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Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico

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Abstract

We report the effects of an invasive tree (*Syzygium jambos*, Myrtaceace) on species composition, plant diversity patterns, and forest regeneration in primary and secondary forest in the Luquillo Mountains of northeastern Puerto Rico, including the area in and around the Caribbean National Forest (CNF) and the Luquillo Long Term Ecological Research site (Luquillo LTER). Land use history was reconstructed using aerial photographs from 1936 to 1989 and study sites were categorized into four groups that corresponded to their status in 1936: unforested, young secondary, mature secondary, and primary forests. In randomly selected forest stands in each forest type, we measured the abundance of invasive and native tree species, seedling recruitment for *S. jambos* as well as soil nutrient pools and tested for the effects of land use history on *S. jambos* density and diversity. A partial Mantel test was used to control for historical and elevational differences across study sites. The results indicate that *S. jambos* density was highest in habitats classified in 1936 as unforested, young, or mature secondary forests. Compared to all other forest classes, species diversity was significantly higher in primary forests. However, there was no statistically significant difference between observed and estimated species richness across the four forest types. *S. jambos* density and species diversity were strongly negatively correlated, even after controlling for land use history and elevation. There was significantly higher *S. jambos* seedling recruitment in areas that were either unforested or had young secondary forests in 1936. The results also indicate that *S. jambos* is able to establish viable populations in habitats with different soil nutrient status. *S. jambos* has also altered vegetation composition and diversity patterns in habitats where it is the dominant tree species. After nearly 185 years since its introduction to the island, *S. jambos* is not only well established within 30 m of stream channels, its presence does not appear to be limited by topographic, soil nutrient, or elevational conditions. This study suggests that land use change and subsequent plant invasions have produced a new vegetation assemblage that has led to potentially long-term changes in community structure, species composition, and successional trajectory in regenerating secondary forests in the Luquillo Mountains.

Keywords: Secondary forest; Forest regeneration; Disturbance; Land use history; Invasive plants; Luquillo Experimental Forest (LEF); *Syzygium jambos*

1. Introduction

Invasive plant species can affect all components of an environment, from ecosystem processes (Vitousek and Walker, 1989; Dyer and Rice, 1999; Bart and Hartman, 2000; Mack et al., 2001; Ehrenfeld, 2003) to biodiversity patterns (Brown and Gurevitch, 2004) to community structure (García-Robledo and Murcia, 2005; Gratton and Denno, 2005). Generally, nonnative invasive trees colonize open and degraded habitats that are recovering from some sort of perturbation. However, invasive species that are shade-tolerant can also establish viable populations in mature tropical forests (Rejmánek, 1996; Fine, 2002). Nevertheless, the extent and degree to which nonnative invasive tree species influence vegetation structure and composition in mature tropical forests remains a point of considerable debate (Fine, 2002; Lugo, 2004). One of the fundamental questions in this debate is whether nonnative invasive trees are transient or persistent members of the plant community. If an invader's dominance is ephemeral in a secondary forest, its establishment maybe considered as an

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initial step in a series of events leading to the recovery of mature native forests (Lugo, 2004). In this case, the community assemblage will then converge on the pre-disturbance community at a rate that depends on the intensity, frequency, and time since the disturbance (Terbourgh et al., 1996; Grau et al., 1997). Alternatively, if the invaders do endure, fundamental, long lasting shifts in forest diversity patterns and community structure can result and a novel vegetation composition and assemblage may develop (*sensu* Lugo, 2004).

It has become increasingly apparent that the legacy of large-scale land uses remain imprinted on the recovered system for many decades after the perturbation event (Foster et al., 1999; Thompson et al., 2002; Chinea and Helmer, 2003). These disturbances influence subsequent soil conditions, available propagules, species composition, and community structure and diversity patterns. In recent years, with the abandonment of tracts of forest once used for agricultural purposes, large regions of secondary tropical forests have regenerated (Brown and Lugo, 1990; Aide et al., 1996, 2000; Finegan, 1996; Pascarella et al., 2000; Aragón and Morales, 2003). The initial colonization of nonnative invasive plants into regenerating secondary forests is a function of arriving propagules from source locations, such as abandoned farms, pastures, or other managed systems (Aragón and Morales, 2003). The removal of dominant native trees facilitates nonnative plant establishment in recovering landscapes (Elton, 1958). And nonnative plants that are able to respond favorable to fluctuating post-disturbance conditions will most likely establish and spread. In effect, those nonnative plants that establish during the initial phases of forest regeneration can limit native plant growth or slow the rate of change in species composition (Lichstein et al., 2004; Marcano-Vega et al., 2002).

