Response to Hurricanes of *Pinus caribaea* var *hondurensis* Plantations in Puerto Rico

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Abstract - We studied the response to hurricanes of 2 *Pinus caribaea* Morelet var. *hondurensis* Barr. & Golf. (Honduran Pine) plantations and paired secondary forests over a period of 32 years (1982 to 2014). Plantations differed in age (38 and 53.5 years old), as did the paired secondary forests. The study included the passage of 2 hurricanes (1989 and 1998). The hurricanes altered forest structure by lowering the basal area and tree density, accelerated tree mortality to over 5% per year and ingrowth rate to over 200 stems/ha at the Cubuy plantation, caused variability and reduction in individual tree growth rates, and dramatically changed species composition and dominance of stands. Honduran Pines were heavily affected by the hurricanes, losing dominance, and almost disappearing from the Cubuy site, in effect converting that pine plantation into a secondary forest with few pines. The susceptibility of Honduran Pine to strong winds raises concern about its suitability for plantation forestry in the hurricane belt of the Caribbean. Their use for commercial timber production would have to consider the recurrence of hurricanes in the region.

Introduction

The suitability of introduced species for plantation forestry is usually assessed through planting trials that might or might not last through the expected rotation times for the species under consideration. In regions such as the Caribbean with large and infrequent disturbances (LID), it may be possible to test species suitability during disturbance-free periods and thus miss their response to LID events that can transform stands and uncover a vulnerability to those LID events. This may be the case for *Pinus caribaea* Morelet var. *hondurensis* Barr. & Golf. (Honduran Pine), a lowland tropical pine species variety from Central America that was widely tested and found suitable for plantation forestry in Puerto Rico after several decades of research between the 1960s and 1980s (e.g., Briscoe 1959, 1962; Liegel 1984a; Whitmore and Liegel 1980). That period of time was almost hurricane-free in the island, allowing experimental plantations to accumulate large wood volumes and exhibit high timber yields (Francis 1995, 2000; Liegel 1984a; Lugo 1992). The passage of 2 hurricanes, in 1989 and 1998, over our study sites gave us the opportunity to examine both the immediate and long-term effects of LID events on the suitability of Honduras Pine to the Caribbean island region.

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Field Site Description

The field sites and methods used in this research follow those described by Lugo (1992) for a comparative study of Honduran Pine and *Swietenia macrophylla* King (Big-leaf Mahogany) tree plantations with paired secondary forests. Plantations and paired secondary forests were located next to each other, and had the same aspect and land-use history (Lugo 1992). The study was conducted in the lower elevations of the Luquillo Experimental Forest/El Yunque National Forest, PR, USA (Fig. 1). All sites are in the subtropical wet forest life zone sensu Holdridge (1967).

Methods

We studied the 2 pine plantations and their paired secondary forest stands dominated by native tree species. Plantations were established in 1976 (Guzmán) and 1961 (Cubuy) with tree spacing of 3 m by 3 m (Lugo 1992). Secondary forests were of similar age and grew under similar conditions as their paired tree plantations. We re-measured all study-site trees in 2007 and 2014 and tagged and identified to species untagged trees in a 40 m by 50 m plot in each plantation and paired secondary

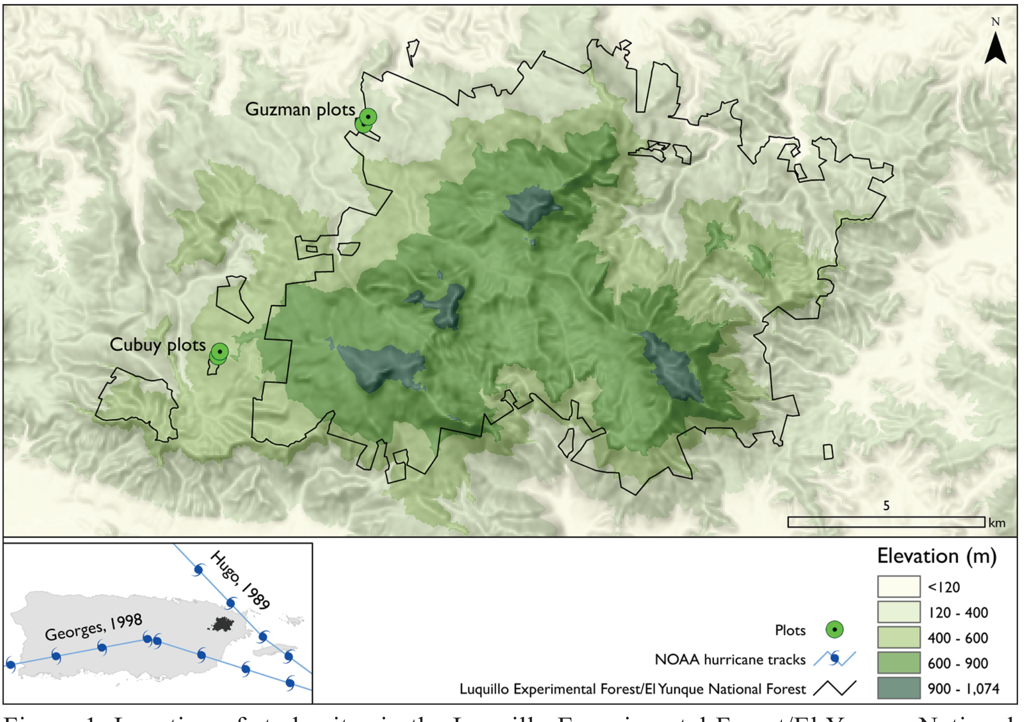

Figure 1. Location of study sites in the Luquillo Experimental Forest/El Yunque National Forest. The plantation and paired secondary forest were adjacent to each other at each site. Topographic elevations and the trajectory of hurricanes Hugo and Georges are shown. The locations correspond to latitude 18°N and longitude 65°W. The plot locations in minutes and seconds of latitude and longitude (respectively) are as follows: Cubuy pine plantation: 16'32.13" and 52'10.03"; Cubuy secondary: 16'36.01" and 52'08.29"; Guzmán pine plantation: 19'49.66" and 49'59.41"; and Guzmán secondary: 19'43.38" and 50'03.34".

forest. All trees with a diameter at breast height (dbh; 1.37 m off the ground) of >4.0 cm were measured and identified to species. Before our 2007 and 2014 measurements, trees had been tagged, identified to species, and measured in 1982, 1984, 1989, and 1990. The Cubuy plantation was also re-measured in 1996. In 2014, the plantations were 38 (Guzmán) and 53.5 (Cubuy) years old.

