Wolfe, 1993; Wunderle, 1997). Parrotta (1993) showed that, after seven years, juvenile tree species establishment in these plantations was initially influenced by the density of *A. lebbek* plantings, which affected understory light conditions (and therefore the relative dominance of competing grasses), nutrient and water availability, and by the distance to nearby secondary forest, which affected the rate of seed dispersal to the site. As the footprint of *A. lebbek* planting density treatments appeared to be largely absent at the time of our study, we hypothesized that juvenile tree density and abundance of animal-dispersed species within the plantation would be mostly related to distance from nearby secondary forest that could act as a seed source. Seven years after the initial planting, Parrotta (1993) found that most of the juvenile tree species regenerating in the *A. lebbek* understory regenerated from seeds dispersed into the site by animals, specifically birds and bats. Thus, we also expected that juvenile tree density and abundance of animal-dispersed species at the site would be higher at the time of our study, 20 years after Parrotta (1993) conducted the last floristic surveys in the *A. lebbek* plantation. In brief, we hypothesized that the abundance of animal-dispersed tree species within this unmanaged plantation would be: (1) greater than in adjacent pastures; (2) greater at distances closer to secondary forest; and (3) increased over the 20 years since floristic surveys were last conducted in the site.

2. Methods

2.1. Study site

The *A. lebbek* experimental plantation was established in 1984 within a University of Puerto Rico (UPR) property in the Toa Baja municipality in northern Puerto Rico (18°26′52″N and 66°09′53″W, 3 m asl; Fig. 1; Parrotta, 1987). The site is now part of the Toa Baja Experimental Farm managed by the Institute for Tropical Ecosystem Studies of UPR, Rio Piedras. The climate is subtropical moist, with a mean annual rainfall of 1567 mm, and average daily temperature ranges from 24 to 29 °C (Ewel and Whitmore, 1973; Parrotta, 1992; NOAA, 2002). The soils are well-drained, moderately alkaline, calcareous sands of recent marine origin with low organic matter and nutrient contents (Parrotta, 1987). The Bayamón River is about 150 m to the east and the Atlantic Ocean is about 250 m to the north of the site. The *A. lebbek* plantation site covers nearly 1 ha, was used for cultivation and grazing, and was affected by sand extraction, leveling, and small fires (Fig. 1; Parrotta, 1987). The entire UPR property covers 4 ha and other experimental plantings of *Acacia auriculiformis*, *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* lie north of the *A. lebbek* plantation site (Fig. 1; Parrotta, 1993, 1995). Secondary forest borders the site to the southeast, roads and urban development border the west, and pastures border the east of the site. No experimental plantings were conducted in this unmanaged adjacent pasture, which was dominated by two grass species –*Megathyrsus maximus* and *Tricholaena repens* – at the time of the *A. lebbek* plantation establishment in 1984. Ever since their establishment, these plantations have been for the most part unmanaged, allowing for natural regeneration to occur. A notable exception was the planting of *L. leucocephala* seedlings in two small areas (⩽10 m^2) within the *A. lebbek* plantation site. With the exception of a few tree-fall gaps, the unmanaged plantation site is now covered by closed canopy forest.

2.2. Field sampling

During 2010–2011, we identified all trees ⩾5 cm in diameter at breast height (DBH) in three parallel 145 × 10 m plots running across the area planted in 1984 with *A. lebbek* (Fig. 1; tree species nomenclature follows Liogier and Martorel, 2000). These parallel plots were spaced 15 m from each other at a distance of 10, 35, and 60 m from the secondary forest located to the southeast of the *A. lebbek* plantation (Fig. 1; secondary forest described in Parrotta, 1993). We conducted the same survey in three 30 × 10 m control plots placed in the same orientation on the unplanted adjacent pasture. These plots were smaller due to the smaller area of the pasture site. Within each of the 0.145-ha plots in the *A. lebbek* plantation, we identified all juvenile trees <5 cm DBH in three randomly placed 10 × 1 m subplots, for a total of nine 10 m^2 subplots. Juvenile tree sampling was not conducted on the adjacent pasture plots due to the high density and dominance of tall grasses (i.e., *Megathyrsus maximus*), which made it evident that juvenile trees would be extremely scarce, if at all present, and also made it unpractical to conduct such sampling as removal of grasses would have been required. An initial visual inspection of the unmanaged pasture found no juvenile tree regeneration beneath the dense grass cover.