In northeast Puerto Rico, the effects of land use history on forest regeneration and present day forest structure have been well-studied at landscape (Foster et al., 1999; Helmer et al., 2002) and community scales (Zimmerman et al., 1995; Aide et al., 1996; Thompson et al., 2002) as well as at the patch level (García-Montiel and Scatena, 1994). Despite this understanding, there is still a dearth of information about how this system responds to the establishment of nonnative plants. This study draws on detailed historical information about past land use in Puerto Rico to ask whether: (1) land use history affected the invasion of an nonnative tree, *Syzygium jambos* (Myrtaceace); (2) soil nutrient dynamics played a role in *S. jambos* establishment patterns; (3) the invasion of *S. jambos* affected species richness, plant diversity, and in turn forest regeneration and successional trajectory.

2. Methods

2.1. Study area

The study was conducted in the Luquillo Mountains of northeastern Puerto Rico (18°18′N, 65°50′W), including the area in and around the Caribbean National Forest (CNF) and the Luquillo Long Term Ecological Research site (Luquillo LTER). The Luquillo Mountains are the dominant physiographic feature of northeastern Puerto Rico and rise abruptly from a narrow coastal plain to an elevation of 1000 m over a distance of 10–20 km. Rain and runoff occur in every month but a drier period typically occurs between late January and April and a wetter season from September to December (García-Martino et al., 1996). Hurricanes are the dominant natural disturbance affecting the area and on average a hurricane will pass close enough to the island to cause severe but localized damage approximately once every 10 years and widespread damage every 50–60 years (Scatena and Larsen, 1991). Mean annual rainfall increases from 1000 mm/yr in the lowlands to nearly 5000 mm/yr at the highest elevations (García-Martino et al., 1996). Corresponding to this climatic gradient are changes in life-zone designation, forest composition and structure (Ewel and Whitmore, 1973; Lugo and Lowe, 1995).

The Luquillo Experimental Forest (LEF) is a United States Department of Agriculture Research Forest and coincident with the CNF. Although there were small European settlements in the area shortly after Columbus landed in 1494, the municipalities of the study area were incorporated between 1772 and 1840. The first large scale impacts to the immediate study area began in the early 1800s (Scatena, 1989), about the same time that *S. jambos* was most likely introduced to the island (Wadsworth, 1943). Thomlinson et al. (1996) reported that by 1936, sugar cane was the dominant land cover in the coastal plain, while upland areas in the Luquillo region supported pasture and small subsistence farms. At this time, dense forest only occupied approximately 15% of northeast Puerto Rico and was generally limited to the upper elevation within the National Forest and along riparian corridors and hedgerows (Thomlinson et al., 1996). By 1996, 66% of northeastern Puerto Rico above 100 m was forested and 13% was shrub lands (Ramos-Gonzalez, 2001). The lowlands formerly covered in sugar cane are now pasture, forest, and urban areas. Additional information on the ecology and management of the site can be found elsewhere (Odum and Pigeon, 1970; Lugo and Lowe, 1995).

2.2. Focal species

The focal species for this study is *S. jambos* (L.) Alston (rose apple). *S. jambos* is a pan-tropical invasive tree species that occurs throughout Puerto Rico. The plant is native to southeast Asia and a major invader in other island tropical forests, including the Galapagos Islands, Hawai'i, Mauritius, La Réunion, Seychelles, and Fiji (Lawesson, 1990). *S. jambos* is typically described as a riparian species that establishes along frequently inundated riverbanks and ephemeral streams (Francis, 1990; Francis and Liogier, 1991). The plant is not exclusively riparian however, as it can be dominant in old pastures, abandoned coffee plantations, and can invade closed-canopy forests (Pascarella et al., 2000).

