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Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico

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Abstract Tropical forests are suffering from increasing intensities and frequency of disturbances. As a result, non-native species accidentally introduced or intentionally planted for farming, plantations, and ornamental purposes may spread and potentially invade undisturbed native forest. It is not known if these introduced species will become invasive, as a result of recurrent natural disturbances such as hurricanes. Using data from three censuses (spanning 15 years) of a 16-ha subtropical wet forest plot, we investigated the impact of two hurricanes on populations of plant species that were planted in farms and plantations that were then abandoned and from the natural spread of species introduced into Puerto Rico in the past. The populations of four species (*Citrus paradis*, *Mangifera indica*, *Musa* sp., and *Simarouba glauca*) changed little over time. Six species (*Artocarpus altilis*, *Calophyllum calaba*, *Genipa americana*, *Hibiscus pernambucensis*, *Syzygium jambos*, and *Swietenia macrophylla*) declined between the first two censuses after Hurricane Hugo, then increased again in Census 3 after Hurricane Georges. *Spathodea campanulata* gradually increased from census to census, while *Coffea arabica* declined. These introduced species represent only a small part of the forest basal area and few show signs of increasing over time. The number of stems per plant, new recruits, and the growth rates of these introduced species were within the ranges of those for native plant species. The mortality rates over both census intervals were significantly lower for introduced species (<5% year^{-1}) than for native ones (15% year^{-1}). Many new recruits established after Hurricane Hugo (prior to this study) had opened the forest canopy and these high mortality rates reflect their death as the canopy recovered. Only *Swietenia macrophylla* and *Syzygium jambos* showed an increase in stem numbers in the closed canopy area of forest that had suffered limited human disturbance in the past. A future increase in frequency of disturbance may enable greater stem numbers of introduced species to establish, while lower-mortality rates compared to native species, may allow them to persist during inter-hurricane intervals. An increase in the population of introduced species, especially for those that grow into large trees, may have an impact on this tropical forest in the future.

Keywords Alien species · Exotic species · Invasive species · Luquillo LFDP · Mature forest · Non-native species

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Introduction

In the tropics, human activities including deforestation, conversion of forests to agriculture, and urbanisation are transforming the landscape and causing loss of forest area, forest fragmentation, and degradation. Changes also occur in the species composition of residual forest stands, and new forests are formed (Lugo and Helmer 2004). A proportion of the species that are successful in anthropogenic landscapes are not native to the area (Horvitz et al. 1998). Many non-native naturalised tree species may have benefits. For example the Central American *Prosopis juliflora* (Sw.) DC. provides economic benefits through employment in harvesting and distribution, in addition to fuel and fodder for the rural poor in India (Muthana and Arora 1983; Pasiecznik et al. 2001). Other naturalised species serve to reforest abandoned pasture, for example *Spathodea campanulata* P. Beauv. in Puerto Rico (Lugo 2004; Lugo and Helmer 2004). However, non-native species are also viewed as having negative impacts through changing ecosystem structure and function, causing the loss of native plants and animals, or changing the genetic structure of native populations through hybridisation (Richardson et al. 2000; Nyoka 2003). Ecologists have not reached a consensus on the implications of the human-mediated changes in species composition of ecosystems (Ewel et al. 1999; Ewel and Putz 2004).

In general, non-native species have a greater opportunity for expansion in deforested or degraded sites and have less success in undisturbed conditions (Elton 1958). However, it is possible that introduced species that would not normally invade a mature native forest might gain a foothold if the forest was periodically disturbed. The effect of hurricane damage on species invasion into mature montane rain forest forests in Jamaica was seen following Hurricane Gilbert, when *Pittosporum undulatum* Vent. became the species with the highest-mean stem density within 6 years (Bellingham et al. 2005). The rate of invasion of *Miconia calvescens* DC. in Tahitian montane forest became more rapid after cyclone damage (Merlin and Florence 1996). In other tropical forests the relative abundance of tree species was not affected by severe cyclones (Burslem et al. 2000). The study of hurricane effects in Puerto Rico is quite extensive and includes short- (Walker 1991; Walker et al. 1992) and long-term effects on the structure and functioning of both wet (Ostertag et al. 2005) and dry forests (Van Bloem et al. 2005). However, little is known about the effects of hurricanes in altering species composition or promoting non-native species invasion. Scatena and Lugo (1995) found no changes in tree species composition after Hurricane Hugo, although Chinea (1999) recorded the appearance and then gradual disappearance of introduced herbaceous species under the hurricane damaged forest canopy. The question remains, however, whether previously established individuals of introduced species would expand their populations after hurricane disturbances and thus slowly change the species composition of mature native forests.

Through repeated censuses of the Luquillo Forest Dynamics Plot (LFDP), we aimed to answer three questions. Are species that were planted within the forest, or arrived through natural dispersal, able to spread in closed canopy forest that had little human disturbance, or are they restricted to previously degraded forest areas? How does hurricane disturbance influence the population dynamics of introduced species? What is the potential long-term outcome of accidental or purposeful introductions of species in a forest stand subsequently protected from human disturbances?

