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Hurricane Disturbance Alters Secondary Forest Recovery in Puerto Rico

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ABSTRACT

Land-use history and large-scale disturbances interact to shape secondary forest structure and composition. How introduced species respond to disturbances such as hurricanes in post-agriculture forest recovery is of particular interest. To examine the effects of hurricane disturbance and previous land use on forest dynamics and composition, we revisited 37 secondary forest stands in former cattle pastures across Puerto Rico representing a range of exposure to the winds of Hurricane Georges in 1998. Stands ranged from 21 to >80 yr since agricultural abandonment and were measured 9 yr posthurricane. Stem density decreased as stands aged, while basal area and species richness tended to increase. Hurricane disturbance exerted contrasting effects on stand structure, contingent on stand age. In older stands, the basal area of large trees fell, shifting to a stand structure characteristic of younger stands, while the basal area of large trees tended to rise in younger stands with increasing hurricane disturbance. These results demonstrate that large-scale natural disturbances can alter the successional trajectory of secondary forest stands recovering from human land use, but stand age, precipitation and soil series were better predictors of changes in stand structure across all study sites. Species composition changed substantially between census intervals, but neither age nor hurricane disturbance consistently predicted species composition change. However, exposure to hurricane winds tended to decrease the abundance of the introduced tree *Spathodea campanulata*, particularly in smaller size classes. In all sites the abundance of the introduced tree *Syzygium jambos* showed a declining trend, again most strongly in smaller size classes, suggesting natural thinning through succession.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: Caribbean; chronosequence; hurricane exposure model; invasive species; secondary succession; wind disturbance.

SECONDARY FOREST COVER HAS INCREASED in many tropical regions due to socioeconomic changes and abandonment of agricultural land and pastures (Rudel *et al.* 2000, Hecht & Saatchi 2007). An estimated 60 percent of the world's forests are now second growth (FAO 2005). These secondary forests may provide many of the services attributed to primary forests including regulation of water quality and flow, erosion control, carbon sequestration, restoration of nutrients and soil properties in former agricultural lands, biodiversity conservation, and enhanced connectivity of fragmented landscapes (Chazdon 2003). Legacies of land use are critical determinants of dynamics in these forests (Zimmerman *et al.* 1995, Foster *et al.* 1999). In addition, many of these secondary forests are subject to landscape-scale disturbances such as hurricanes, which have striking short- and long-term impacts on forest dynamics (Lugo 2008). Thus, the interaction between land use and large-scale disturbance is key to understanding the composition and structure of secondary forests through time.

Numerous studies of secondary forest succession have revealed common patterns in structural and compositional recovery. Basal area tends to increase linearly with stand age, while stem density first increases and then decreases through succession (Aide *et al.* 2000, Guariguata & Ostertag 2001) (Fig. 1, solid lines). Species richness tends to increase linearly with stand age (*e.g.*, Ruiz *et al.* 2005), with light-demanding pioneer species being replaced by a richer group of shade-tolerant species. Shifts in species composition through succession are strongly affected by distance to and characteristics of the remnant forest, as well as soil characteristics and the nature of previous land use (Chazdon 2003). Hurricanes, however, may alter this typical successional trajectory in several ways. Large trees in older stands with high basal area may be particularly susceptible to loss of structure due to hurricane winds, while sites with low basal area may not change greatly in stand structure (Uriarte *et al.* 2004). This process would lead to a greater decrease in basal area for older stands relative to younger ones (Fig. 1), acting in part to return forest stands to an earlier stage in the successional trajectory, at least with respect to light availability. Hurricanes can also accelerate succession if, by opening up the canopy recruitment of intermediate sized trees to larger size classes is

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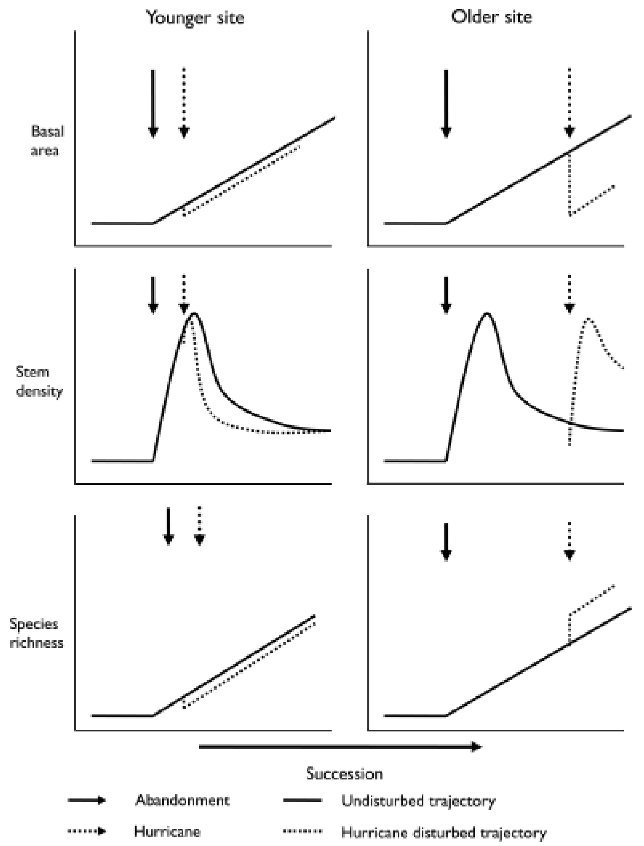