By 1821 *S. jambos* was introduced to tropical botanical gardens throughout the West Indies, including Puerto Rico (Descourtilz, 1829, as seen in Wadsworth, 1943). In Puerto

Rico, it was originally planted for fuelwood and posts, but its sweet, fleshy fruits made it a horticultural favorite (Wadsworth, 1943). There are several possible dispersal routes for *S. jambos* fruits. Several frugivorous bat species in the Luquillo Mountains may facilitate long distance dispersal of *S. jambos* fruits (personal observation). The fruits are too large to be taken far distances by bird species currently inhabiting the Luquillo Mountains, but they may be responsible for localized dispersal directly beneath the parent tree (personal observations). *S. jambos* fruits float and are often seen along floodplains down to the estuary after storms, and so rivers as well as ephemeral streams may be another means for long distance dispersal (personal observation).

2.3. Site classification

The land use history classification of the Luquillo Mountains used in this study is based on Foster et al. (1999), who analyzed forest cover and forest type from 1936 to 1989 based on aerial photos. We relied upon these historical classification maps to reconstruct the 1936 extent, cover, and forest type for our study plots. Three different classes of forests were classified: (1) unforested in 1936; (2) secondary forests in 1936; (3) primary forests in 1936. The maps further classified 1936 canopy cover into three categories: <10% cover; 20–50% cover; 50–80% cover. Using these classifications, we categorized study sites into the following four groups: <10% cover, unforested; 20–50% cover, secondary; 50–80% cover, secondary; 50–80% cover, primary forests. Henceforth, these forests classifications will be referred to as unforested, young secondary, mature secondary and primary forests (Table 1). All of the secondary forests in 1936, including the mature secondary forests were presumably once cleared to at least <10% cover. In contrast, primary forests were never cleared.

2.4. Site location

Vegetation and environmental variables were measured at 11 sites. Each site had one to three 50 m × 4 m plot, for a total of 28 200 m^2 plots sampled for the study (Table 1). Sampling was conducted from January 2001 to April 2001. The 11 sites were randomly established along three of the major watersheds in the Luquillo Mountains. At each site, a 30 m transect was established perpendicular to the river and at 5, 15, and 30 m distances along the perpendicular transect leading away from the river, 50 m × 4 m (200 m^2) plots were established. Each site had one to three 200 m^2 plots that were arranged parallel to the river's edge. Placement of the 200 m^2 plots at 5, 15, and 30 m distances from the river was dependent on the geomorphology of the channels. All the study sites, with the exception of two, were located below 400 m and were therefore within the tabonuco plant association (Ewel and Whitmore, 1973).

2.5. Vegetation sampling

In each 200 m^2 plot, all woody stems >1.5-cm diameter at breast height (DBH) were measured and identified to species. We calculated the plot-level basal area using DBH. Beginning in January 2001, seedlings of *S. jambos* were tagged, measured (height and diameter), and monitored over the next 2 years. Seedlings were surveyed by randomly placing twenty 1 m^2 quadrats within the 200 m^2 plots. Individuals were classified as seedlings if they were between 1 and 50 cm in height; they were further classified as new germinants (those with cotyledons still present) or established seedlings. Tagged plants were re-surveyed in January 2002 and January 2003. The per-capita recruitment rate was calculated as the ratio of number of new recruits to the number of *S. jambos* trees >1.5 cm DBH in a given plot in a given year. A new recruit was any *S. jambos* plant 1–4 cm in height that was encountered in the 2002 census but

Table 1
Environmental characteristics and the average importance values (IV) for sites within the different land use history classifications

Sites within land use classification	Plots per site	Elevation (m)	Importance values		
			Natives	*Syzygium jambos*	Other nonnatives
Unforested					
Sab-1	2	96	0.50	0.76	0.01
Sab-2	3	107	0.38	0.68	0.01
Sab-3	3	115	0.10	0.36	0.04
Esp-2	1	405	0.22	1.07	0.00
Young secondary					
Sab-4	3	125	0.35	0.93	0.01
Esp-1	3	106	0.32	0.81	0.14
Mature secondary					
Sab-5	3	145	0.60	0.56	0.03
Mam-2	3	99	0.32	0.88	0.03
Mam-3	2	245	0.27	0.79	0.09
Primary					
Mam-4	3	331	1.17	0.00	0.00
Queb-1	2	485	1.02	0.08	0.00

Plots/site refers to the number of 200 m^2 plots that were surveyed at each site. Importance values were calculated from relative dominance and relative abundance (maximum IV = 2.00). Site elevation (m) and IV were calculated by averaging measurements for all plots at a site.

not in the 2001 census. The same criterion was used for the 2002–2003 census. Untagged, new plants >20-cm high were considered stems missed in the previous year, rather than as new recruits.