Methods

Study area and site

This study was conducted in the El Verde Research Area of the University of Puerto Rico (18°20′ N, 65°49′ W) in the Luquillo Experimental Forest, Luquillo Mountains, Puerto Rico (Waide and Reagan 1996). The El Verde Research Area is in vegetation and on topography typical of the *tabonuco* (*Dacryodes excelsa* Vahl.) forest zone, below 600 m a.s.l. (Brown et al. 1983; Lugo and Scatena 1995) in an area where parts of the forest has experienced human disturbance (Foster et al. 1999). Rainfall at the nearby El Verde Field Station averages 3,500 mm year^{-1}. March and April tend to have less rainfall than other months, but there is usually no month with <200 mm (Brown et al. 1983). The average return interval for hurricanes that cause widespread damage in this area is 50–60 years (Scatena and Larson 1991), however, two hurricanes that affected this study occurred only 9 years apart (see below). In addition to these hurricanes, the forest also suffered disturbance from a drought in 1994.

The study site was the 16-ha (320 × 500 m) LFDP which is part of the Luquillo Experimental Forest Long-Term Ecological Research (LTER) program, and the Center for Tropical Forest Science network of forest plots. The LFDP is divided into 400 20 × 20 m plots and each plot is divided into 16 5 × 5 m sub-plots.

Elevation, topography, and soils

Topography on the LFDP includes northwest-running drainages that form steep northeast- and southwest-facing slopes with an elevation range from 333 m a.s.l. at the northern end of the LFDP to 428 m at the south (Thompson et al. 2002). There are two permanent streams running through the plot from east to west and several small ephemeral stream channels. The soils are clays formed from volcaniclastic sandstone (USDA Soil Survey Staff 1995) with small amounts of Fluaquents in and along the stream channels. The distribution of the soil types across the plot, have little impact on forest composition when compared with the effects of previous land use history (Thompson et al. 2002).

Land use history

Information on the history of land use in and around the LFDP was obtained from interviews with local inhabitants, public documents, forest surveys, a Forest Service cruise survey (Gerhart 1934), and other United States Forest Service documents. The destruction of farms by hurricanes in 1928 and 1932 contributed to the abandonment of agriculture in this area (Gerhart 1934). Evidence of human disturbance was also found in aerial photographs of the forest that were taken in 1936 (Foster et al. 1999). Using the aerial photographs the LFDP was divided into four areas representing different intensities of human disturbance. Canopy cover class 1 with <20% forest canopy cover, cover class 2 with 20–50%, cover class 3 with 50–80%, had all suffered forest clearing and farming prior to 1934, while cover class 4, with >80% canopy cover in 1936, was never cleared but was subjected to limited selective logging in the 1940s. Canopy cover class 4 will, hereafter, be described as undisturbed. More details of the land use history and species composition of the LFDP can be found in Thompson et al. (2002); for introduced species see Table 1.

LFDP censuses and hurricane impacts

The LFDP was established under the auspices of the LTER Research Program, after Hurricane Hugo (category 4, September 1989) caused severe damage to the forest at El Verde (Walker 1991; Walker et al. 1992; Zimmerman et al. 1994). The first LFDP census data comprised inventories of stems ≥10 cm diameter at breast height measured at 1.3 m from the ground (dbh); June 1990–February 1992) and stems ≥1 cm < 10 cm dbh (February 1992–September 1993). The census of smaller stems started approximately 2.5 years after Hurricane Hugo struck the forest in September 1989, therefore, many of the small stems recorded as part of the first census were likely to have been recruited as a result of the canopy being opened by the hurricane. In the second (November 1994–October 1996) and third census (July 2000–April 2002) all woody stems ≥1 dbh were recorded concurrently. Between the second and third census Hurricane Georges (category 3, in September 1998) struck the forest and, as in Census 1, many of the small stems recorded during Census 3 were likely recruited after Hurricane Georges opened the forest canopy. Differences in stem numbers between those reported here and in previous papers result from data corrections.

Inventory of stems

For each census of the LFDP we identified, tagged and marked the location on a map of all self-supporting woody stems ≥1 cm dbh. Census methods generally followed Condit (1998), except that all stems ≥1 cm dbh on a multiple-stemmed plant were individually tagged and measured and the connections among stems recorded. *Musa* sp. are herbaceous and only the number of culms and not diameter was recorded.

In the second and subsequent censuses a plant was recorded as alive if there was evidence from sprouts,

Table 1 Introduced species characteristics including status of introduction (Little and Woodbury 1976; Francis and Logier 1991), mode of dispersal and response to shade

Species	Status	Seed dispersal	Vegetative growth	Shade response
Artocarpus altilis (Parkinson, Fosberg)	A	Animal	Root sprouting[d]	Intolerant
Calophyllum calaba (Jacq.)	N/P	Animal		Intolerant
Citrus paradis (Macfad.)	A	Animal		Intolerant
Coffea arabica (L.)	A	Animal		Tolerant
Genipa americana (L.)	N	Animal		Intolerant
Hibiscus pernambucensis (Arruda)	I/N[a]	Animal	Roots from fallen stems	Intolerant
Mangifera indica (L.)	A	Animal		Intolerant
Musa sp.	A		Culms[b]	Intolerant
Simarouba glauca (DC)	P	Animal		Intolerant
Spathodea campanulata (Beauv.)	E	Wind[c]		Intolerant
Swietenia macrophylla (King)	P	Wind		Intolerant
Syzygium jambos ((L.) Alston)	E	Animal		Tolerant[e]

A, Exotic planted for agricultural use; E, Naturalised (sensu Richardson et al. 2000) exotic; N, native species planted for agricultural or ornamental use; P, plantation species for timber.