Hurricanes Hugo (in 1989) and Georges (in 1998) affected the stands after they were first measured in 1982 to 1984 by Lugo (1992). Rodríguez Pedraza (1993) reported the immediate effects of Hurricane Hugo on all plantations and paired secondary forest sites and reported the changes in basal area and tree density between 1982 and 1990 used here.

We added 2007 and 2014 estimates of basal area, tree density, species density and importance value (IV), tree ingrowth rates, tree mortality rates, and tree basal-area growth rates to available data from previous measurements in both pine plantations and paired secondary forest stands. Stand basal area was the sum of individual tree basal area divided by plot area. Individual tree basal area was derived from dbh measurements. Tree density was the number of trees divided by plot area. Species density was the number of tree species per area sampled (0.2 ha). A species IV is its relative density plus its relative basal area expressed in percent. Species relative tree density and relative basal area are expressed in percent of the stand's total tree density and basal area, respectively. We ranked species by their IV and constructed IV curves sensu Whittaker (1970). We also calculated the Sørensen similarity index (Sørensen 1948) for plantation and secondary forest species assemblages at different times throughout the study.

Tree ingrowth rates were the number of trees entering the 4-cm dbh class since the previous re-measurement divided by the elapsed time in years. Similarly, tree mortality was the number of trees that died between measurement intervals divided by the elapsed time between measurements. Mortality rates were also expressed as the percent of trees dying relative to the number of live trees at the beginning of the interval, divided by the time elapsed. We estimated individual tree growth by species at the Cubuy site for 6 time intervals: 1982–1990, 1982–1996, 1990–1996, 1990–2007, 1996–2007, and 2007–2014. Estimates were based on the change in basal area of tagged trees during the interval divided by the elapsed time in years.

Results

Forest structure

Tree density declined before the 1989 hurricane in all stands (Fig. 2). Tree density also declined in all stands after the 1989 hurricane and reached a low value in the 1996 measurement of the Cubuy plantation. By 2007, all stands had higher tree densities than when initially measured in 1982, with the exception of the Cubuy secondary forest. Between 2007 and 2014, all stands exhibited a reduction in tree density (Fig. 2). Between 1982 and 1990, tree density in the Cubuy secondary forest was higher than in the paired pine plantation, and the pattern reversed between 2007 and 2014, with the pine plantation exhibiting a higher tree density than the paired secondary forest. The opposite pattern was observed in the paired Guzmán plantation and secondary forest, with higher initial tree density in the Guzmán plantation and higher tree density in the paired secondary forest than in the Guzmán plantation between 2007 and 2014 (Fig. 2).

Basal area in the Cubuy plantation declined after the 1989 hurricane, reaching a low value just before the 1998 hurricane (Fig. 3). The post-hurricane increase in basal area after 1996 was relatively slow at the Cubuy plantation, and values

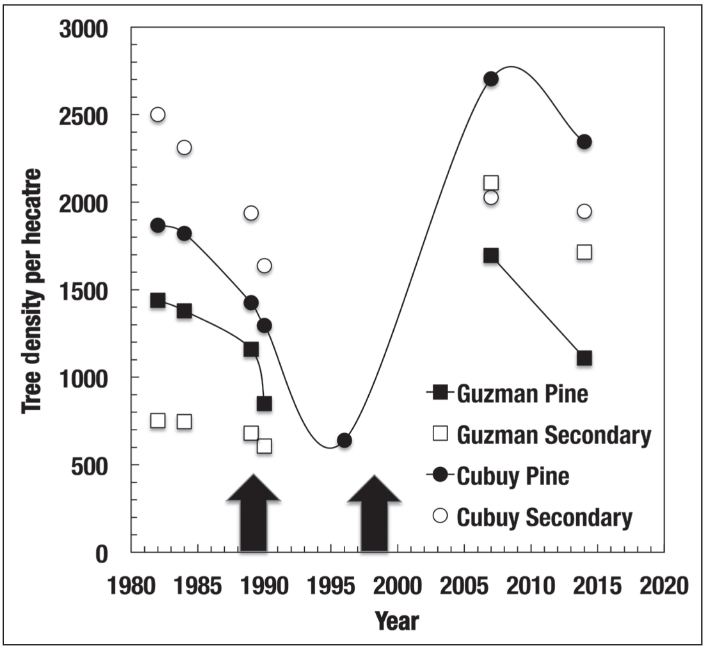

Figure 2. Tree density in *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations and paired secondary forests at 2 sites in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998 (black arrows). Data are for all trees with dbh > 4 cm. The lines connecting data points are for illustrative purposes only.