2.6. Soil sampling

Soil samples were taken with a 1.5 cm corer to a depth of 10 cm. A total of 10 cores were taken from each 200 m^2 plot, with a soil core extracted every 5 m. Bulk density was calculated using the ten 1.5 cm diameter soil core samples that were extracted from a depth of 0–10 cm from each plot. Soils were analyzed at the International Institute of Tropical Forestry for exchangeable Ca and K and available P and N. Chemical extractions for exchangeable Ca were made with 1N KCl. Extractions for exchangeable K and available P follow a modified Olsen's method (Hunter, 1982). A Beckman plasma emission spectrometer was used to analyze the soil extracts. Nitrogen was analyzed with a Kjeldahl process (Bremner and Mulvaney, 1982). Nutrient pool size per unit area was calculated from the product of bulk density, soil volume to 10 cm depth, and nutrient concentration.

3. Analytical methods

3.1. Diversity indices and importance values (IV)

Two measures were used to characterize plant diversity; each emphasizes a different aspect of diversity. They were as follows: Shannon's diversity index ($H = -\sum_{i=1}^{s} p_i \ln p_i$, where p_i is the proportion relative to the total number of species per plot), which accords greater weight to contrasts in rare species; and estimated species richness (S_{max}). To calculate S_{max}, species accumulation curves were projected using EstimateS (Colwell and Coddington, 1994). Then, S_{max} was estimated for each plot by fitting the mean accumulation curves to a two-parameter hyperbola, using a nonlinear regression equation. The equation:

$$S(n) = \frac{S_{max} \times N}{B + n},$$

describes $S(n)$, species per sub-plot generated from the species accumulation data, S_{max} (maximum number of species in each plot), B (species overlap), and n (the number of sub-plots in each 200 m^2 plot). The S_{max} is a fitted constant that describes the asymptote, and B is a fitted constant that describes the amount of species overlap at a site. Estimated species richness or S_{max} allowed a more accurate estimate of floristic richness by using the survey data to extrapolate to a larger sample area.

Species-specific importance values were calculated by summing the relative dominance and relative abundance in each plot. Importance values were calculated for all species:

1. Relative dominance $= \sum \mathrm{DBH}_{ij}^2 / \sum \mathrm{DBH}_i^2$, where DBH_{ij} refers to species j at site i and DBH_i refers to the DBH of all species at site i.
2. Relative abundance $= \sum S_{ij} / \sum N_i$, where S_{ij} refers to the number of individuals for the jth species at site i and N_i refers to the total number of individuals of all species at a site i.
3. Importance values (IV) = relative dominance + relative abundance. Importance values are dimensionless and for this study may sum to a maximum value of 2.00.

3.2. Statistical analyses

The effects of land use history on *S. jambos* density, plant diversity, and plant species richness were tested using separate single-classification ANOVAs. The data for sites with the same 1936 classifications were pooled. A single-classification ANOVA was used to assess the relationship between soil nutrients and *S. jambos* presence. A two-way ANOVA was used to test the effects of land use on *S. jambos* seedling recruitment. Seedling recruitment data were also pooled, arcsine square root transformed, and tested for significance at $P < 0.05$ using the Tukey–Kramer procedure. The figures show back-transformed data. We calculated correlations between *S. jambos* density, Shannon's diversity index, and S_{max} for all plots (i.e., plots within sites analyzed separately). A Shapiro–Wilk test was used to test for normality. Instances when bivariate normality was not satisfied, non-parametric tests were used—specifically Kendall's coefficient of rank correlation (τ) and the Kruskal–Wallis test.