I/N[a] Either introduced (Little and Woodbury 1976) or native (Logier 1994)

[b] Spread by sprouting new culms

[c] Francis (2000a)

[d] Francis (2000b)

[e] Parrota (1994)

Nomenclature follows Logier (1985, 1988, 1994, 1995, 1997)

leaves or live tissue within the stem that it was still living, even if the stems had broken or died back and no stems $\geq$1 cm dbh remained.

Population dynamics

The mean number of sprouts per individual was calculated for each species from the total number of stems of each species, divided by total number of individuals alive at each census. For the comparison of mean stem numbers with native species, palms were not included as they do not sprout.

Absolute growth rate (cm year^{-1}) was calculated for all stems that survived from one census to another as in Burslem et al. (2000). Stems that were not measured at the same place in consecutive censuses were omitted from growth rate calculations over mean census intervals.

Mean annual mortality rates m and recruitment r for each species in percent was calculated as in Burslem et al. (2000) and expressed according to the following equations:

$$m = 1 - (1 - (N_0 - N_1)/N_0)^{1/t}$$

where N_0 and N_1 are the number of stems at the beginning and end of the census interval in t (years);

$$r = 1 - (1 - n_r/N_t)^{1/t}$$

where n_r is the number of recruits and N_t the number of stems present at the end of the census interval t.

Palm stems of *Prestoea acuminata* (Willd.) H. E. Moore var. *montana* were included as recruits as part of the native species calculation when their newest leaf arose from the stem at 1.3 m from the ground.

Differences in mean stem numbers per individual and mean species growth rate were assessed with a t-test to compare the native species versus introduced species. Percent recruitment and mortality rates were also compared after arcsine square root transformation of the data. The distributions of the native versus introduced species data were assessed for equal variance (Haber and Runyan 1973), and most results given below are quoted using the model assuming unequal variances for the *t*-test. None of the outcomes of the comparisons between native and introduced species were changed as a result of calculating *t* assuming unequal variance.

Spatial aggregation

For each of the 12 introduced species at each census, we calculated an aggregation index (He et al. 2000; McGarigal et al. 2002). The analysis was computed at a 5-m scale, as that was the lowest-spatial resolution common among the censuses. For each 5 × 5 m quadrat that contained a stem of the study species, the method assesses the presence or absence of that species in each adjacent 5 × 5 m quadrat. The aggregation index is then calculated from the number of contiguous quadrats with that species present.

Results

Changes in stem numbers and basal area

The total numbers (ha^{-1}) of individuals (not separate stems) of most of the introduced species were relatively small and changed little among censuses (Fig. 1a). *Calophyllum calaba*, *Genipa americana*, and *Hibiscus pernambucensis* declined between Census 1 and Census 2 then increased in numbers in Census 3. *Coffea arabica* increased from Census 1 to 2 then declined. *Syzygium jambos*, *Artocarpus altilis*, *Swietenia macrophylla, Musa* sp., and *Spathodea campanulata* showed a gradual increase from the first to the third census, and three species, *Simarouba glauca*, *Mangifera indica*, and *Citrus paradis* showed essentially no change across the three censuses. The basal area (m^2 ha^{-1}) of introduced species (Fig. 1b) was also very low and for most species changed little among the censuses, largely reflecting the change in total stem numbers (Table 2). The maximum total basal area of introduced species was <1% of the total for the stand in all three censuses with *Calophyllum calaba* having the largest basal area in Census 1 (0.45% of the total LFDP).