FIGURE 1. Potential effects of hurricane disturbance on secondary forest structural changes. Alteration of the successional trajectory by hurricane disturbance may depend on site age, with younger sites having little decrease in basal area, accelerated decline in stem density, and reduced species richness, while older sites experience substantial declines in basal area, rapid increases in stem density, and increases in species richness.

favored and in the following several years the stand stem density is reduced.

The interaction between human and hurricane disturbances will also affect species composition. Human disturbance increases the regional abundance of secondary forest species, and these species are often less resistant to storm disturbance than primary forest species (Zimmerman *et al.* 1994, Foster *et al.* 1998, Thompson *et al.* 2002). By opening up the canopy, storm disturbance may assist in maintaining secondary species in forests with a history of human disturbance, thereby providing a positive feedback between human and natural disturbance (Foster *et al.* 1999, Grove *et al.* 2000, Boucher *et al.* 2001, Pascarella *et al.* 2004, Zhao *et al.* 2006). Alternatively, large-scale disturbance may hasten the reestablishment of primary forest species through advanced regeneration, leading to dissipation of land use legacies (Yih *et al.* 1991). The effect of this interaction among these two dominant forest dynamics drivers remains unclear for secondary forests. Equally uncertain is the fate of introduced tree species in this process. Although the novel communities formed by introduced species may only persist for a few decades as native species recovery (Pascarella *et al.* 2000), hurricane disturbance could accelerate the decline of introduced species, but it could also facilitate the spread of these species. For the purpose of this study, we consider a decline in abundance and number of introduced species to reflect an acceleration of the successional pathway because previous research has demonstrated a decrease in the importance of some invasive trees in older stands in Puerto Rico (Lugo 2008).

Studies on the effects of land use history and hurricane disturbance on forest structure, composition, and recovery require long-term data sets, which span a broad range of land use histories, since chronosequences alone (*i.e.*, space-for-time substitution) do not necessarily predict the rate of change in forest dynamics (Chazdon *et al.* 2007, Johnson & Miyanishi 2008). Here, we investigate how land use history and hurricane disturbance interact to determine the structure, composition, and successional dynamics of secondary forests in Puerto Rico, with a particular focus on the fate of two key introduced species. We couple pre- and posthurricane censuses of 37 secondary forest stands that range in age from 20 to >80 yr since agricultural abandonment with a landscape-scale topographic model of exposure (Boose *et al.* 1994, 2004) to Hurricane Georges (1998), the last severe tropical storm to hit the island. With this information we address the following questions: (1) How does hurricane disturbance alter expected changes in basal area and stand structure through succession along this post-agriculture chronosequence? (2) Does hurricane disturbance alter the composition of species present in these forest stands? Particularly, do introduced tree species increase or decrease in importance as a result of hurricane disturbance?

We propose two alternative potential changes in the successional pathway, depending on the interaction between age since abandonment and hurricane disturbance. If hurricane disturbance acts to delay secondary succession in stands recovering from agriculture, older stands hit harder by hurricane winds will have lower basal area and higher stem density compared with similar-aged stands that experienced less hurricane disturbance (Fig. 1). Conversely, if hurricane disturbance acts to accelerate secondary succession, younger stands hit harder by hurricane winds will have greater basal area and lower stem density compared with stands that escaped disturbance. Species richness may rise in older sites due to influx of early-succession species in light gaps (Vandermeer *et al.* 2000), and species composition may shift more rapidly to a more mature composition as early-successional species may suffer proportionally greater wind damage (Canham *et al.* 2009, Zimmerman *et al.* 1994). Delayed succession as a result of hurricanes may also be manifested by steady or even increasing prevalence of introduced species between the census years, while accelerated succession would be reflected by more rapid reductions of introduced species. These changes are likely to occur at the scale of several years to a decade following a hurricane, requiring research to cover an extended time frame.