It is often difficult to assess the impact of land use history on diversity as these impacts can also be confounded by differences in elevation, invasive plant establishment, and events during successional time. To statistically control for these potentially confounding factors, we used partial Mantel tests (Smouse et al., 1986; Fortin and Gurevitch, 2001) to evaluate the correlations between *S. jambos* invasion and plant diversity patterns. The Mantel test is a non-parametric randomization procedure based upon distance matrices that allowed us to test whether the relationship between *S. jambos* invasion and plant diversity was independent of land use history. The statistical significance of the correlation between two distance matrices is tested by re-randomizing one of the matrices many times. Partial correlations can be constructed to evaluate the correlation between two distance matrices (e.g., *S. jambos* invasion and species diversity) while holding the values in a third matrix (e.g., land use) statistically constant. Mantel distance matrices were created for diversity (using H′), *S. jambos* density, land use history, and elevation. The distance matrix for invasion was based on the relative abundance (proportion of stems) of nonnative plants in each plot. The distance matrix for land use history was based on ranking each site according to its 1936 forest cover percentage. Sites that had lower cover percentages in 1936 were assigned a higher perturbation ranking than other forest types (e.g., perturbation ranking for unforested sites = 4 and perturbation ranking for primary forest sites = 1). Mantel tests were carried out using PASSAGE (Rosenberg, 2005). Each test represents a Mantel test with 999 permutations.

4. Results

4.1. Effect of S. jambos on species richness, diversity and forest regeneration

Analysis of the vegetation patterns suggests that recolonization of unforested areas and regeneration of secondary forests were disproportionately affected by *S. jambos* presence. The importance values for native and nonnative species were significantly different across all forest types (Fig. 1). The IVs were significantly higher for all nonnative species than for native species in all forest types, except in primary forests (Fig. 1). The most dominant and abundant nonnative species was *S. jambos* (Fig. 1 and Table 1). Unforested, young and mature secondary forests had significantly higher *S. jambos* densities than primary ($F = 7.82$, $P < 0.0008$, Fig. 2). Plant diversity was significantly higher in primary forests than in all other forest classes (Fig. 2). Kendall's coefficient of rank correlation revealed that *S. jambos* density and Shannon's diversity (H′) were significantly negatively correlated ($\tau = -0.6309$, $P = 0.0001$, Fig. 3A). However, there were no observable patterns between estimated species richness (S_{max}) and *S. jambos* density ($\tau = 0.0442$, $P > 0.7326$, Fig. 3B).

S. jambos density and plant species diversity remained strongly, negatively correlated even after controlling for land use history ($r_{Mantel} = -0.939$, $P = 0.001$). While lower-elevation sites were more likely to be disturbed than those at higher altitudes, the association between invasion and diversity is not simply an artifact of covariation with elevation. *S. jambos* density and diversity remained strongly, negatively correlated when altitude was statistically held constant ($r_{Mantel} = -0.921$, $P = 0.001$).

Land use history significantly influenced *Syzygium* seedling recruitment. Relative to the mature secondary and primary forests, there was significantly higher seedling recruitment of *S. jambos* in the unforested and young secondary forests ($F_{1,3} = 4.033$, $P < 0.014$, Fig. 4). There was a statistically significant increase in recruitment rates over the 2-year study period in unforested and young secondary forests ($F_{1,3} = 6.120$, $P < 0.018$, Fig. 4). Both mature secondary and primary forests showed an increase in established *S. jambos* seedlings from the years 2001 to 2003, but the difference was not statistically significant. There was no significant interaction between land use history and year in 2002 or 2003.

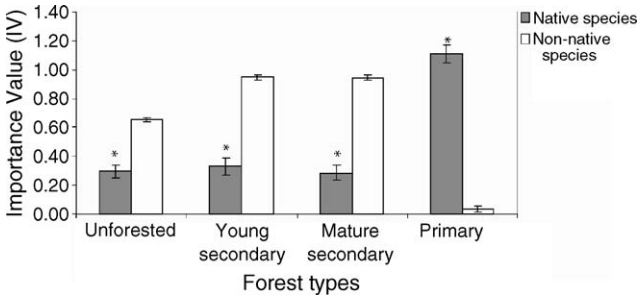

Fig. 1. Importance values (IV) for native and nonnative plant species in the four 1936 forest types. The IVs were calculated based on relative dominance and relative abundance (see text for more details). Asterisk indicate significance at $P < 0.05$ level based on the Kruskal–Wallis test. Error bars are ±1S.E.