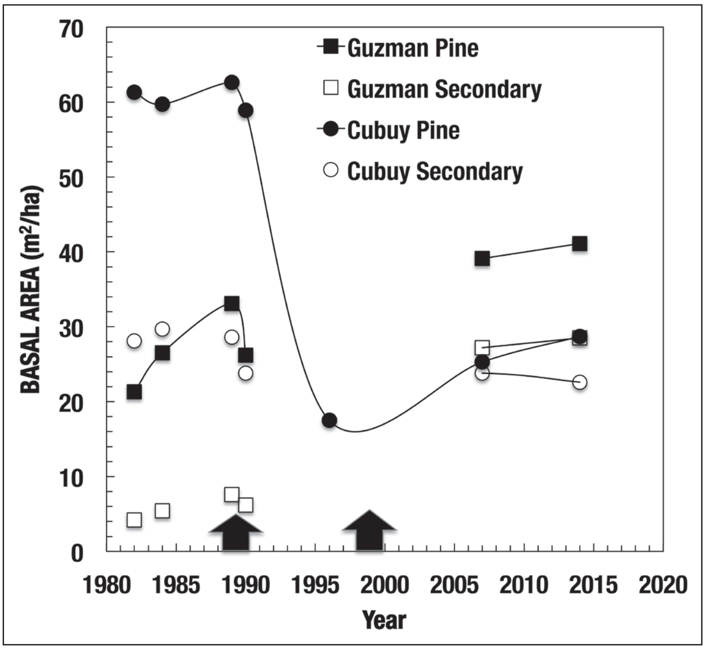

Figure 3. Tree basal area in *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations and paired secondary forests at 2 sites in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998 (black arrows). Data are for all trees with dbh > 4 cm. The lines connecting data points are for illustrative purposes only.

remained below those at the beginning of the study in 1982. However, the basal area of the Guzmán plantation was increasing before the 1989 hurricane, decreased as a result of the hurricane, and reached its highest values between 2007 and 2014. The two pine plantation stands always had higher basal area than the corresponding paired secondary forest. After the passage of the 1998 hurricane, the Guzmán plantation had a higher basal area than the Cubuy plantation. The Cubuy secondary forest lost some basal area after the 1989 hurricane but in general retained a similar level of its pre-hurricane basal area. The Guzmán secondary forest also lost some basal area after the 1989 hurricane but by 2014 had a higher basal area than the Cubuy secondary forest (Fig. 3). Both secondary forests had a lower basal area than their paired plantations.

Forest processes

Annual tree mortality exceeded 5% in all stands immediately after hurricane Hugo in 1989 and was 6.8% in 2007 at the Cubuy plantation 9 years after the passage of hurricane Georges in 1998 (Fig. 4). Before 1989 and by 2014, annual tree mortality rates were well below 5% in all stands. The Guzmán plantation experienced almost 3 times the tree mortality rate observed in the Cubuy plantation after the 1989 hurricane. After the 1989 hurricane, the Cubuy plantation experienced less tree mortality than both of the secondary forests, but the Cubuy secondary forest

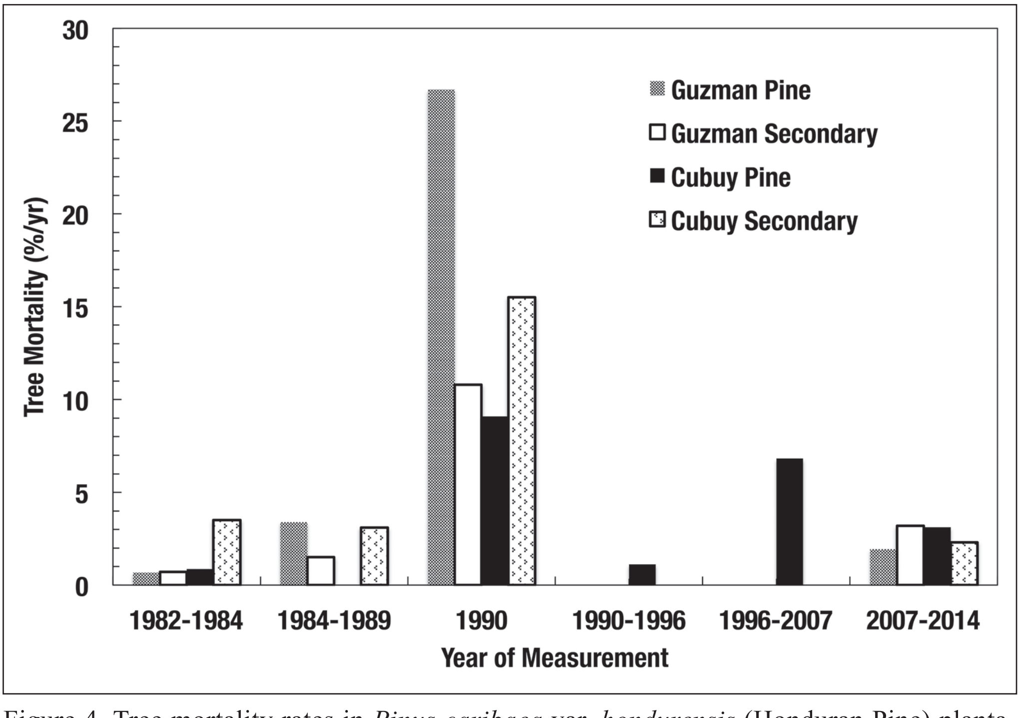

Figure 4. Tree mortality rates in *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations and paired secondary forests at 2 sites in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998. The 1990 data represents the instantaneous hurricane-induced tree mortality. Data are for all trees with dbh > 4 cm.

experienced higher tree mortality than the Guzmán secondary forest or the Cubuy plantation. All forest stands had similar low levels of tree mortality in 2014.

By 2007, the Cubuy plantation had a high rate of tree ingrowth and so did the other three stands but at much lower levels (Fig. 5). In 2014, ingrowth levels in all stands were lower than before the 1989 hurricane.