METHODS

STUDY SITES AND DATA COLLECTION.—In May–July 2007, we sampled 37 secondary forest stands distributed throughout Puerto

Rico. The three regions studied consisted of the Luquillo Mountains in the northeast (18°20′ N, 65°44′ W), Carite in the southeast part of the Cordillera Central (18°4′ N, 66°4′ W), and the *mogotes* in the north-central Ciales region (18°20′ N, 66°29′ W; Fig. 2). These sites represent a range of ages since abandonment, with 20–80 yr of regrowth in 2008. In addition, these sites spanned a range of potential exposure to the winds of the last major hurricane to hit the island, Hurricane Georges in 1998 (see below). Hurricane Georges hit Puerto Rico as a Category 3 hurricane, causing widespread damage across the island. This hurricane moved from southeastern to western Puerto Rico over the central mountain range (Bennet & Mojica 1998), delivering winds of 130–167 km/h and gusts of 148–209 km/h for approximately 18 h. Rainfall totals exceeded 63.5 cm in many mountainous areas.

Previous studies had separately censused 94 forest stands in 1995/6 in former cattle pastures (Aide *et al.* 1996, Rivera & Aide 1998, Pascarella *et al.* 2000). Sites were initially identified by examining aerial photographs from 1936 to 1994 and interviewing local landowners, to establish which stands had been active pastures and when they had been abandoned. To examine the immediate effects of hurricane disturbance on forest composition, Pascarella *et al.* (2004) re-visited 15 of these sites 2 yr after Hurricane Georges.

To account for a broader range of exposures to hurricane winds and examine the effects of hurricane winds on changes in forest structure and composition over a longer time interval, our study included 37 sites of the 94 sites studied in 1995/6. Sites were located using maps and original field notes, and were sampled using a uniform methodology, following Pascarella *et al.* (2000). For all sites, vegetation 1–10 cm dbh was measured in four parallel 1 × 50 m transects 10 m from each other, and vegetation > 10 cm dbh was sampled in two 10 × 50 m transects between the four parallel transects set up perpendicular to the slope. In some cases, due to topography or encroachment from neighboring pastures, these transects were arranged end-to-end rather than in parallel, but in all cases the total area sampled equaled 1200 m^2 (0.12 ha). We did not sample woody vines, epiphytes, or herbaceous plants. Nomenclature follows Liogier (1982). Voucher specimens were kept throughout the study period to ensure consistent species identifications.

To reconstruct wind conditions (sustained wind speed, peak gust speed, and wind direction) at our study sites, we used Expos, a simple model that combines information on the track and intensity of a hurricane (Boose *et al.* 1994, 2005). The model assumes that movement over land decreases sustained wind speeds and increases inflow angles, and then calculates spatial variation in sustained damage in the Fujita scale. This model has been shown to accurately reconstruct historical exposure to hurricane winds in Puerto Rico at the landscape scale, when compared with historical records (Boose *et al.* 1994, 2004; Foster *et al.* 1999).

We then used a simple landscape-level topographic model (Boose *et al.* 1994, 2005) to estimate the degree of landscape exposure to winds given a specific wind direction and a digital elevation map (derived from the Shuttle Radar Topography Mission, Farr *et al.* 2007). Our implementation of this exposure model is identical to that of Boose *et al.* (1994), except that we modified this procedure to estimate potential exposure as a continuous variable, ranging from maximum exposure at high sites with no topographic protection from the maximum wind speeds of the hurricane at that location, to minimum exposure in sites largely protected topographically from the direction of maximum wind speeds (Fig. 2). For simplicity we assign sites to 'exposed' or 'protected' classes based on the mean exposure values of each of the four corners of the