2.3. Data analysis

We estimated tree species importance values for each 0.145-ha plot based on relative tree density and basal area for trees ⩾5 cm DBH (IV$_{>5}$ = [relative density + relative basal area]/2 × 100), and based on relative tree density and frequency across the three 0.03-ha subplots for juvenile trees (IV$_{<5}$ = [relative density + relative frequency]/2 × 100). We also estimated site-level species importance values for trees ⩾5 cm DBH and for juvenile trees as the mean importance value per species across the three 0.145-ha plots. We classified each species as native to Puerto Rico or introduced from elsewhere (including naturalized non-natives), and
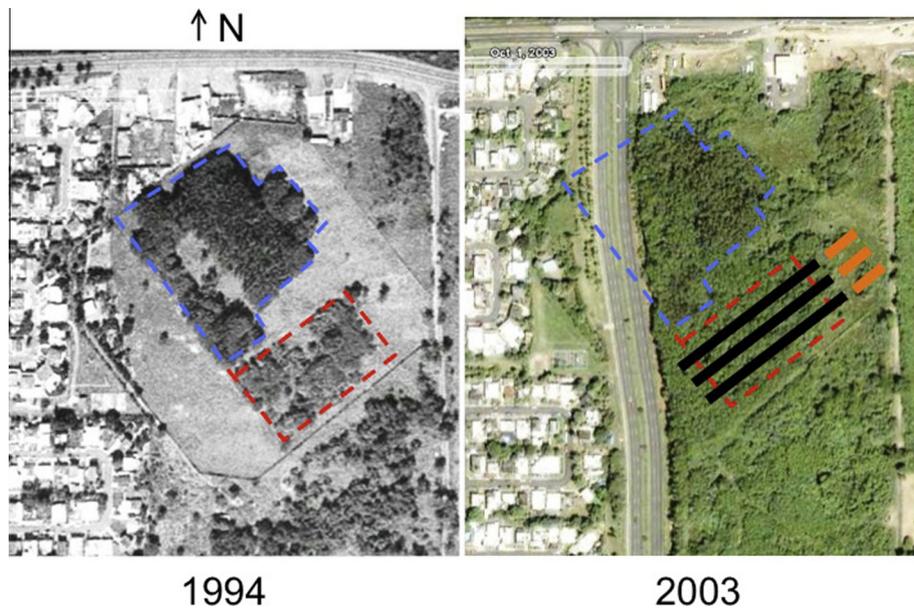
Fig. 1. Aerial photographs of the study site in 1994 and 2003 showing the original area of the *Albizia lebbek* plantation (dashed red line), the plantations of other species (dashed blue line), and the location of plots sampled for tree structure and species composition on the *A. lebbek* experimental plantation site (black bars atop 2003 photo) and on the adjacent pasture (orange bars) in relation to the adjacent secondary forest to the southeast of the *A. lebbek* plantation site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determined seed dispersal syndrome based on fruit morphology (Van der Pijl, 1969; Liogier and Martorel, 2000). We used ANOVA to compare tree density, basal area, and relative abundance (percentage of the total number of species found) and pooled importance value of animal-dispersed and native tree species ⩾5 cm DBH between plots on the *A. lebbek* plantation site vs. on the adjacent pasture. We also used ANOVA to test for differences in juvenile tree density, species richness, and relative abundance and density of animal-dispersed and native species between subplots grouped by distance from secondary forest. The Shapiro-Wilks test was used to assess data normality and the *F*-max test for homogeneity of variances. Non-parametric ANOVA was used when normality requirements were not achieved. We used non-metric multi-dimensional scaling (NMS) and Pearson correlations to evaluate the effect of distance from secondary forest on tree species composition using species importance values per 0.145-ha plot for trees ⩾5 cm DBH and for juvenile trees. We performed all statistics on Infostat software (Di Rienzo et al., 2003) except for NMS, which was conducted on PC-Ord software (McCune and Mefford, 1999).