The basal area growth rate of trees in the Cubuy plantation exhibited a shift in the frequency of observed growth rates from prior to the hurricanes during 1982–1990 to after the hurricanes during 2007–2014 (Fig. 6). Before the hurricanes,

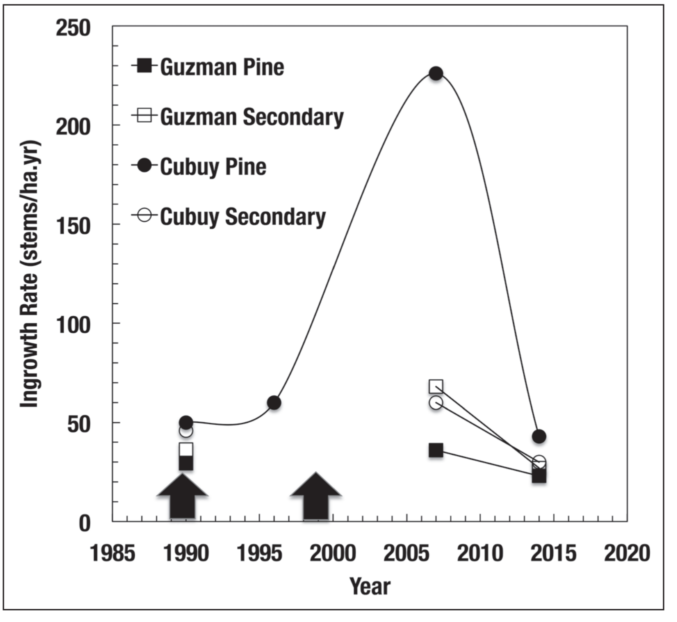

Figure 5. Tree ingrowth to the 4-cm diameter class or higher in *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations and paired secondary forests at 2 sites in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998 (black arrows). Data are for all trees regardless of species. The lines connecting data points are for illustrative purposes only.

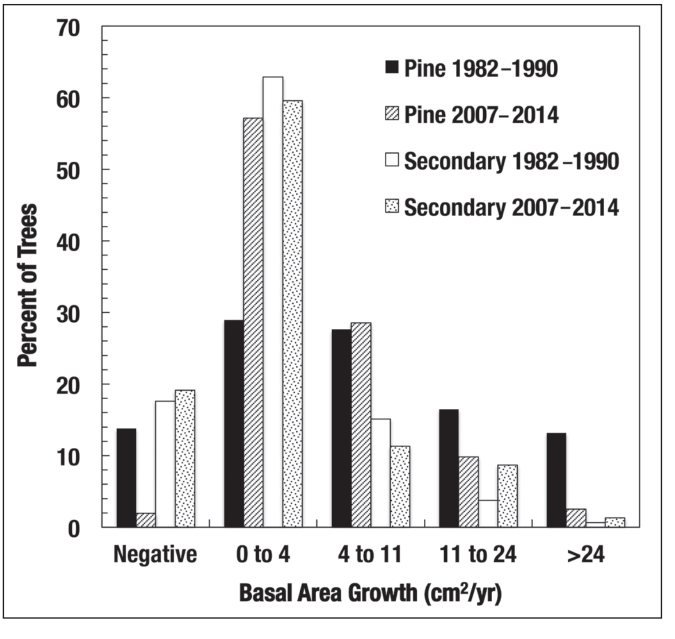

Figure 6. Histogram of basal area tree growth in *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations and paired secondary forests in Cubuy, Luquillo Experimental Forest. Hurricanes affected the site in 1989 and 1998. Data are for all trees with dbh > 4 cm.

~30% of the trees in the plantation grew at rates that exceeded 11 cm^2/yr and the slower growing trees (0 to 4 cm^2/yr) comprised ~28% of plantation trees. In the 2007–2014 interval, fast growing trees represented ~10% of the trees while ~60% of the trees were growing at rates below 4 cm^2/yr. Basal area growth in the Cubuy secondary forest did not change over the same time interval, as slower growing trees were always prevalent at this site (Fig. 6).

The average growth rate of pines was always faster and more variable than tree growth of non-plantation species at Cubuy, except after the 1998 hurricane when surviving trees grew at very low rates, resuming faster growth rates between 2007 and 2014 (Fig. 7). During the 2007–2014 interval, 2 common secondary forest species growing in the pine plantation exhibited contrasting growth rates, with the native *Tabebuia heterophylla* (DC.) Britton (White Cedar) sustaining a faster growth rate than the non-native *Syzygium jambos* (L.) Alston (Rose Apple) (Fig. 8).

Forest species composition and dominance

The species density of the surveyed stands changed throughout this study, with a convergence by 2014 among stands in the number of species (Fig. 9). In general, the plantations gained species while the secondary forests lost species. The species IV curves (Fig. 10) show that dominance (the IV for the species ranked 1) was higher in the plantations than in the paired secondary forest and tended to decline over time. Also, as the dominance decreased, the IV curve had more species and the initial steepness of the curve for the top ranked species declined. As plantations

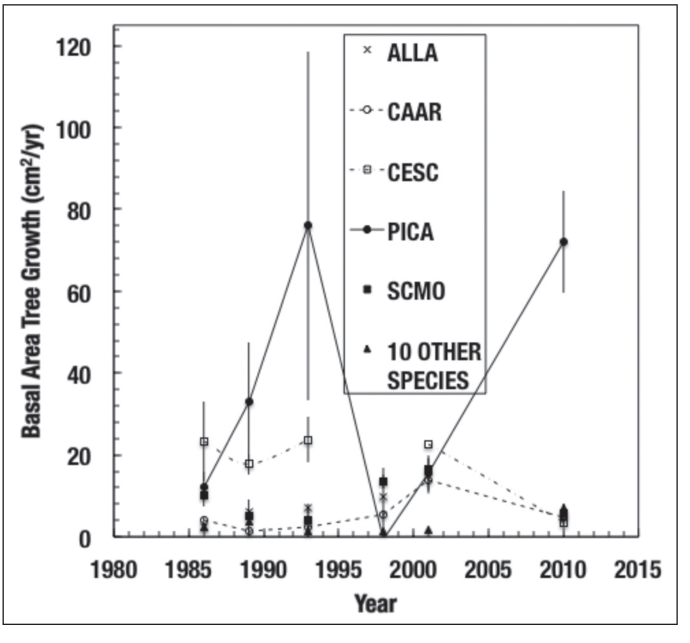

Figure 7. Basal area growth of selected tree species in a *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantation in Cubuy, Luquillo Experimental Forest. Hurricanes affected the site in 1989 and 1998. The species codes and number of trees (for 1982–1990, 1982–1996, 1990–1996, 1990–2007, 1996–2007, and 2007–2014 intervals) respectively, are: *Alchornea latifolia* (ALLA: 3, 2, 3, 1, 0, 28), *Casearia* arborea (CAAR: 17, 5, 8, 7, 4, 190), *Cecropia schreberiana* (CESC: 10, 4, 5, 0, 1, 30), *Pinus caribaea* var *hondurensis* (PICA: 79, 15, 10, 4, 1, 3). *Didymopanax morototoni* (synonymous with *Schefflera morototoni*; SCMO: 40, 18, 21, 13, 6, 41), other 10 species: 5, 3, 5, 1, 1, and 65. Error bars correspond to the standard error of the mean. Data are for trees with dbh > 4 cm.