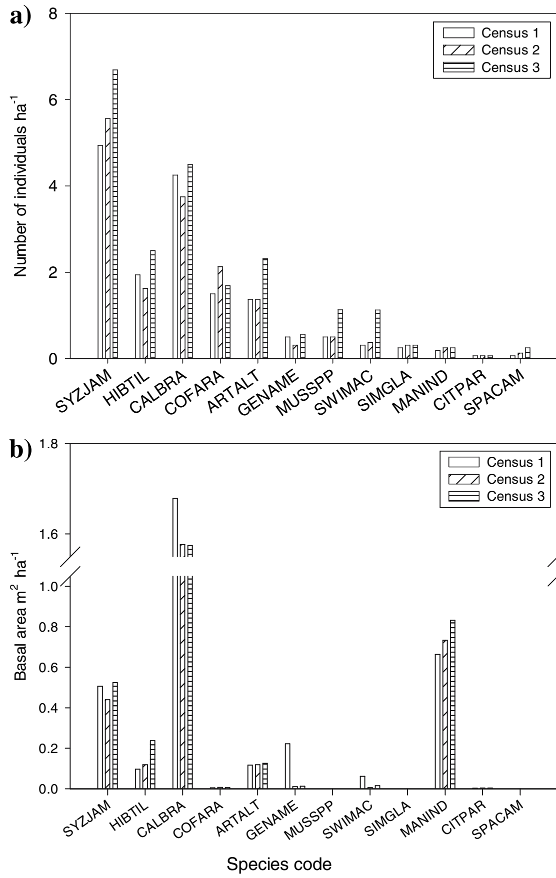

Fig. 1 (**a**) Number ha^{-1} of alive individual plants (with a stem ≥1 cm dbh in at least one census) of introduced species in three censuses over 15 years of the LFDP. (**b**) Total basal area m^2 ha^{-1} all stems (≥1 cm dbh ha^{-1} in at least one census) of introduced species in three censuses over 15 years of the LFDP. Species codes are: ARTALT *Artocarpus altilis*, CALBRA *Calophyllum calaba*, GENAME *Genipa americana*, CITPAR *Citrus paradis*, COFARA *Coffea arabica*, HIBTIL *Hibiscus pernambucensis*, MANIND *Mangifera indica*, MUSSPP *Musa* sp., SIMGLA *Simarouba glauca*, SWIMAC *Swietenia macrophylla*, SYZJAM *Syzygium jambos*, SPACAM *Spathodea campanulata*

Of the introduced species *Hibiscus pernambucensis* had the most stems with 0.34% of the total stems in Census 3 (Table 2). The mean number of stems per individual plant changed little (range 1–2), except for *H. pernambucensis* which had stem numbers increasing from 2.6 to 7.2 stems per individual plant from Census 1 to Census 3. There was no significant difference between the native and introduced species in mean number of stems per individual in any census interval.

Table 2 Mean number of sprouts on each plant of introduced species and mean for all species present in each census

Species	Census 1		Census 2		Census 3	
	Mean number of sprouts	Number of stems	Mean number of sprouts	Number of stems	Mean number of sprouts	Number of stems
Artocarpus altilis	1.04	24	1.09	24	1.3	36
Calophyllum calaba	1.03	70	1.02	61	1.07	76
Citrus paradis	1	1	1	1	1	1
Coffee arabica	1.08	26	1.11	38	1.26	29
Genipa americana	1.25	10	1	6	1	1
Hibiscus pernambucensis	2.62	81	3.61	83	7.18	280
Mangifera indica	1	3	1	4	1	4
Musa sp.	2.5	2	1.25	8	5	25
Simarouba glauca	1	4	1	5	1	4
Spathodea campanulata	1	1	1	2	1	4
Swietenia macrophylla	1.1	11	1	11	1	18
Syzygium jambos	2.08	164	1.87	161	2.1	210
Mean no. stems introduced sp.	1.39 (0.18)	395	1.32 (0.22)	406	1.38 (0.04)	697
Mean no. stems native species*	1.26 (0.39)	103,438	1.27 (0.44)	83,532	1.39 (0.68)	76,730

* Not including the palm *Prestoea acuminata* var. *montana* as this does not sprout

The growth, mortality and recruitment rates, and the relative rank order among all species for both census intervals show that the introduced species covered almost the full range of values achieved by native plant species (Table 3). Differences between native and introduced species were only significant for mortality at 15% versus 5% for the both census intervals. Six out of the 12 introduced species recruited more individuals from Census 2 to 3 than the first two censuses. Excluding the herbaceous *Musa* sp., *Hibiscus pernambucensis* had the largest recruitment rate (29.5% year^{-1}) of the introduced species as a result of the many sprouts that developed on a few large fallen trees. Three others *Genipa*, *Swietenia*, and *Spathodea* had high recruitment rates of almost 12% year^{-1} (Table 3) also between Census 2 and 3 but these represent a small number of stems.

Species distribution and land use history

Most of the introduced species were planted for agriculture prior to 1932 and have remained as relic populations in the previously farmed areas, without spreading into mature non-disturbed forest. *Coffea arabica* slowly diminished in numbers and reduced its distribution across the plot, remaining in previously farmed areas and where this area abuts the mature forest (Fig. 2). *Artocarpus altilis*, *Hibiscus pernambucensis*, *Mangifera indica*, and *Musa* sp. remained as small clusters of stems in previously farmed areas *Genipa americana* was mainly near other fruit trees and was likely to have been planted (Francis 1993), but is native to Puerto Rico and did extend its range with a few individuals found in the mature forest. The majority of *Syzygium jambos* were clustered in large groups as a result of sprouting mainly in human disturbed areas but stem numbers increased from Census 1 to Census 3 in the undisturbed part of the plot (Fig. 3). *Swietenia macrophylla* had similar stem numbers in both human disturbed and undisturbed parts of the plot by Census 3 that were well-dispersed (Fig. 4). *Spathodea campanulata* (not shown) was found in both human disturbed and undisturbed areas by Census 3 but had only four individuals. *Simarouba glauca* (not shown) was the only introduced species found only in mature forest (cover class 4). In Census 3 four *S. glauca* were at the corner of the LFDP closest to the trial planting outside the plot.