3. Results

Density and basal area of trees ⩾5 cm DBH was significantly higher on the *A. lebbek* plantation than on the adjacent pasture (*F*[1, 4] = 51.97, *P* = 0.002; *F*[1, 4] = 32.20, *P* = 0.004; respectively; Table 1). We found 18 species of trees ⩾5 cm DBH in the *A. lebbek* plantation and three in the adjacent pasture (total area sampled was 0.435 and 0.09 ha, respectively; Table 2). Of all identified tree species ⩾5 cm DBH, 67% were both animal-dispersed and native (Table 2). The relative abundance and importance value of animal-dispersed tree species ⩾5 cm DBH in the *A. lebbek* plantation and adjacent pasture were not significantly different (*H*[1, 4] = 3.86, *P* = 0.1; and *H*[1, 4] = 1.19, *P* = 0.3; respectively; Table 1). Only one out of three species found in the pasture was animal-dispersed (Table 2). We found no native tree species in the adjacent pasture and were thus unable to statistically compare the abundance and importance value of native tree species between these

Table 1
Tree density, basal area, and relative abundance and importance value of animal-dispersed and native tree species ⩾5 cm diameter at breast height found in three 0.145-ha plots located in the 27-year-old *Albizia lebbek* plantation and three 0.03-ha subplots located in the adjacent pasture.

	Albizia lebbek plantation	Adjacent pasture
Tree density (trees/ha)	**1241** (*118*)	**222** (*78*)
Basal area (m²/ha)	**17.6** (*1.0*)	**4.3** (*2.0*)
Animal-dispersed species (% of species found)	70.3 (*1.8*)	11.1 (*11.1*)
Pooled importance value of animal-dispersed species (%)	35.1 (*8.9*)	14.2 (*14.2*)
Native species (% of species found)	62.0 (*1.8*)	0.0 (*0.0*)
Pooled importance value[a] of native species (%)	27.1 (*8.3*)	0.0 (*0.0*)

Notes: Numbers in parenthesis and italics are standard errors. Mean values in bold are significantly different at *P* < 0.05.

[a] $IV_{>5}$ = [relative density + relative basal area]/2 × 100.

treatments. The dominant tree species ⩾5 cm DBH in the *A. lebbek* plantation was *L. leucocephala* followed by *Cordia laevigata*, *Citharexylum spinosum*, and *A. lebbek* (Table 2).

Juvenile tree density was significantly higher in the *A. lebbek* plantation plot located 35 m from the adjacent secondary forest than in the more distant (60 m) plot (Table 3; *F*[2, 6] = 5.44, *P* = 0.04). However, juvenile tree species richness, the relative abundance and density of animal-dispersed juvenile tree species, and the relative abundance and density of native juvenile tree species were not different between subplots located within the *A. lebbek* plantation at different distances from the secondary forest (*H*[2, 6] = 0.16, *P* = 0.9; *H*[2, 6] = 0.02, *P* = 1; *F*[2, 6] = 0.45, *P* = 0.7; *H*[2, 6] = 0.36, *P* = 0.9; and *F*[2, 6] = 0.09, *P* = 0.9; respectively; Table 3). We found 22 juvenile tree species on the *A. lebbek* plantation site of which 90.5% are animal-dispersed and 76.2% are native (Table 4). The dominant juvenile tree species in the *A. lebbek* plantation was also *L. leucocephala*, followed by *A. lebbek*, *Eugenia biflora*, *Bursera simarouba*, and *C. laevigata*. These were also the only juvenile tree species with importance values >5% across the site (Table 4). We observed that the dominant juvenile tree species on the *A. lebbek* plantation, *L. leucocephala*, was relatively less

Table 2

Importance value (%) in two sites, seed dispersal mode, and origin of tree species ⩾5 cm diameter at breast height found in three 0.145-ha plots in the 27-year-old *Albizia lebbek* plantation and three 0.03-ha plots in the adjacent pasture.