aged, they lost dominance and gained species. The dominance of secondary forests remained more similar within stands as they aged.

The identity and IV of the top 2 ranked species changed throughout the study in all stands (Table 1). There was no change in the top-ranked species at the Guzmán site, but the second-ranked species changed in both the plantation and paired secondary forest. The second-ranked species gained IV over time. At the Cubuy plantation, the top-ranked, but not the second-ranked, species changed. At the Cubuy secondary

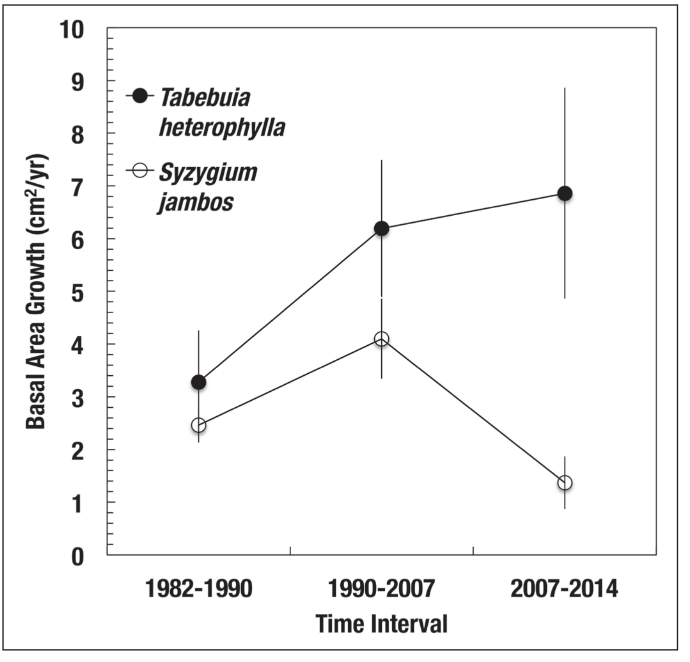

Figure 8. Basal area tree growth of 2 species inside a *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantation in Cubuy, Luquillo Experimental Forest. Hurricanes affected the site in 1989 and 1998. The species codes and number of trees for the 1982–1990, 1990–2007, and 2007–2014 intervals, respectively, are: *Tabebuia heterophylla* (TAHE, 35, 23, 28) and *Syzygium jambos* (45, 21, 65). Error bars correspond to the standard error of the mean. Data are for trees with dbh > 4 cm.

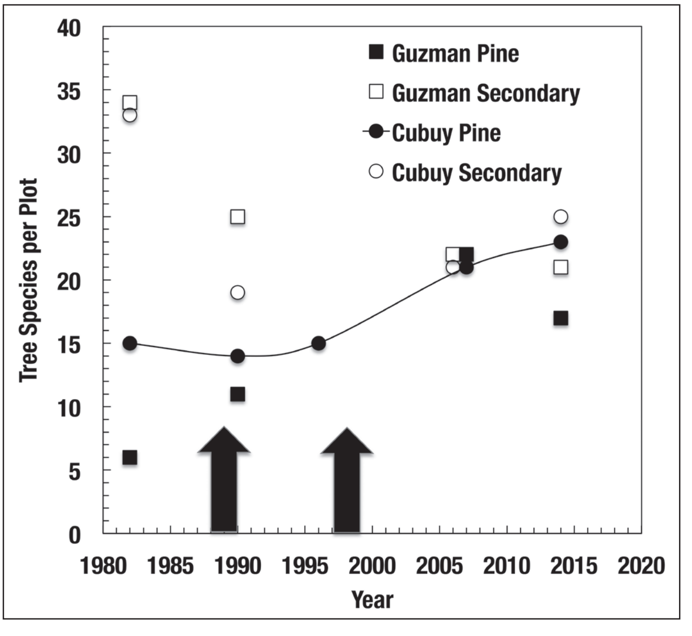

Figure 9. Species density in *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations and paired secondary forests at 2 sites in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998 (black arrows). The line connecting data points is for illustrative purposes only. Data are for trees with dbh > 4 cm in 0.2-ha plots.

forest, the top-ranked species changed in 2007 but regained top ranking in 2014, after alternating with the second-ranked species. The IV of pines declined in both plantations throughout the study (Fig. 11). In Cubuy, pines almost disappeared, while at Guzmán they lost almost half of their original IV. The distribution of trees by diameter class at the Cubuy plantation in 2014 showed the dominance of the 5–10-cm dbh class and the loss of the large pines measured in 1982 (Fig. 12).

Discussion

The results of this study are influenced by stand age, temporal succession, hurricane effects, and by the characteristics of the species involved. When these stands were first surveyed in 1982, the plantations were 4 years and 18.5 years old. While the study stands maintained their age differential at the time of this later study, they were 32 years older and thus temporal successional effects had come into play as well as the age of the forest.