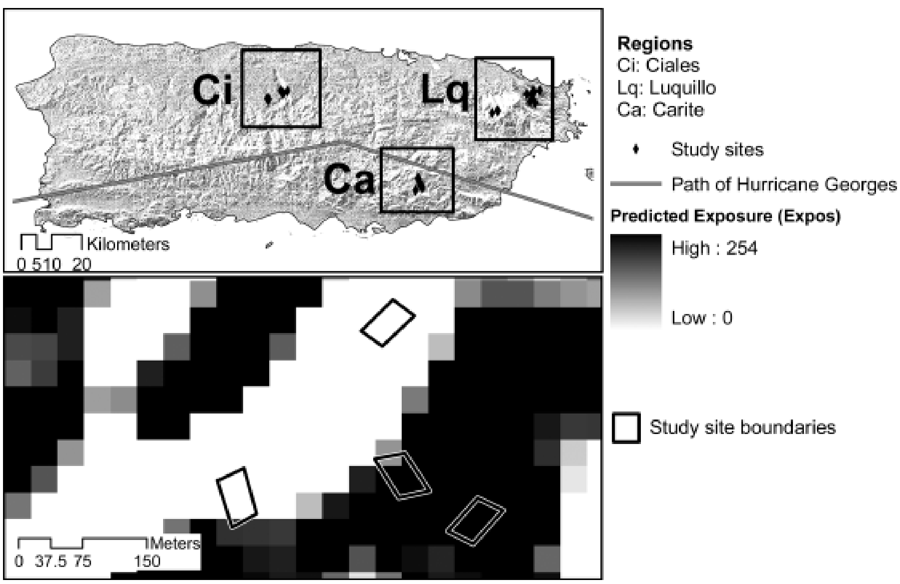

FIGURE 2. Locations of the three study regions that include the 37 secondary forest plots, and an example from Carite of the predicted exposure to winds from Hurricane Georges, based on the hurricane track, maximum wind speed, and topography. Note that two sites had high predicted exposure, while two adjacent sites, on the other side of a ridge, were much more protected.

site; if two corners were assigned exposure values of at least 0.5, the site was classified as exposed.

ANALYSES.—For each site, we calculated basal area (m^2/ha), stem density (number/ha), and species richness (number of species/ 0.12 ha). From these values, we derived importance values (IV), a measure of the average of the relative basal area and relative abundance of each species in a site. While we are confident that our study areas overlapped almost entirely with the original study areas, it was not possible to track growth or mortality of individual trees. To examine successional trajectories at our study sites, we relied on changes in stand composition and structure change for small trees, defined as trees $\leq$ 10 cm dbh, and large trees, those trees $>$ 10 cm dbh.

To assess how species composition changed between the two census periods, 3 yr before and 9 yr after Hurricane Georges, we used two approaches. First, we investigated how introduced tree species changed in relative importance in the stands. For each site we calculated the importance value (IV) for each species, then summarized these values within each region, distinguishing between sites exposed or protected from Hurricane Georges. We then examined the composition of the resulting species lists to assess how hurricane exposure affected abundance of introduced species.

Second, we looked at the changes in the overall community composition for the sites censused in both 1995/6 and 2007. In this analysis, we compared the identity and abundance of species found in a particular site between the two census periods using Chao's abundance-based index of similarity (Chao *et al.* 2005), which measures similarity in species composition of a given site between the censuses after accounting for differences in stem densities. We calculated the change in composition for both small and large trees and assessed differences in composition between age classes (three groups; under 40, 40–60, or $>$ 60 yr since abandonment) using one-way analyses of variance (ANOVA) and between exposure classes (two groups) using *t*-tests.

For stand structure, we used generalized linear models to: (1) focus on how stand age, exposure to the winds of Hurricane Georges (derived from our hurricane exposure model), and the interaction of these two factors determined the change in basal area and stem density; and (2) use stand age, exposure, and environmental factors to identify the strongest predictors of these changes. Environmental covariates included soil series, which can influence some aspects of stand structure (Pascarella *et al.* 2000) and composition (Thompson *et al.* 2002); elevation; and mean annual precipitation (Table 1). Models were compared using Akaike Information Criterion values. These two analyses were separated because age was correlated with elevation, and exposure with precipitation, complicating interpretation of the effects of stand age and exposure of forest structure (Table S1). All analyses were done using the statistical programming environment R (v2.6.2, R Development Core Team 2007).

RESULTS

The hurricane exposure model predicted a range of values for the 37 study sites of 0–0.7 (in unitless exposure values, with a potential maximum of 1; Fig. 2). Sites were predicted to be exposed and protected in each of the three study regions for Hurricane Georges, with overall mean value across the sites of 0.3. Predicted hurricane exposures were only correlated with precipitation (Table S1).

TABLE 1. *Summary of environmental covariates and sources used in this study.*

Variable	Range	Source
Age in 2007 (yr)	21–88	Pascarella *et al.* (2000), Rivera & Aide (1998)
Elevation (m)	30–710	Digital elevation model (SRTM)
Exposure	0–1	Expos model
Soil series	11 soil series	International Institute of Tropical Forestry, USDA
Region	Luquillo, Carite, Ciales	Geographic

STAND STRUCTURE.—As expected in a natural successional trajectory, stem density of small trees tended to decrease with age since abandonment, regardless of wind exposure, while both basal area and stem density of large trees increased (Table 2). Among large trees, exposure to the winds of Hurricane Georges, as calculated by the Expos model, increased stem density and basal area. The effect of the hurricane interacted with age since abandonment in the case of basal area, such that older sites experienced decreases in the basal area of large trees with increased exposure while younger sites experienced increases (Table 2; Fig. 3A and B). Thus, exposure interacted with age to make older sites resemble the stand structure of younger sites (delayed succession), in contrast to the hypothesis of accelerated succession.