Species	*Albizia lebbek* plantation	Pasture control	Dispersal	Origin
Leucaena leucocephala	56.0	19.2	W	I
Citharexylum spinosum	12.3		A	N
Albizia lebbek	7.7	66.6	W	I
Cordia laevigata	7.3		A	N
Terminalia catappa	5.2		A	I
Bursera simaruba	3.7		A	N
Schinus terbinthifolius	3.3	14.2	A	I
Rauvolfia nitida	2.0		A	N
Eugenia biflora	0.6		A	N
Tabebuia heterophylla	0.4		W	N
Zanthoxylum martinicense	0.3		A	N
Acacia falciformis	0.3		W	I
Lonchocarpus pentaphyllus	0.2		W	N
Unknown 1	0.1			
Calophyllum calaba	0.1		A	N
Andira inermis	0.1		A	N
Unknown 2	0.1			
Unknown 3	0.1			
Total	100.0	100.0		

Notes: A: animal-dispersed, W: water- or wind-dispersed; I: introduced, N: native. Empty cells in 'pasture control' columns correspond to absence of the species. Empty cells in the 'dispersal' and 'origin' columns correspond to unknown unidentified species. Site-level species importance values were estimated as the mean importance value (IV$_{>5}$ = [relative density + relative basal area]/2 × 100) for each species across the three 0.145-ha plots.

Table 3

Juvenile tree density, species richness, and relative abundance and density of animal-dispersed and native tree species in three 10 m^2 plots located within the 27-year-old *Albizia lebbek* plantation at different distances from adjacent secondary forest.

	Albizia lebbek plantation plot distance to secondary forest		
	10 m	35 m	60 m
Tree density (trees/m^2)	**20.0**[a,b] (*2.7*)	**23.1**[a] (*1.5*)	**14.7**[b] (*1.7*)
Species richness	8 (*1.2*)	9 (*2.3*)	8 (*1.0*)
Animal-dispersed species (% of species found)	80.4 (*1.6*)	78.2 (*5.8*)	79.6 (*1.8*)
Density of animal-dispersed species (% of individuals found)	10.6 (*1.0*)	14.7 (*6.6*)	15.8 (*0.5*)
Native species (% of species found)	71.1 (*4.4*)	69.0 (*7.6*)	72.2 (*8.5*)
Density of native species (% of individuals found)	9.9 (*1.4*)	13.3 (*5.3*)	14.0 (*1.5*)

Notes: Numbers in parenthesis and italics are standard errors. Bold means denoted with different letters are significantly different at $P < 0.05$.

dominant on the mid-point plot located between the adjacent secondary forest and experimental plantations (35 m; Table 5).

The composition of trees ⩾5 cm DBH within the experimental *A. lebbek* plantation was similar across plots and very dissimilar to that of the adjacent pasture (Fig. 2). Likewise, tree species composition within the *A. lebbek* plantation displayed higher similarity within tree size class than within plot distance from nearby secondary forest (Fig. 3). Pearson correlation coefficients of NMS scores of species composition of trees ⩾5 cm DBH and juvenile trees to distance from secondary forest were not significant (R^2 = 0.053 and 0.052 for Figs. 2 and 3, respectively; $P > 0.1$). The juvenile tree species composition of the *A. lebbek* plantation plot closest to the secondary forest was the most similar to that of trees ⩾5 cm DBH found throughout the *A. lebbek* plantation (Fig. 3).

We found 22 juvenile tree species, the same number that Parrotta (1993) found seven years after the establishment of the *A. lebbek* plantation (Table 4). However, the area sampled for juvenile tree species in this study was lower than that sampled by Parrotta (1993) in 1991 (90 vs. 192 m^2, respectively). Nevertheless, juvenile tree density increased by an order of magnitude, and the abundance and density of animal-dispersed species increased by 15% and 40%, respectively, between 1991 and 2011 (Table 6). The increase in juvenile tree density was largely due to *L. leucocephala* (Tables 4 and 6). The abundance and density of native juvenile tree species also increased between 1991 and 2011 although to a lesser degree (Table 6). Out of the 22 juvenile

tree species we found in this study, only ten were recorded by Parrotta (1993) in 1991 (Table 4). Unknown species (five in Parrotta's (1993) dataset; one in ours) preclude a more accurate description of species turnover, yet it is possible to make some general observations. Except for *L. leucocephala*, animals disperse all of the additional species we identified in 2011 that were not present in 1991 (Table 4). Parrotta (1993) identified seven juvenile tree species that we did not find in 2011 (Table 4). Out of those seven species, *Albizia procera*, *Psidium guajava*, and *Spathodea campanulata* are light-demanding tree species that were very likely shaded out from the *A. lebbek* plantation as canopy closure occurred. Of those seven species, three are dispersed by wind and we only recorded one of them, native *Lonchocarpus pentaphyllus*, occurring only as a tree ⩾5 cm DBH on the *A. lebbek* plantation in 2011 (Table 2). Within the 20 year time span between sampling dates, two introduced species appeared and three disappeared from the juvenile tree species composition of the *A. lebbek* plantation (Tables 4 and 6).