Table 3 Recruitment and mortality rates (% year^{-1}) and growth rates (cm year^{-1}) for the introduced species with the mean and standard error (SE) for all species in the LFDP, between Censuses 1 and 2 (1990 and 1995) and Censuses 2 and 3 (1995 and 2000)

Species	Recruitment % stems year^{-1}				Mortality % stems year^{-1}				Growth rate cm year^{-1} (number of stems)			
	1990–1995	Rank	1995–2000	Rank	1990–1995	Rank	1995–2000	Rank	1990–1995	Rank	1995–2000	Rank
Artocarpus altilis	2.9	47	3.4	43	1.4	25	8.0	90	0.119 (22)	75	0.108 (10)	63
Calophyllum calaba	0.8	29	6.5	66	4.1	54	2.8	47	0.442 (59)	134	0.399 (52)	122
Citrus paradis	0	1	0	1	0	1	0	1	0.043 (1)	28	0.164 (1)	84
Coffea arabica	14.3	131	4.7	53	0	1	6.9	85	0.061 (22)	42	0.036 (20)	18
Genipa americana	6.1	90	11.9	98	18.4	108	0	1	0.059 (5)	41	0.075 (5)	45
Hibiscus pernambucensis	17.3	133	29.5	125	15.8	102	11.8	104	0.336 (47)	125	0.229 (38)	105
Mangifera indica	6.3	95	0	1	0	1	0	1	0.731 (3)	139	0.757 (4)	127
Musa sp.	38.5	143	21.1	120	0	1	8.3	93	–	–	–	–
Simarouba glauca	8.0	106	0	1	0	1	0	1	0.151 (4)	89	0.164 (4)	85
Spathodea campanulata	21.3	137	11.9	100	0	1	0	1	0.056 (1)	33	0.189 (2)	94
Swietenia macrophylla	6.8	99	11.9	97	6.2	71	3.6	54	0.397 (8)	132	0.303 (9)	116
Syzygium jambos	4.7	73	7.4	74	3.9	51	2.3	37	0.128 (139)	81	0.172 (136)	90
Introduced species mean (SE)	10.5 (3.1)		10.5 (2.7)		4.15* (1.81)		3.6* (1.2)		0.23 (0.07)		0.26 (0.06)	
Native mean (SE)	5.0 (0.68)[a]		7.5 (0.95)[a]		15.2 (2.25)		15.5 (2.39)		0.17 (0.03)[b]		0.15 (0.013)[b]	

The rank order of the introduced species relative to the other species in the LFDP population is also given. Rank order is from lowest to highest in each category; species with no recruitment all have rank 1 Rank numbers were assigned so that species with the same value were ordered alphabetically and given the same rank number. The species with the next highest value was the total number of species with a lower value +1 in order to preserve the relative rank position among the total species pool. For example rank order 47 for *Artocarpus altilis* shows that 46 species had lower recruitment than *A. altilis* between Census 1 and 2 even though many of these species had the same, zero recruitment rate. For growth rate values the number of stems used for calculations are given in parenthesis. Census time interval was calculated as mean time in years for each species from one census to the next. No growth rate for *Musa* sp. is available as only number of culms was recorded and not diameter

*Results of *t*-test significant results ($p < 0.05$)

[a] Including *Prestoea acuminata* var. *montana* as recruits when newest leaf arose from stem at 1.3 m from the ground

[b] Including palms *Prestoea acuminata* var. *montana* only if diameter was measured at 1.3 m from the ground

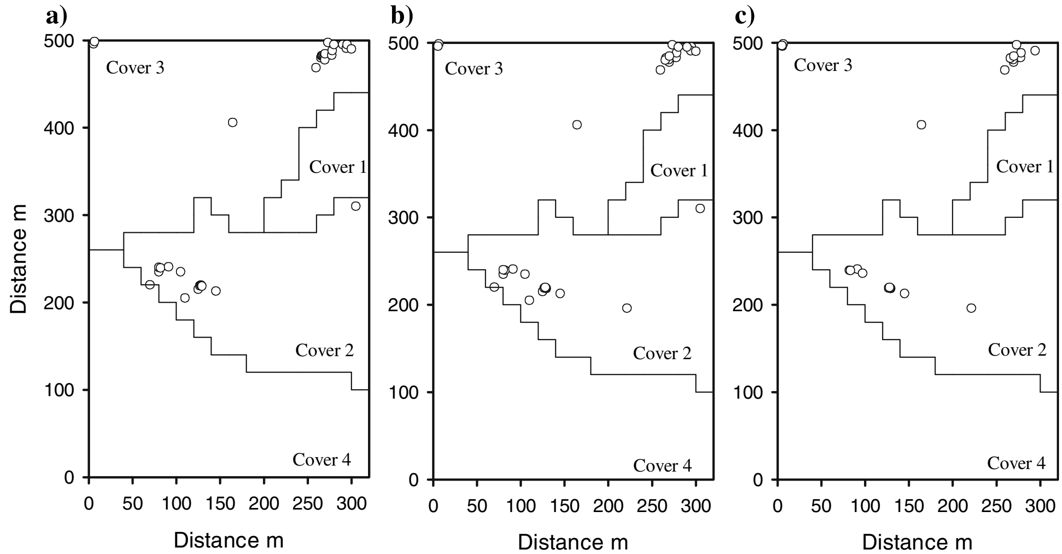

Fig. 2 Distribution of *Coffea arabica* in the LFDP in three censuses over 15 years. (**a**) Census 1 (1990), (**b**) Census 2 (1995), (**c**) Census 3 (2000). Open symbols are trees $\geq 1 \leq 10$ cm dbh, filled symbols ≥ 10 cm dbh. Canopy cover classes seen in aerial photographs taken in 1936 and indicative of intensity of land use history in each subplot are indicated