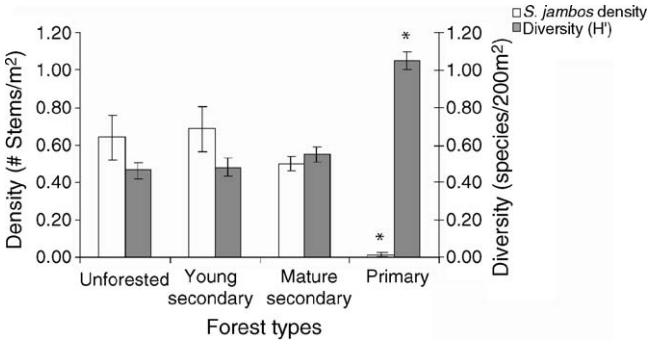

Fig. 2. *Syzygium jambos* density and Shannon's diversity index (see text for formula) in the four 1936 forest types. Data given for mature individuals >1.5 cm DBH. Asterisk indicate significance at $P < 0.05$ level based on a single-classification ANOVA. Error bars are ±1S.E.

4.2. Effects of soil nutrients on S. jambos

There were significant differences between several soil nutrient properties and sites where *S. jambos* was present and sites where it was absent. There were significant differences between phosphorous, calcium and potassium soil nutrient pools in high density *S. jambos* sites and sites where the plant

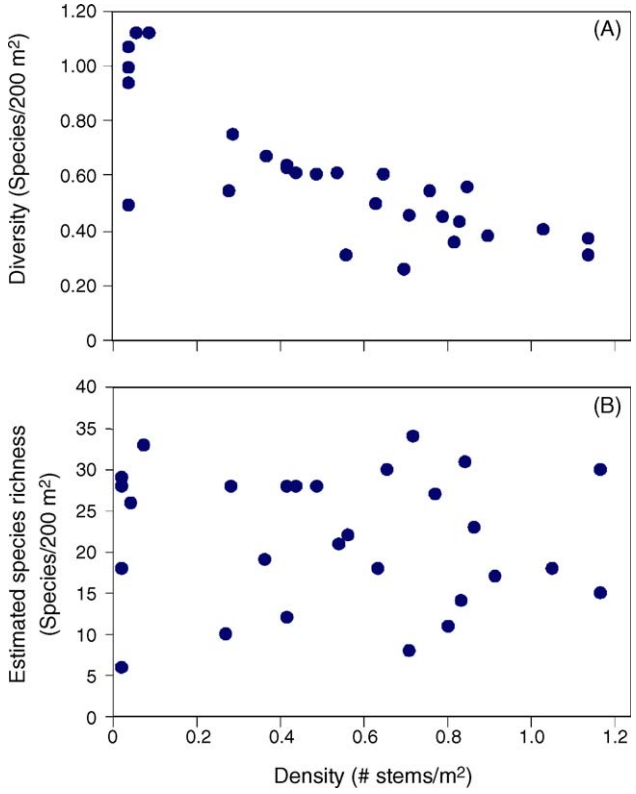

Fig. 3. (A) Association between *S. jambos* density and Shannon diversity (see text for formula). (B) Association between *S. jambos* density and estimated species richness (S_{max}). Data given for mature individuals >1.5 cm DBH. All study plots are shown.