4. Discussion

The difference in tree density, basal area, and species composition between the experimental *A. lebbek* plantation and the adjacent pasture is striking yet expected (Table 1; Fig. 2). It is evident that following the initial planting and growth of the *A. lebbek*

Table 4

Density, frequency, importance value, origin, and dispersal mode of juvenile tree species found in the *Albizia lebbek* plantation in 2011 from this study, and density of juvenile trees found in the same plantation by Parrotta (1993) in 1991.

Species	Density (trees/m²)	Density (%)	Frequency (%)	Importance value (%)	Density (trees/m²) in 1991	Density (%) in 1991	Dispersal	Origin
Leucaena leucocephala	14.77	76.9	12.0	44.5			W	I
Albizia lebbek	1.76	9.2	8.0	8.6	0.72	25.7	W	I
Eugenia biflora	0.76	4.0	10.7	7.4			A	N
Bursera simarouba	0.59	3.1	10.6	6.8	0.04	1.3	A	N
Cordia laevigata	0.48	2.5	9.4	5.9			A	N
Citharexylum spinossum	0.13	0.7	8.1	4.4	0.97	34.5	A	N
Terminalia catappa	0.17	0.9	5.3	3.1	0.01	0.2	A	I
Roystonea borinquena	0.05	0.2	5.3	2.8	0.06	2.0	A	N
Calophyllum calaba	0.14	0.7	4.1	2.4	0.05	1.7	A	N
Casearia guianensis	0.05	0.3	4.0	2.1			A	N
Eugenia monticola	0.10	0.5	2.7	1.6	0.10	3.5	A	N
Ixora coccinea	0.07	0.3	2.7	1.5			A	I
Schinus terbinthifolius	0.04	0.2	2.7	1.4	0.05	1.9	A	I
Rauvolfia nitida	0.02	0.1	2.7	1.4	0.16	5.7	A	N
Pimenta racemosa	0.02	0.1	2.6	1.4			A	N
Guaiacum officinale	0.01	0.1	1.3	0.7			A	N
Andira inermis	0.01	0.0	1.3	0.7	0.03	0.9	A	N
Siderolylon foetidissimum	0.01	0.0	1.3	0.7			A	N
Guarea guidonia	0.01	0.1	1.3	0.7			A	N
Coccoloba diversifolia	0.01	0.1	1.3	0.7			A	N
Zanthoxylum martiniscence	0.01	0.1	1.3	0.7			A	N
Unknown (1 species)	0.01	0.1	1.3	0.7				
Lonchocarpus pentaphyllus					0.23	8.3	W	N
Cordia polycephala					0.15	5.2	A	N
Boureria succulenta					0.12	4.1	A	N
Spathodea campanulata					0.09	3.2	W	I
Psidium guajava					0.01	0.4	A	I
Trichilia hirta					0.01	0.2	A	N
Albizia procera					0.01	0.2	W	I
Unknown (5 species)					0.04	1.3		
Total	19.20	100.0	100.0	100.0	2.82	100.0		

Notes: A: animal-dispersed, W: water- or wind-dispersed; I: introduced, N: native. Empty cells correspond to absence of the species. Empty cells in the 'dispersal' and 'origin' columns correspond to unknown unidentified species. Site-level species importance values in this study were estimated as the mean importance value (IV$_{<5}$ = [relative density + relative frequency]/2 × 100) for each species across the three 0.145-ha plots.

Table 5

Importance value (%) of *Leucaena leucocephala* amongst trees ⩾5 cm diameter at breast height (DBH) and juvenile trees on plots located within the 27-year-old *Albizia lebbek* experimental plantation at different distances from secondary forest and experimental plantation plots of *Acacia auriculiformis*, *Casuarina equisetifolia*, *Eucalyptus robusta*, and *L. leucocephala* (Parrotta, 1995).