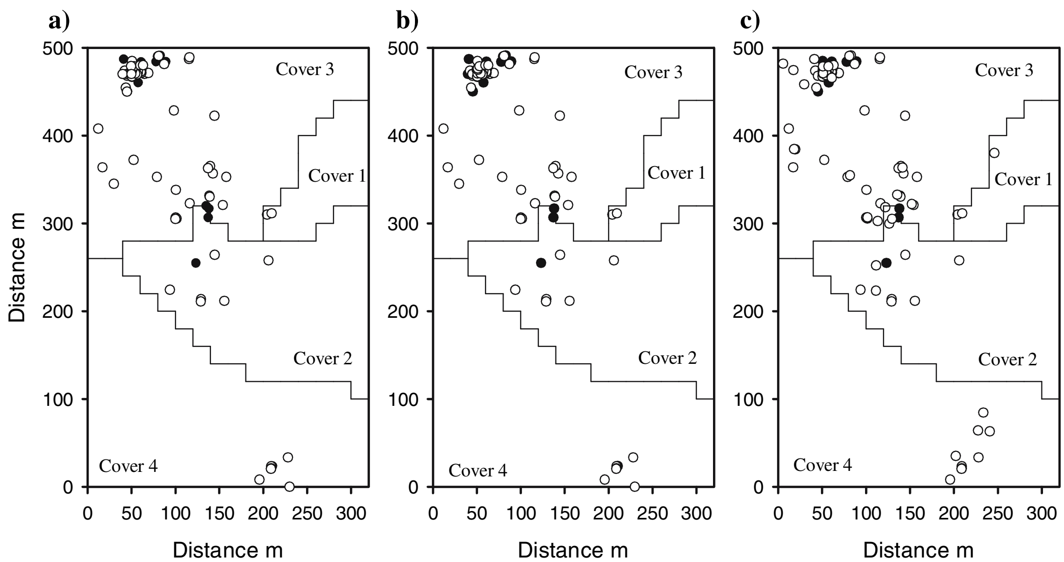

Fig. 3 Distribution of *Syzygium jambos* in the LFDP in three censuses over 15 years. (**a**) Census 1 (1990), (**b**) Census 2 (1995), (**c**) Census 3 (2000). Open symbols are trees $\geq 1 \leq 10$ cm dbh, filled symbols ≥ 10 cm dbh. Canopy cover classes seen in aerial photographs taken in 1936 and indicative of intensity of land use history in each subplot are indicated

Two species were highly aggregated, *Artocarpus altilis* and *Hibiscus pernambucensis* (Fig. 5a) and both of these species demonstrated an increase in aggregation index between Census 2 and Census 3. The high aggregation index reflects the low number of individuals with many sprouts, which means they are found clustered together. Six other species had low aggregation indices, and with only one exception,

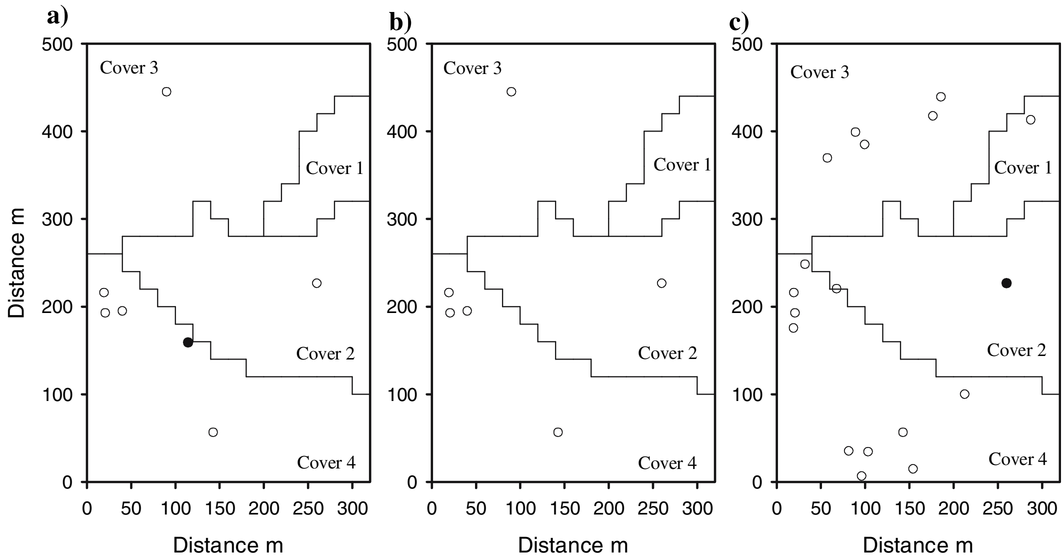

Fig. 4 Distribution of *Swietenia macrophylla* in the LFDP in three censuses over 15 years. (**a**) Census 1 (1990), (**b**) Census 2 (1995), (**c**) Census 3 (2000). Open symbols are trees ≥1 ≤10 cm dbh, filled symbols ≥10 cm dbh. Canopy cover classes seen in aerial photographs taken in 1936 and indicative of intensity of land use history in each subplot are indicated