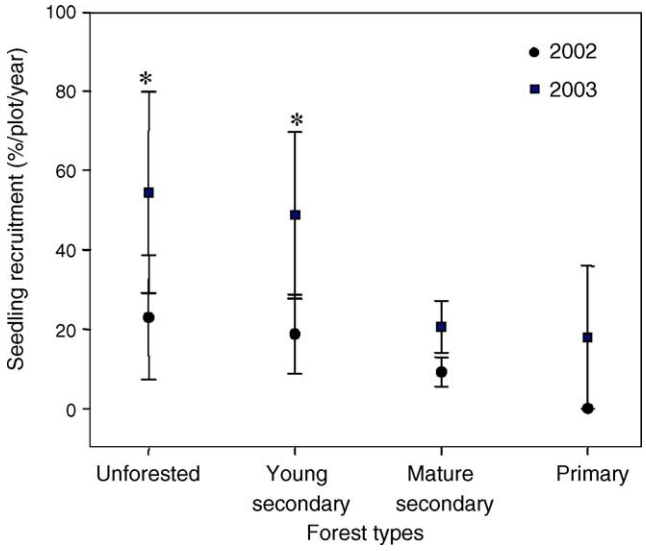

Fig. 4. *S. jambos* seedling recruitment from years 2002 to 2003 vs. 1936 forest types. See text for designation of seedling size. Asterisk indicate significance at $P < 0.05$ level based on a two-way ANOVA. Error bars are ±1S.E.

Table 2
The ANOVA table for soil nutrient pools in *S. jambos* and non-*S. jambos* sites

	N (kg/ha)	P (kg/ha)	C (kg/ha)	Ca (kg/ha)	K (kg/ha)
Invasion type (*Syzygium* vs. no *Syzygium*)					
d.f., within = 1					
d.f., among = 26					
d.f., total = 27					
F-value	4.39	5.39	1.58	3.95	13.7
P	0.059	**0.031**	0.239	**0.039**	**0.001**
Forest types					
Unforested	29.6	13.0	392.4	595.5	115.3
Young secondary	26.0	10.3	344.7	831.0	114.8
Mature secondary	24.2	11.9	306.7	959.1	116.3
Primary	22.9	5.3	343.1	654.0	75.10

Total N, total C, exchangeable Ca, exchangeable K, and available P are from 0 to 10 cm soil depth (kg/ha). Bold indicates significance at $P < 0.05$. Invasion type refers to sites where *S. jambos* is present (i.e., *Syzygium* sites) and *S. jambos* is absent (i.e., no *Syzygium*). The mean values for each soil nutrient in the four forest types are shown.

was absent (Table 2). On average, phosphorous, calcium, and potassium were higher in dense *S. jambos* patches.

5. Discussion

5.1. Community structure and diversity patterns

S. jambos is currently a dominant member of secondary forests that had relatively open canopies in 1936. Those habitats now have the highest *S. jambos* densities and the lowest plant diversity and the species appears to be the overriding force driving vegetation and diversity patterns. *S. jambos* abundance is also strongly associated with a reduction in plant species diversity. However, there was no detectable relationship between S_{max} (estimated species richness) and *S. jambos* and to date its presence has not had a measurable effect on species richness. However, the invader–extinction relationship may not show up in the Luquillo Mountains because there are few if any riparian tree specialists (Heartsill-Scalley and Aide, 2003). These finding supports the assertion made by Gurevitch and Padilla (2004) that the direct causative link between plant invaders and purported extinctions of native plants is tenuous.

While the presence of *S. jambos* is not directly linked to the extinctions or exclusions of native tree species, the diversity, physiognomy, and native plant abundance in habitats dominated by *S. jambos* are distinct from non-*Syzygium* habitats. In sites where the plant is well established it has apparently remained for several decades and these sites have not yet begun to converge upon the pre-disturbance vegetation assemblage. The abundance of seedlings and the high levels of recruitment observed in this study also suggest that it will continue to be a dominant in the areas where it is established. Whether these shifts are considered permanent or temporary depends in part on the time scale considered. The results of this study demonstrate that the plant has persisted for long periods in Puerto Rico (i.e., from 1821 to 2006) and that it has remained a dominant riparian species for at least 70 years in the Luquillo Mountains (i.e., 1936–2006). Evidence from studies in other tropical systems support the enduring influence of plant invasions on community and diversity patterns in the Luquillo Mountains (Brown and Gurevitch, 2004; Lichstein et al., 2004).

Syzyzium jambos was dominant in habitats with large pools of phosphorous, calcium, and potassium. It is presence was not related to the soil pools of nitrogen and carbon. These analyses also suggest that *S. jambos* can establish viable populations in habitats with tremendously variable soil and edaphic properties within the Luquillo Mountains. It is unclear whether *S. jambos* invasion is a cause or consequence of the observed soil conditions.