Distance from secondary forest (m)	10	35	60
Distance from plantation plots (m)	60	35	10
Trees ⩾5 cm DBH[a]	65.1	37.5	58.8
Juvenile trees[b]	48.7	37.0	47.7

[a] IV$_{>5}$ = [relative density + relative basal area]/2 × 100.

[b] V$_{<5}$ = [relative density + relative frequency]/2 × 100.

Fig. 2. Non-metric multidimensional scaling of species importance values of trees ⩾5 cm diameter at breast height on the *Albizia lebbek* plantation and adjacent pasture plots. Triangles represent *A. lebbek* plantation plots (Al1, Al2, and Al3), and squares represent pasture plots (P1, P2, and P3). The ordination solution was one-dimensional with a final stress of 0 and a final instability of 0.00005 in 52 iterations. Species occurring in only one plot were excluded and data were arcsine square-root transformed to obtain a valid solution. Axis 1 explained 95.5% of the variation in species composition. The weight of each symbol represents the distance from secondary forests, being larger for plots furthest from secondary forests.

plantation, the driver of these differences became the replacement of *A. lebbek* by *L. leucocephala* as the dominant canopy species. We had aimed to detect differences in the abundance of animal-dispersed species between *A. lebbek* and the adjacent pasture. However, we were unable to test this with more rigorous parametric tests due to the near complete absence of animal-dispersed tree species, or any tree species for that matter, in the pasture (Tables 1 and 2). Coupled with the total absence of native species in the pasture, this is indication of the success of this *A. lebbek* experimental plantation in catalyzing native forest regeneration on this chronically degraded site. We cannot overlook that the site is now dominated by another introduced species, *L. leucocephala*, which has become naturalized and invades disturbed lands throughout lowland and dry areas in Puerto Rico (Parrotta, 2000a; Molina Colón et al., 2011). However, overall our results provide additional evidence that both *A. lebbek* and *L. leucocephala* catalyze tree species
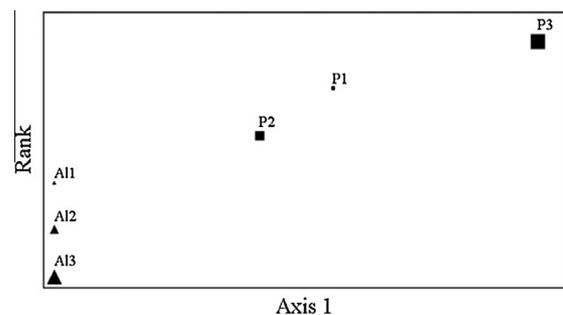
establishment by suppressing dominant grasses, attracting seed-dispersing wildlife, and creating favorable understory and soil conditions for the germination and growth of colonizing tree species (*see below*; Parrotta, 1992, 1993, 1995, 1999; Chinea, 2002; Molina Colón and Lugo, 2006; Pérez Martínez, 2007).

The finding of lower juvenile tree density in the plot furthest away from the secondary forest suggests an influence of distance to seed sources upon tree establishment (Table 3). However,
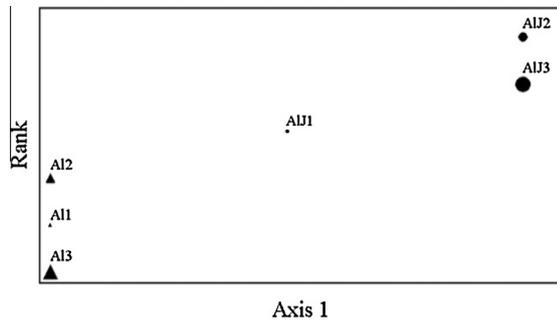
Fig. 3. Non-metric multidimensional scaling of species importance values of trees ⩾5 cm and juvenile trees <5 cm diameter at breast height (DBH) on *Albizia lebbek* plantation plots. Triangles represent trees ⩾5 cm DBH (Al1, Al2, and Al3) and circles represent juvenile trees in three plots (AlJ1, AlJ2, and AlJ3). The ordination solution was one-dimensional with a final stress of 0.00026 and a final instability of 0.00001 in 64 iterations. Species occurring in only one plot were excluded and data were arcsine square-root transformed to obtain a valid solution. Axis 1 explained 88.7% of the variation in species composition. The weight of each symbol follows Fig. 2.