Temporal succession affects the pattern of change in parameters, whereas age effects influence the level that parameters reach at a given moment. Therefore, the differences in tree density (Fig. 2), basal area (Fig. 3), and species density (Fig. 9)

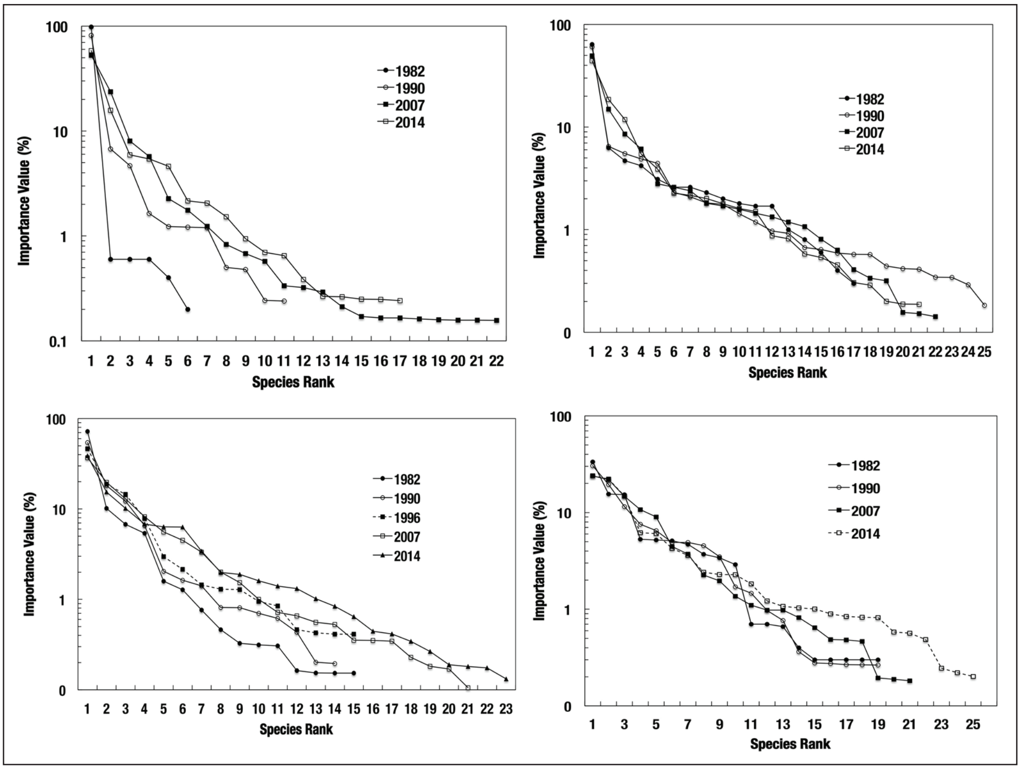

Figure 10. Importance value curves for different years for *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantations (left column) and paired secondary forests (right column) at 2 sites (Guzmán [top panels]; and Cubuy [bottom panels]) in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998. Data are for trees with dbh > 4 cm.

before 1989 reflect age differences between stands, while the direction of change in these parameters reflect temporal successional phenomena such as stand thinning and growth reflected in basal area increases. Succession processes also explain stand changes between 2007 and 2014 (Figs. 2, 3, 4, 5), which reflect stand thinning, growth of trees, and low tree mortality and ingrowth a decade or more after the passage of the 2 hurricanes.

Tree mortality (Fig. 4) and ingrowth (Fig. 5) rates were low during the early and end periods of the study relative to elevated rates in the years more immediately following the hurricanes. Lugo and Scatena (1996) suggested that tropical forests typically had background rates of tree mortality lower than 5% per year. The passage of hurricane Hugo changed stand structural and functional parameters as well as the immediate direction of successional processes.

Table 1. The first and second ranked species in Honduran Pine plantations and paired secondary forests at 2 sites in the Luquillo Experimental Forest, PR, over time. Importance value (IV) for each is given below the species name. The years correspond to the inventory of vegetation. Hurricanes Hugo and Georges affected the sites in 1989 and 1998, respectively. *Schefflera morototoni* (Aubl.) Maguire, Steyerm., & Frodin (Matchwood) is synonymous with *Didymopanax morototoni* (Aubl.) Decne. & Planch.

Site/	Pine plantation		Secondary forest	
year	First rank	Second rank	First rank	Second rank
Guzmán				
1982	*Pinus caribaea** 97.7	*Myrcia splendens* 0.6	*Tabebuia heterophylla* 63.8	*Miconia prasina* 3.1
1990	*Pinus caribaea** 81.8	*Miconia prasina* 6.8	*Tabebuia heterophylla* 61	*Psidium guajava** 6.5
1996				
2007	*Pinus caribaea** 52.8	*Miconia tetranda* 23.7	*Tabebuia heterophylla* 49.46	*Calophylum calaba* 15
2014	*Pinus caribaea** 58.6	*Miconia tetranda* 15.8	*Tabebuia heterophylla* 44.1	*Calophylum calaba* 18.6
Cubuy				
1982	*Pinus caribaea** 72	*Schefflera morototoni* 10.2	*Tabebuia heterophylla* 33.4	*Syzygium jambos** 15.5
1990	*Pinus caribaea** 71.5	*Schefflera morototoni* 10.4	*Tabebuia heterophylla* 30.4	*Syzygium jambos** 19.5
1996	*Pinus caribaea** 46.1	*Schefflera morototoni* 18.8		
2007	*Cyathea arborea* 37	*Schefflera morototoni* 19.8	*Syzygium jambos** 23.9	*Tabebuia heterophylla* 21.9
2014	*Cyathea arborea* 38.8	*Schefflera morototoni* 15.4	*Tabebuia heterophylla* 24.1	*Syzygium jambos** 22.2

* Naturalized species.