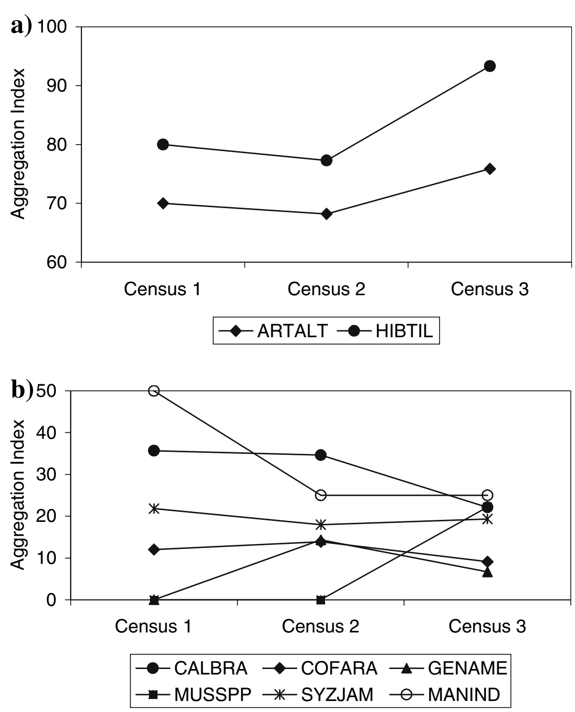

Fig. 5 Aggregation Index for (**a**) ARTALT *Artocarpus altilis* and HIBTIL *Hibiscus pernambucensis* and (**b**) CALBRA *Calophyllum calaba*, COFARA *Coffea arabica*, GENAME *Genipa americana*, MUSSPP *Musa* sp. and SYZJAM *Syzygium jambos*, in the LFDP in three censuses over 15 years

Musa sp., the index declined over time (Fig. 5b). The other four species had an aggregation index of zero but very few stems were available to compute the index.

Discussion

These three forest censuses of the LFDP were conducted soon after Hurricane Hugo, 5 years later and then again soon after Hurricane Georges damaged the forest and, therefore, the population changes were very dynamic. Canopy trees that had suffered direct hurricane damage were slowly dying, while the damaged canopy allowed the rapid recruitment of large numbers of plants, which then soon died as the canopy recovered and closed. The combined effect of the two hurricanes is difficult to disentangle. The forest census of small stems (≥1 ≤ 10 cm dbh) starting in 1992 and the full census of all stems that started in 2000 meant that small stems were recorded at a mean time approximately 2.5 years after a hurricane, by which time many saplings had reached census size. The comparisons among censuses for recruitment, growth, and mortality rates are calculated for the few stems of the introduced species (max. 280 for *Hibiscus pernambucensis*) and a wide range of abundances for native species ranging from single individuals to, for example, around 11,000 stems for *Cecropia schreberiana* Miq. and this must be borne in mind when considering the statistical results.

Overall, the introduced species survived over the 15 years of study and remained as small components of the forest and, those that spread, did so over relatively small distances with few individuals establishing in the mature forest. Our results for growth, recruitment and mortality rates were similar to those found after cyclone damage on Kolombangara in the Solomon Islands (Burslem et al. 2000). Our results for mean mortality rate (5–15% year^{-1}) were greater than that for 205 species in tropical forest that is not affected by hurricanes on Barro Colorado Island (c. 3% year^{-1}) (Condit et al. 1995). The difference between the LFDP and BCI is the combined result of hurricane damaged large trees slowly dying, and the high-mortality rate (as the canopy recovered) of the large numbers of small stems that were recruited soon after the hurricane damage opened the forest canopy. The lower mean mortality rate for introduced species relative to natives indicates the possibility that the introduced species may survive to increase their populations relative to native species if hurricanes occur frequently.

Species life history characteristics heavily influence the level of success of each species under different ecological conditions. Even though *Spathodea campanulata* is naturalised in Puerto Rico and being wind dispersed is likely to reach the forest, it is shade intolerant and, therefore, is unlikely to prosper in closed canopy mature forests unless recurrent disturbances maintain canopy openings. Under the historical return frequency of hurricane disturbances (50–60 years, Scatena and Larson 1991), the rapid recovery of the native canopy species will keep shade-intolerant introduced species relatively rare over the long-term. Although *Swietenia macrophylla* is light demanding and colonises after catastrophic disturbances (Snook 1996; Shono and Snook 2006), it is able to survive in shaded conditions for long periods of time (Medina et al. 2003). The shade tolerant *Syzygium jambos* has the capacity to maintain populations in mature native forests in the Luquillo Mountains (Brown et al. 2006), but so far they have not become a common species in the forest area of the LFDP.