contrary to our expectations, we did not find differences in the abundance of animal-dispersed juvenile tree species at different distances from the nearby secondary forest (Table 3). We identified some possible causes for the lack of a clear distance effect upon animal-dispersed species, which had been noted 20 years earlier at this site (Parrotta, 1993). First, the proximity of the *A. lebbek* plantation plots to other experimental plantations could have facilitated the establishment of wind-dispersed *L. leucocephala*, which was present in adjacent experimental plantation plots as well as within two smaller subplots within the site (Fig. 1; Table 5; Parrotta, 1995, 2000a). The higher similarity in juvenile tree species composition between plots found closest to the plantations to the north may be due to the influence of both the nearby and within site dominance of *L. leucocephala* over local seed rain and juvenile tree species establishment (Figs. 1 and 3; Tables 2 and 5). Secondly, seed dispersal may not be limited within the *A. lebbek* plantation due to the covered spatial scale. Other studies have suggested that seed dispersal is limited at distances ⩾30 m from forest edges (Holl, 1999; Zimmerman et al., 2000; Cubiña and Aide, 2001). Since the area of the *A. lebbek* plantation covers about 80 m from secondary forest to the adjacent plantations, seed dispersal to the interior of the *A. lebbek* plantation may have been limited during its initial years of establishment but not afterwards as canopy closure was occurring. In addition, even after understory grasses were suppressed by *A. lebbek*, processes such as litter decomposition and changes in soil microfauna that improved conditions for regeneration by the production of an organic topsoil layer could have taken several years to develop. Distance effects would have been diminished as the *A. lebbek* trees and other species that regenerated naturally in the site eventually grew to reproductive maturity and produced seed within the site as well.

Most of the juvenile tree species we found are dispersed by animals, mainly bats and birds, as we had expected (Tables 1–4; Parrotta, 1993; Wunderle, 1997; Carlo et al., 2003; Rodríguez Durán, 2005). Compared with the forest regeneration observed in

Table 6
Juvenile tree density and abundance of native and animal-dispersed species in the *Albizia lebbek* plantation in 1991 (Parrotta, 1993) and 2011.

Parameter	1991	2011
Tree density (trees/m²)	2.8	19.2
Animal-dispersed species (% of species found)	76.5	90.5
Density of animal-dispersed species (trees/m²)	1.7	2.7
Native species (% of species found)	64.7	76.2
Density of native species (trees/m²)	1.9	2.4

1991, seven years after the *A. lebbek* plantation's establishment, juvenile tree density and the abundance of animal-dispersed and native species increased by 10–40% between 1991 and 2011 (Table 6). This conclusion could be questioned because we could not account for the dispersal mode of some unidentified species encountered at both sampling dates (Table 4). Yet overall, our results show that planting highly degraded lands with tree species with desirable traits can accelerate native tree species establishment by providing a canopy that shades out tall grasses and that provides perches and possibly habitat for animal seed dispersers. Our results also show that the role of distance to seed sources in shaping tree species regeneration may be overshadowed by the availability of species within or near the site with particularly favorable traits for fast growth under degraded soils. This is illustrated by the overwhelming dominance of *L. leucocephala* (Table 5).

We found low importance values of *A. lebbek* amongst trees ⩾5 cm DBH and juvenile trees, which suggests that poor regeneration of this species has allowed others to grow and become dominant on the site (Tables 2 and 4). There may be several reasons for this. First, it is likely that *A. lebbek*'s shade intolerance has not allowed it to thrive as a juvenile tree at the site (Parrotta, 2000b). Second, high N-fixation rates can lead to phosphorous limitation in *Albizia* plantations, which could facilitate overgrowth by other species (García Montiel and Binkley, 1998). However, subsequent dominance in the site by another fast-growing and light-demanding N-fixer, *L. leucocephala*, suggests light and phosphorous availability may be non-limiting, at least for the latter species. On the other hand, it is very likely that *A. lebbek* trees were killed by *Fusarium* sp., a fungal pathogen that was already affecting the species five years after the plantation's establishment (Parrotta, 1990). *A. lebbek* can thrive in dry to wet climates, yet the moist climate of the site may have made it more susceptible to fungal disease compared to drier climates in Puerto Rico. In all, this illustrates that introduced tree species with favorable traits for facilitating forest regeneration, such as fast growth and N-fixation capacity, may also possess unfavorable traits, such as high susceptibility to pathogens in their novel location. This combination of favorable and unfavorable traits in *A. lebbek* may accelerate native forest regeneration by facilitating the quick turnover of the planted species.