Hurricane effects

The immediate (less than a decade) effects of hurricanes on the structure of tropical forests have been well documented and understood, and our results are consistent with published literature (Lugo 2008). Hurricane winds open forest canopies; cause greater effects on large trees relative to small ones (Fig. 12), cause elevated tree mortality rates above 5% per year (Fig. 4), reduce tree growth rates (Fig. 6), increase the variability of individual tree growth rate (Fig. 7), accelerate tree ingrowth rates (Fig. 5), cause lag effects on post-hurricane mortality (e.g., the 6.8% per year 9 years

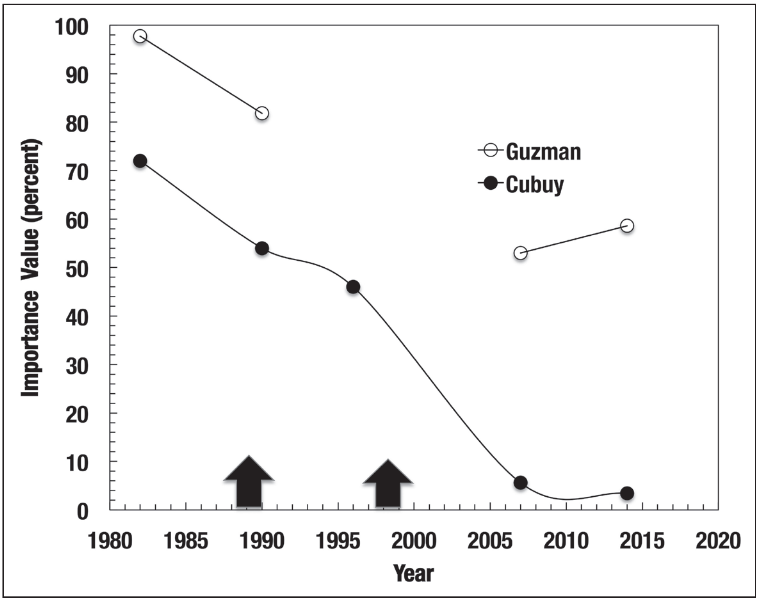

Figure 11. Importance value of *Pinus caribaea* var. *hondurensis* (Honduran Pine) over time at 2 sites in the Luquillo Experimental Forest. Hurricanes affected the sites in 1989 and 1998 (black arrows). Data are for trees with dbh > 4 cm.

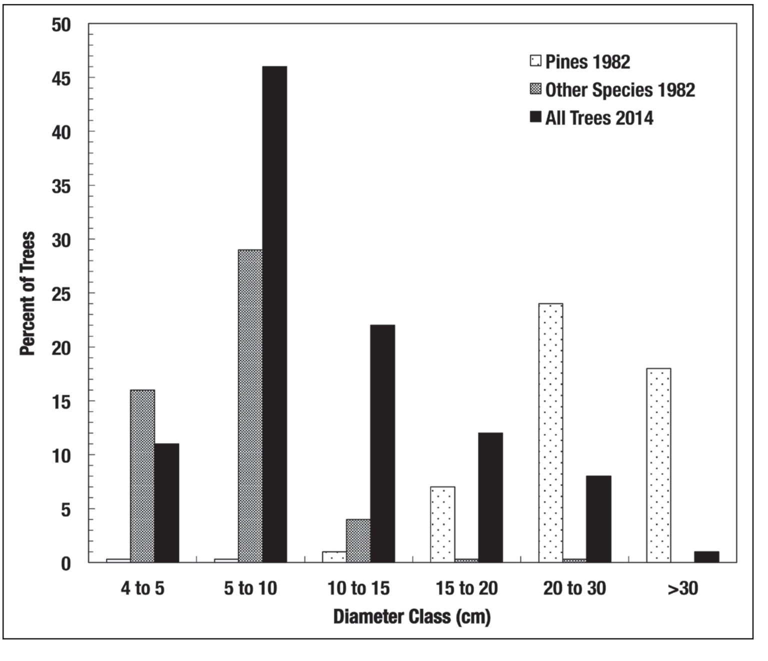

Figure 12. Histogram of tree diameter classes at a *Pinus caribaea* var. *hondurensis* (Honduran Pine) plantation in Cubuy, Luquillo Experimental Forest in 1982 and 2014. Hurricanes affected the site in 1989 and 1998.

after Hurricane Georges in Fig. 4), and cause dramatic changes in tree density and basal area (Figs. 2, 3). The maximum basal area measured in the Guzmán plantation was half the basal area observed in the Cubuy plantation at similar ages (Fig. 3). We attribute this lower value to the cumulative effects of the 2 hurricanes, which greatly affected and killed the fast-growing pines.

A surprising finding was the disproportional effect of hurricane winds on Honduran Pine growth (Fig. 6) and IV (Fig. 11). Surviving pines experienced a reduction in growth, and an increased variability in growth rates after the hurricanes as a result of canopy and branch loss (Rodríguez Pedraza 1993). Pines also lost dominance in the plantations and almost disappeared in the Cubuy plantation, resulting in the transformation of the plantation into a secondary forest dominated by non-plantation tree species (Fig. 9, Table 1). As the pines lost dominance, the difference in IV between the top- and second-ranked species diminished, reflecting the increasing number of species in the stands as a result of increasing ingrowth rates in the developing secondary forests (Fig. 5).

The hurricanes had a greater effect on pine trees that had reached large diameter classes (Fig. 12). With the fall of these large trees, the canopy opened to a greater extent than it would have opened by slower tree mortality due to age. A succession of non-plantation tree species was initiated as a result of the loss of canopy due to the hurricanes. The plantations became enriched with other tree species at the expense of the declining pines (Fig. 9). The growth of non-plantation tree species in plantations varied by species (Fig. 8), thus affecting which species would prevail over the long-term. In Cubuy, the dominant species was *Cyathea arborea* (L.) J.E. Smith (West Indian Treefern), a species that requires high levels of light and whose presence reflected the large canopy openings as a result of the fall of large pine trees. Nearby *Prestoea montana* (Graham) G. Nicholson (Sierran Palm) brakes had similar changes in their top dominant species when the same hurricanes affected them (Lugo and Frangi 2016). While *C. arborea* increased in IV in the palm brakes after the hurricanes, the species that dominated in those forests was *Cecropia schreberiana* Miq. (Yagrumo Hembra), another indicator species for large canopy openings.