However, changes in structure across all stands were in general most strongly predicted by stand age, precipitation, and soil type, rather than exposure to Hurricane Georges (Table S2). In particular, greater precipitation lead to increases in basal area and species richness for both small and large trees, as well as increase in basal area, stem density, and species richness of large trees. Different soil series exhibited strong effects on stand structure and composition. For example, stands on Caguabo soils demonstrated increases in the basal area, stem density, and species richness of large trees. Stem density of all trees and basal area of small trees decreased with stand age.

COMMUNITY COMPOSITION.—For all three regions, introduced species remained large components of the forest community between the 1995/6 censuses and 2007, but with substantial decreases in abundance and size, as reflected in changes in importance values (IV; Table S3). The two main introduced tree species, *Syzygium jambos* (Malagasy apple) and *Spathodea campanulata* (African tulip tree; hereafter both referred to by genus) demonstrated different patterns of change. *Spathodea* decreased sharply in importance in the Ciales region where it is most prevalent, regardless of hurricane exposure. This decrease, for both small and large trees, represented the largest change in IV across all species in Ciales, significantly

TABLE 2. *Summary of generalized linear model (GLM) results for change in stem density, species richness, and basal area from 1995/6 to 2007 due to stand age and exposure to the winds of Hurricane Georges, separately for small (dbh $\leq$ 10 cm) and large ($>$ 10 cm) trees.*

	Small Trees				Large Trees			
	Estimate	SE	*t*	*P*	Estimate	SE	*t*	*P*
Change in basal area								
Age	− 0.1	0.1	− 1.48		0.2	0.1	3.74	***
Exposure	43.7	21.9	1.99	†	38.0	16.0	2.37	*
Age × Exposure	− 1.0	0.5	− 1.87	†	− 0.901	0.4	− 2.31	*
Change in stem density								
Age	− 3.7	12.8	− 0.29	†	5.3	1.2	4.42	***
Exposure	2024	3825	0.53		750	357	2.10	*
Age × Exposure	− 28.6	93.3	− 0.31		− 16.7	8.7	− 1.92	†
Change in rarefied species richness								
Age	0.0	0.0	− 0.61		0.1	0.0	3.11	**
Exposure	− 1.7	5.8	− 0.30		7.2	5.2	1.38	
Age × Exposure	0.0	0.1	− 0.01		− 0.1	0.1	− 0.78	

†$0.1 < P < 0.05$; *$0.05 \geq P$; **$0.01 \geq P$; ***$0.001 < P$.

larger than any other species ($P < 0.001$, one-sample *t*-test for change in IV). Looking across all sites, *Spathodea* density tended to decline in sites exposed to the winds of Hurricane Georges ($P > 0.1$ for both large and small stems, two-sample *t*-test; Fig. 4). *Syzygium* fell in stem density overall in both exposed and protected sites, with no significant differences for tree size or site exposure ($P > 0.1$ for