The low numbers of stems of species that remain in the forest from those planted by farmers in the 1930s, or that have established after natural disturbance, and the relatively small impact that the two hurricanes had on their populations suggest that under the current disturbance regime most of these species are unlikely to reach large population sizes. Assuming the native canopies remain dominant and future disturbances are no more devastating or frequent than Hurricanes Hugo or Georges, the introduced species currently established in the Luquillo Forest do not appear likely to expand in significant numbers in the near future. Furthermore, recent observations in the LFDP, 8 years after Hurricane Georges indicate that many of the stems in the understory that were recorded in the third census have since died (J. Thompson pers. obs.).

The dynamics and spread of introduced species in tropical forest depend on a number of factors and site conditions (e.g., Horvitz et al. 1998; Ewel and Putz 2004; Bellingham et al. 2005; Brown et al. 2006; Küffer 2006). Site specific and species differences may explain the invasion of the exotic *Pittosporum undulatum* in Jamaica following Hurricane Gilbert (Bellingham et al. 2005) and the lack of a similar invasion in the LFDP after Hurricanes Georges and Hugo. The damage in Jamaica after Hurricane Gilbert was greater than was experienced at LFDP in either Hurricane Hugo or Georges, and a different forest type was studied. *Pittosporum* had been present close to the forest in Jamaica since the late 19th century without spreading, and it required extensive hurricane damage to initiate its invasion. This reinforces the idea that it is difficult for an introduced species to become invasive in closed-canopy forest. The results in the forest in LFDP might have been different given more extensive hurricane damage.

The Luquillo forest has only one-third of the numbers of introduced species in comparison to human-disturbed forest in Florida that also experiences hurricanes, where invasive non-indigenous species reached 24% of the total species present (not including vines) in the 2 years after Hurricane Andrew (Horvitz et al. 1998). Only 1% of stems in our study were of non-native species compared to 10–50% in the study by Horvitz et al. (1998). These authors concluded that the non-indigenous species did compete with native species in Florida. However, the effects of Hurricane Andrew in Florida were much greater than the effects of Hurricanes Hugo or Georges at El Verde and it is difficult to separate the effect of the hurricane from other confounding factors.

As a result of canopy opening from hurricane damage in the LFDP, the populations of eight species increased from Census 1 to Census 3 but most species remained in the same human disturbed area of the plot in which they were originally planted. *Syzygium jambos* and *Swietenia macrophylla* were the only two introduced species that increased in numbers in the undisturbed part of the plot, and of these only *S macrophylla* had a similar number of stems in both the human disturbed and non-disturbed area by Census 3. Our results for *Syzygium jambos* agree with Brown et al. (2006) that this species is found in closed canopy wet forest particularly in areas that have suffered human disturbances. In some areas of the Luquillo mountain *tabonuco* forests *S. jambos* has already established at high densities and had a significant effect on species diversity (Brown et al. 2006). The plots used by Brown et al. (2006) were within 30 m of streams and it may be only a matter of time following its establishment along these streams before this species has more impact in the LFDP. The distribution of *S. jambos* in the LFDP reflects its propensity to establish in abandoned coffee plantations (Pascarella et al. 2000). Despite the fact that the species has been described as a major invader on other tropical islands (Lawesson 1990), in the 70 years since farming ceased in the LFDP *S. jambos* only represented a very small fraction of the biomass and stem number in this study. As noted above *Swietenia macrophylla*, once established, is able to survive in shaded conditions for long periods of time (Medina et al. 2003) and after reaching the undisturbed part of the forest following hurricane damage it may be able to maintain its population for some time.

Most species that could be expected to spread rapidly are those that display a low aggregation index. Most of the introduced species that have low values also have very few stems but three species combine low aggregation and larger numbers of stems: *Syzygium jambos*, *Calophyllum calaba*, and *Coffea arabica*. Of these, the numbers of *Calophyllum* and *Coffea* have remained more or less steady over the 15 years of this study, but *Syzygium jambos* has increased. Combined with its high dispersal (low aggregation) and shade tolerance (Francis 2000b), *S. jambos* is the most likely of the introduced species to continue to spread throughout the LFDP.

Conclusion

We found little evidence that introduced species are able to invade closed canopy *tabonuco* forest. Despite two damaging hurricanes, introduced species showed little increase, if at all, relative to native species or survived to make a large contribution to the population. At the current frequency of hurricane disturbance of *c*. 50–60 years, the species remaining from the abandoned farms that have survived since 1934 are likely to gradually disappear as they die without successful replacement, or they will remain in low numbers, and disperse over short distances. Introduced species that become naturalised and native species that are introduced to a different forest type can persist within mature forests and coexist with native flora. To persist, however, these species must be able to complete their life cycles within the constraints of the natural disturbance regimes that in the Luquillo Mountains include periodic hurricanes and droughts. The long-term outcome of introductions of species in land areas subsequently protected from human disturbance may result in the eventual dominance of native tree species, with the introduced species remaining in subordinate roles at low population numbers, except where dramatic canopy opening allows the invasion of introduced species.

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