Change in species dominance of stands is a function of the strength of hurricane effects, which in turn is influenced by the aspect of forests (Boose et al. 1994). Our results are consistent with those of Lugo and Frangi (2016) for palm brakes and *Dacryodes excelsa* Vahl (Tabonuco) forests nearby. They suggest that the Guzmán plantation was located windward to the 1989 hurricane Hugo's winds and leeward to those of 1998 hurricane Georges. The Cubuy plantation had the opposite aspect effect, i.e., it was windward to hurricane Georges and leeward to hurricane Hugo winds. Figure 1 illustrates the positioning of the plots relative to the trajectory of the hurricanes. Thus, the Guzmán plantation was more affected by hurricane Hugo, and the Cubuy plantation was most affected by hurricane Georges. By 2014, forest processes had returned to pre-hurricane rates while stand structure and species composition had not because stand age and temporal successional effects precluded a return to 1982 values.

Comparison of plantations with secondary forests

Before the 1989 hurricane, the plantations had lower tree density, higher basal areas, lower species densities, and higher dominance than the paired secondary forests (Figs. 2, 3, 9, 10). Tree growth rates (Fig. 6) were faster in the plantation (because of the pines; Fig. 7) than in paired secondary forests, but rates of tree mortality and ingrowth were similar (Figs. 4, 5). Plantations experienced a greater loss of basal area and biomass after hurricane Hugo than did the secondary forests (Rodríguez Pedraza 1993), but the hurricane-induced rates of tree mortality were different (Fig. 4). The differences in biomass and basal area reduction probably reflect the greater structural development of the plantations relative to the secondary forests. Also, plantation trees allocate less biomass to roots than secondary forests (Lugo 1992). The observed differences in tree mortality rates were probably due to aspect in relation to wind direction (discussed above). Convergence in tree density, basal area, and species density occurred among paired stands as species composition changed in the plantations with the loss of pine dominance and ingrowth of non-plantation tree species, i.e., the plantations became secondary forests and in so doing, gained species, had smaller and younger trees, and had more of them.

Over the course of the study, the species assemblages of plantations and secondary forests changed in composition resulting in dramatic differences in their similarity (Table 2). The Cubuy plantation species assemblage of 1982 was 60% similar to its 1996 species assemblage and 67% similar to its 2007 species assemblage. By 2014, the Cubuy plantation species assemblage was 90% similar to its 2007 species assemblage but only 36% similar to the paired secondary forest. Low similarity values were also observed in the paired Guzmán plots, which suggest that the plantations are evolving with species assemblages that are different from those of the secondary forests.

Honduran pine vulnerability to wind and implications to plantation forestry

The US Forest Service introduced pines to Puerto Rico in 1932 as a plantation species with multiple uses (Briscoe 1959, Francis 2000, Wadsworth 1976). Honduran pines not only yield large volumes of high quality lumber but they are also used

Table 2. Sørensen similarity index for various combinations of plantations and paired secondary forests.

Comparison	Similarity (%)
Cubuy pine 2007 vs. 2014	93
Guzmán secondary 2007 vs. 2014	90
Cubuy secondary 2007 vs. 2014	84
Guzmán pine 2007 vs. 2014	79
Cubuy pine 1996 vs. 2007	67
Cubuy pine 1982 vs. 1996	60
Guzmán pine 2014 vs. Guzmán secondary 2014	54
Cubuy pine 2007 vs. Cubuy secondary 2007	45
Guzmán pine 2007 vs. Guzmán secondary 2007	42
Cubuy pine 2014 vs. Cubuy secondary 2014	36

for posts, furniture, making paper, ornamental purposes, resins, tannins, fuelwood, rehabilitation of degraded soils, and many other applications. Honduran Pine was planted in many areas globally, including widely throughout the Caribbean, particularly in Jamaica where large-scale plans for a timber-exporting industry were formulated and initiated in the Blue Mountain region (Greig and Foster 1982). The passage of hurricane Allen over the region in 1980 caused extensive reductions in the standing timber on pine plantations and exacerbated attacks of the fungus *Fomes annosus* (now *Heterobasidion annosum* (Fr.) Bref.), which causes disease and mortality to pines (Thompson 1983). Thirty percent pine mortality due to this fungus was observed in the first thinning before the hurricane, and the problem increased after the hurricane (Greig and Foster 1982). Subsequent studies demonstrated the susceptibility of Honduran pines to windthrow and to mortality as a result of windstorms in Puerto Rico (Liegel 1982, 1984 b, 1984c; Rodríguez Pedraza 1993; this study), the Dominican Republic (Gannon and Martin 2014), and Central America (Boucher et al. 1990).

Our long-term study of paired plantations and secondary forests documented the reduction in the IV of Honduran Pine after the hurricanes and the establishment of non-plantation tree species in the recovering forest stands. The suitability of Honduran Pine as a plantation species is thus diminished in the Caribbean by its vulnerability to hurricane winds, but the importance of the species for forestry purposes remains high because of its many advantages, including rapid growth, low nutrient requirements, growth versatility under varied environmental conditions, high wood quality, and diversity of uses (Francis 2000). Wadsworth (1976) pointed out that even if hurricanes were to affect plantations of Honduran Pine, its wood could be salvaged for other uses, even at the early age of 5 yr. Moreover, ecological research suggests the compatibility of pine plantations with some plant (Lugo 1992, this study) and animal taxa (Collazo and Bonilla Martínez 1988, Cruz 1998, Lugo 1992, Lugo et al. 2012, Mott et al. 2010) and the desirability of using Honduran Pine for the restoration of tree species diversity and productivity on degraded sites to "jump-start" succession (Lugo 1997). Clearly the use of Honduran Pine for whatever purposes must be based on sound silvicultural and ecological precautions as traditionally done by professional foresters, who usually plant pines on degraded lands. Conversion of mature native forests for plantation purposes is usually not recommended.

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