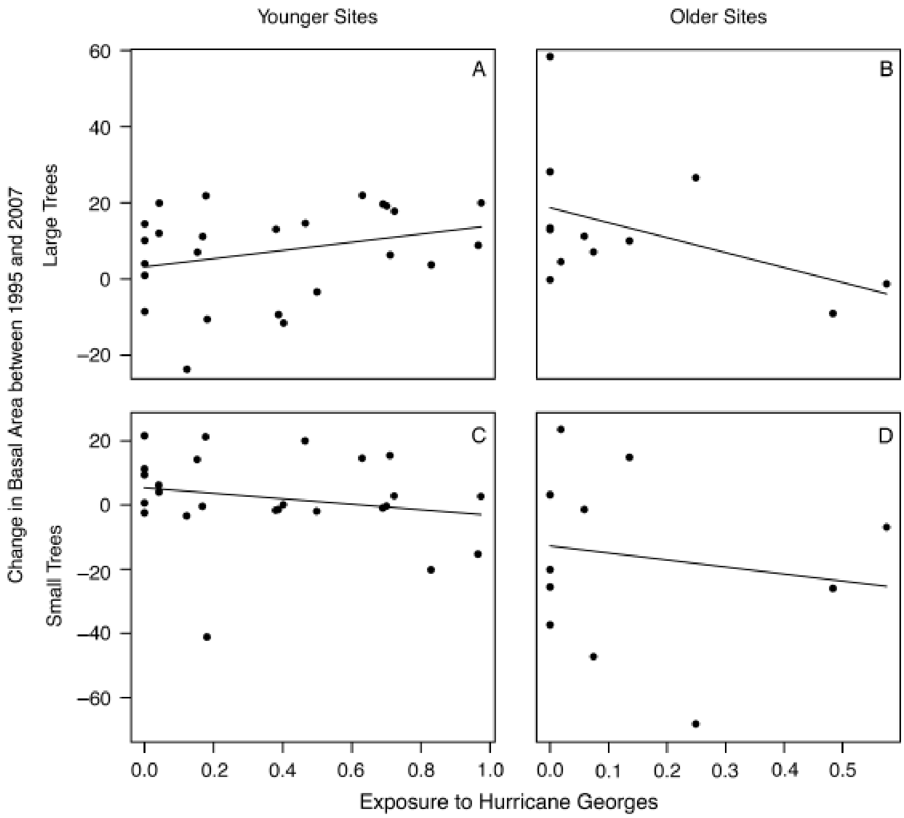

FIGURE 3. Change in the basal area of trees $>$ 10 cm dbh (A–B) and $\leq$ 10 cm dbh (C–D) in sites of potential exposure to Hurricane Georges (1998). Age classes: Younger: $\leq$ 50, Older: $>$ 50 yr since abandonment.

both large and small stems; Fig. 4). In the Luquillo region this species also declined in importance more than any other species ($P < 0.001$, one-sample *t*-test, both large and small trees), while in Carite it significantly increased in importance ($P < 0.001$, one-sample *t*-test, large trees; Table S3).

Species richness of large trees rose with stand age, but was not significantly influenced by hurricane exposure (Table 2; Fig. 5A and B). Among all drivers, greater precipitation drove higher species richness, as did different soil types to varying extents (Table S2). Looking in detail at species composition change using Chao's similarity index, we found that composition of small trees (dbh $\leq$ 10 cm) did not differ significantly across site ages (Fig. 5C). Exposure to Hurricane Georges (Fig. 5B) did not alter the compositional similarity of small trees ($t = 0.36$, $P = 0.71$). For large trees, compositional similarity rose with site age class ($F_{2,34} = 11.2$, $P = 0.002$), but did not change with exposure to hurricane winds ($t = 1.66$, $P = 0.10$).

DISCUSSION

These results present a mix of stand-level responses to the interaction between time since abandonment and hurricane disturbance. Changes in both basal area and stem density of large trees were influenced by hurricane disturbance, in ways that interacted with age since abandonment. Hurricane exposure and age interacted to result in an increase in basal area of large trees in young sites (accelerated succession) and decrease in basal area of large trees in older sites (delayed succession). However, site age and environmental drivers such as precipitation and soil type explain more of the change in stand structure than the hurricane exposure $\times$ age interaction. Changes in species composition demonstrated no clear patterns with stand age and hurricane disturbance, except that older sites had less species turnover. Overall, these results show that hurricane exposure can influence successional trajectory of forest stands, particularly by making older sites more similar in structure to younger sites. It is important to note that this study focuses on the effects of a Category 3 hurricane, which was relatively mild in strength compared with more severe hurricanes examined in other studies (*e.g.*, Vandermeer *et al.* 2000). Over 90 percent of the hurricanes in the Atlantic basin are Category 1–3 (NOAA, http://www.csc.noaa.gov/).

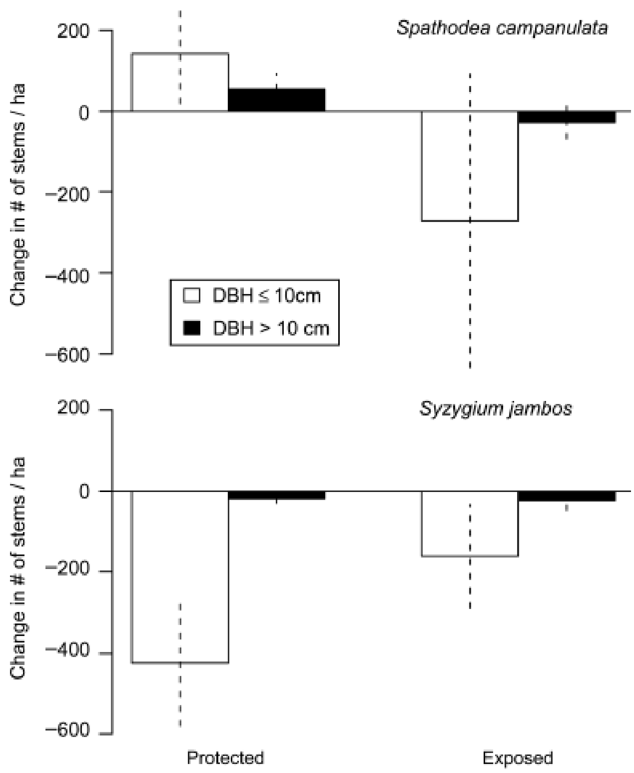

FIGURE 4. Change in number of small ($\leq$ 10 cm dbh) and large (> 10 cm dbh) stems per hectare between 1995 and 2007 of two introduced species, *Spathodea campanulata* and *Syzygium jambos*, in sites exposed or protected from winds of Hurricane Georges. Bars represent mean $\pm$ SE.