6. Conclusion

Historic agricultural land uses in the Luquillo Mountains removed dominant, native tree species from portions of the landscape. When these areas were abandoned they were colonized by *S. jambos*. As forest regeneration continued, established populations of *S. jambos* spread, until some areas, typically riparian zones, became dominated by *S. jambos*. In these previously disturbed areas, it has been a permanent member of the community for over 70 years. In the meantime, it has continued to expand into and establish in mature and primary forests. Presently, *S. jambos* is a shade-tolerant, long-lived tree that can colonize mature primary forests in the Luquillo Mountains. The plant's ability to invade open areas and withstand lengthy periods in the understory are important life history traits that help account for its success in the Luquillo Mountains. Whether the plant will eventually establish dominant populations in mature forests is still unknown. Nevertheless, this study indicates that *S. jambos* will remain a permanent member of the tree community in the Luquillo Mountains and over the environmental conditions considered here it is not limited by land use history, soil, or topographic factors.

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Appendix A. Species list

Forest type			
Unforested ($n = 9$)	Young secondary ($n = 6$)	Mature secondary ($n = 8$)	Primary ($n = 5$)
Alchornea latifolia	*A. latifolia*	*A. latifolia*	*A. latifolia*
Artocarpus altilis[a]	*C. brasiliense*	*Alchorneopsis portoricensis*	*Buchenavia capitata*
Calophyllum brasiliense	*Casearia arborea*	*Andira inermis*	*Byrsonima spicata*
Casearia sylvestris	*Casearia guianensis*	*A. altilis*[a]	*C. brasiliense*
Cecropia scheberiana	*C. sylvestris*	*C. brasiliense*	*C. guianensis*
Citharexylum caudatum	*Coccoloba pyrifolia*	*C. scheberiana*	*C. borinquensis*
Citrus aurantium[a]	*Cyathea arborea*	*Cestrum macrophyllum*	*C. arborea*
Clusia rosea	*Dendropanax arboreus*	*C. arborea*	*C. borinquena*
Cordia borinquensis	*Faramea occidentalis*	*Cyathea borinquena*	*D. excelsa*
Guarea guidonia	*Gonzalagunia spicata*	*Dacryodes excelsa*	*Eugenia stahlii*
Inga laurina	*Hirtella rugosa*	*D. arboreus*	*Guarea glabra*
Mangifera indica[a]	*I. laurina*	*G. guidonia*	*G. guidonia*
Miconia tetrandra	*Ixora ferrea*	*Guatteria caribaea*	*H. rugosa*
Miconia prasina	*M. indica*[a]	*H. rugosa*	*Homalium racemosum*
Miconia racemosa	*Manilkara bidentata*	*I. laurina*	*I. laurina*
Myrcia deflexa	*M. racemosa*	*Inga vera*	*I. vera*
Myrcia Splendens	*M. prasina*	*M. bidentata*	*M. bidentata*
Ocotea leucoxylon	*M. deflexa*	*M. prasina*	*Matayba domingensis*
Palicourea riparia	*M. splendens*	*M. racemosa*	*M. prasina*
Piper hispidum	*P. berteriana*	*M. deflexa*	*M. tetrandra*
Pouteria multiflora	*P. indicus*[a]	*M. splendens*	*Myrcia leptoclada*
Prestoea montana	*S. morototoni*	*O. leucoxylon*	*M. splendens*
Psychotria berteriana	*S. macrophylla*[a]	*P. riparia*	*O. leucoxylon*
Pterocarpus indicus[a]	*S. jambos*[a]	*P. hispidum*	*P. riparia*
Schefflera morototoni	*T. heterophylla*	*P. multiflora*	*P. montana*
Swietenia macrophylla[a]	*Vitex divaricata*	*P. montana*	*P. berteriana*
Syzygium jambos[a]		*P. berteriana*	*S. morototoni*
Tabebuia heterophylla		*P. indicus*[a]	*S. berteriana*
Trichilia pallida		*S. morototoni*	*T. heterophylla*
		Sloanea berteriana	*Urera baccifera*
		S. jambos[a]	*V. divaricata*
		T. heterophylla	
		Tetragastris balsamifera	
		T. pallida	

[a]Indicates nonnative tree species.

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