The dominance of *L. leucocephala* at the site obscures any difference we may have observed from the initial planting density of *A. lebbek* upon tree species composition across the site, as it was observed in earlier studies (Table 5; Parrotta, 1987, 1992). We observed that most *L. leucocephala* juvenile trees (~90%) were about 20 cm tall, which is likely due to the light-demanding requirements of this species. We expect that the high density of juveniles of *L. leucocephala* (Table 4) will persist until there is a major change in the composition of the forest canopy. Natural disturbances such as hurricanes might accelerate the turnover of *L. leucocephala* (e.g., Flynn et al., 2010) or perpetuate its dominance through the stimulation of stem and root sprouting (Van Bloem et al., 2003, 2005). The many studies on tree species regeneration under *L. leucocephala* canopies in Puerto Rico have also found high density of con-specific juvenile trees along with an array of native tree species that are protected from disturbances, such as hurricanes and fire, by the forest canopy (Van Bloem et al., 2005; Molina Colón and Lugo, 2006; Pérez Martínez, 2007; Santiago García et al., 2008; Molina Colón et al., 2011). The degree of persistence of *L. leucocephala* and its co-existence with native species will necessarily be related to the frequency and intensity of natural and anthropogenic disturbances. Although native species have returned to this site, it is unlikely that species composition will return to the original conditions found before deforestation. Instead, it is likely that introduced species with traits favorable under human disturbance regimes, such as *L. leucocephala*, will persist and perpetuate the novel ecosystem conditions at the site

(Hobbs et al., 2006; Molina Colón et al., 2011; Wolfe and Van Bloem, 2012). Besides restoring the integrity of ecosystem properties and processes, these novel forests are expected to contribute to the conservation of native species in human-modified rural to urban areas such as this one, which remain understudied (Lugo, 2009, 2010; Kowarik, 2011).

The spatial connectivity and proximity between forested areas is critical for the regeneration of forest tree species in rural to urban areas worldwide (Turner et al., 1996; Norden et al., 2009). In Puerto Rico, the role of animal dispersers in facilitating the establishment of native tree species in secondary forest growth has been widely documented (Wunderle, 1997; Carlo et al., 2003; Abelleira Martínez, 2010). The proximity of the *A. lebbek* plantation site to secondary forests and to urban areas planted with animal-dispersed tree species aided the recovery of native species. We were particularly surprised to find juvenile trees of *Guaiacum officinale*, a native and endangered tree species of Caribbean and Mesoamerican dry forests (IUCN, 2011), growing in this site (Table 4). In Puerto Rico, populations of this species are naturally restricted to dry forests in the southern coast (Axelrod, 2011; UPRRP Herbarium). It is possible that natural populations existed in the northern coast in pre-Hispanic times yet this has not been documented. Although only one individual of this species was found within the plots we sampled, we observed about ten juvenile trees of this species ranging from 0.2 to 2 m in height growing across the *A. lebbek* plantation site. It is most likely that these were dispersed from trees planted in nearby urban areas since *G. officinale* is a popular ornamental shade tree and appears to grow well and produce seed when planted in the northern coast. In its native range, *G. officinale* is dispersed by birds and forest roaming mammals (Francis, 2000), and a very closely related yet less common species, *Guaiacum sanctum*, is also dispersed by birds (Wendelken and Martin, 1987). The prospect of *G. officinale* being dispersed from planted shade trees to this experimental *A. lebbek* plantation and becoming established was something we had not expected to find. We cannot be sure that these *G. officinale* juvenile trees will grow to maturity and reproduce. However, finding naturally regenerating individuals of *G. officinale* in such a site is both surprising and encouraging, and illustrates how the natural establishment of new populations that extend an endangered species' range into previously undocumented areas can be possible. In this case, the establishment and expansion of native tree species, including endangered *G. officinale*, to this novel urban forest in northern Puerto Rico was catalyzed by the planting of an introduced species with desirable traits in chronically degraded land.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.08.008. These data include Google maps of the most important areas described in this article.

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