Time since abandonment of agriculture was the strongest and most consistent predictor of stand structure, following the pattern of steadily increasing basal area and declining stem density over the decades, as has been observed across Neotropical forests (Chazdon *et al.* 2007). In older sites with high hurricane exposure, larger trees declined in basal area, returning stands to an earlier successional stage (Fig. 3B and C). One possible mechanism may account for the divergence in the effects of hurricane exposure between old and young stands. We are assuming that larger trees are (1) more prevalent in older sites and (2) more susceptible to damage from hurricane winds (Xi *et al.* 2008). Therefore, older sites would be expected to experience a reduction in basal area and an increase in stem density as advanced regeneration of smaller trees took place over the scale of a decade following the hurricane.

Forest stands gained species in the mature size class as stands aged, again in accordance with previously observed trajectories of recovery (Chazdon 2003). However, community composition changes were large for all sites, particularly young sites, regardless of hurricane disturbance. No change in species richness was detected with varying exposure to hurricane winds, providing no support for previous observations of enhanced richness following a Category 4 hurricane (Vandermeer *et al.* 2000), and in contrast to the decrease in species richness observed by Pascarella *et al.* (2004) in a subset of these sites soon after Hurricane Georges. More important than overall patterns of species turnover or richness are the observed changes in the two most important introduced species in Puerto Rico, *Spathodea campanulata* and *Syzygium jambos*.

Agricultural history has a distinct and long-lasting effect on forest species composition (Chinea & Helmer 2003). For example, using some of the same sites as were used in this study, a recent study found that species composition between old growth forests and abandoned pastures remained distinct even after 80 yr, despite very rapid recovery of soil chemistry characteristics (Marin-Spiotta *et al.* 2007, 2008). Increased prominence of introduced species is one of the signatures of past agricultural use. Because the native pioneer species which start the successional pathway may not be able to colonize and persist in degraded agricultural land (Zimmerman

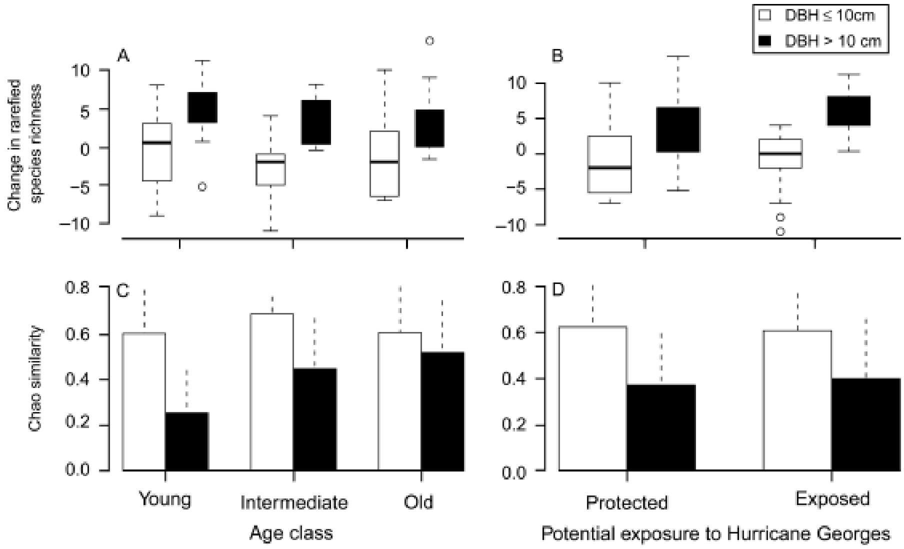

FIGURE 5. Comparison of species composition of sites in 1995 and 2007, using the Chao's abundance-based measure of vegetation dissimilarity (A and B) and change in sample-based rarefied species richness (C and D) for young, intermediate, or old sites or between sites exposed or protected to Hurricane Georges. Bars in A–B represents mean ± SE; whiskers in C–D represent 95% CI.

et al. 2000, Lugo 2004), introduced species can become dominant players in abandoned land. These novel communities, with many individuals of introduced species, may last for decades (Martin *et al.* 2004). Some forest managers argue that this phenomenon need not be viewed negatively, because it may be a necessary step for forest rehabilitation (Lugo 2004).

Spathodea and *Syzygium* together account for up to 15 percent of the forest importance value island-wide (Lugo 2004) and the latest forest inventory of the island calculated that *Spathodea* alone accounts for a third of island-wide tree volume in Puerto Rico (Brandeis *et al.* 2007). Although *Spathodea*, originally introduced as an ornamental and briefly used as coffee shade (Little & Wadsworth 1964), dominated abandoned pasture sites in north-central Puerto Rico, the dominance of shade-tolerant native species in the understory suggested that these species would eventually displace *Spathodea* (Little & Wadsworth 1964, Rivera & Aide 1998). This observation is consistent with the idea of introduced tree species in Puerto Rico having largely beneficial effects, in their ability to colonize degraded habitats and then gradually be replaced (Lugo 2004); we therefore take the point of view that declines in these introduced species constitute advancement along in the successional pathway. However, demographic work on *Syzygium* populations has shown that this species can persist and even expand its range within closed-canopy stands, regardless of soil nutrient status or distance to rivers (Brown *et al.* 2006). Thus, the question of whether these species will become wide-spread invasives or minor forest components as more of Puerto Rico's land reverts to forest remains open.

Introduced species such as *Spathodea* often have much greater susceptibility to wind effects than native trees (Lomascolo & Aide 2001), but some researchers argue that ability to rapidly re-grow may trump any heightened vulnerability to wind effects, allowing them to persist in hurricane-dominated landscapes (Lugo 2008). Our results show declines in *Spathodea* in all stands based on importance value, with a tendency for stronger declines in sites exposed to hurricane winds. *Syzygium* fell in importance in the Luquillo region, but continues to spread in the Carite region, with no difference in sites exposed to Hurricane Georges. Herbivory on *Syzygium* appears to have increased overall in recent years, particularly in gaps formed by hurricane blowdowns (M. Caraballo Ortiz, pers. obs.), indicating the potential for an indirect effect of hurricane effects on plant–animal interactions (Pascarella 1998).

Other recent work found that *Syzygium* abundance increased in areas disturbed by Hurricane Georges, and that *Spathodea* gradually increased in abundance regardless of hurricane disturbance (Thompson *et al.* 2007). The difference in results between the two studies is likely due to differences in particular location of the study sites. The results of Thompson and colleagues are drawn from a long-term forest dynamics study in the Luquillo mountains, where the most recent agricultural activity was in 1932, and both species were minor components of that forest (both under 0.6 m^2 ha). In contrast, we report results of decreased abundance and basal area of *Syzygium* and *Spathodea* in sites with a more recent range of agricultural use, and including several *Spathodea*-dominated sites in the Ciales region.

Recovery from hurricane disturbance can alter post-agricultural forest regrowth in several ways. Typically, the abundance of pioneer species decreases through succession. However, pioneer species have been observed to suffer much greater breakage, and resprout at lower rates as a consequence of strong hurricanes than nonpioneer species (Walker 1991, Zimmerman *et al.* 1994, Boucher *et al.* 2001). In addition, factors such as growth rate and stem density influence the amount of breakage experienced by trees (Lugo & Scatena 1996). Thus, we would expect that hurricane disturbance would decrease their abundance accelerating the expected change in species composition. The alteration of changes in stand structure, however, requires further study. Much of the variations in dynamics among plots may be due to differences in the landscape surrounding our plots, which we did not directly examine here.

We have shown that stands of different ages respond in contrasting ways to hurricane disturbance, such that the hurricane event led to more rapid declines in the density and basal area of large trees in older sites. This result suggests a homogenizing effect of hurricane disturbance on stand structure, as older and younger forest stands become more similar in forest structure. However, age and environmental factors remain the strongest predictors of changes in stand structure and composition. If confirmed by further study, our results indicate that management of forest stocks in an age of widespread forest transitions (Rudel *et al.* 2005) and increased hurricane activity (Webster *et al.* 2005) should consider how to integrate both land use history and predicted exposure to hurricane winds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Spearman correlation coefficients between predictor variables of stand structure and composition.*

TABLE S2. *Summary of best-fit generalized linear model (GLM) results for change in basal area, stem density, and species richness from 1995/6 to 2007, separately for small and large trees.*

TABLE S3. *The ten largest changes in importance value (IV) in sites of each study region protected from and exposed to Hurricane Georges (1998), as estimated by the Expos model.*

LITERATURE CITED

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