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Long-Term Response of Caribbean Palm Forests to Hurricanes

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Abstract - We studied the response of *Prestoea montana* (Sierra Palm, herefter Palm) brakes and a Palm floodplain forest to hurricanes in the Luquillo Experimental Forest in Puerto Rico. Over a span of 78 years, 3 hurricanes passed over the study sites for which we have 64 years of measurements for Palm brakes and 20 years for the Palm floodplain forest. For each stand, species composition, species density, basal area, tree density, rates of tree ingrowth and mortality, and importance value of tree species were assessed. We also estimated stand and Palm population aboveground biomass for the Palm floodplain forest. We found that different forest attributes such as basal area and tree density exhibited different temporal response patterns to hurricanes. The passing of 2 hurricanes in less than 10 years shifted the forest-response pattern of Palm brakes into a different trajectory with wider oscillations than before the 1989 hurricane. Neither Palm forest type reached steady state during the period of observation. Palm brakes spent about 50 of 64 years of the study in a transition state, and during the last 14 of those years, *Cecropia schreberiana* (Yagrumo) displaced the Palms as the species with the highest importance value, likely due to hurricane effects. The Palm floodplain forest remained in a transition mode over the 20-year span of the study. The results of the study showed that stands located on the leeward of hurricanes experienced less structural and species-composition changes and had more time to recover from hurricane effects than those exposed to the windward path of the hurricane. Caribbean Palm forests are dynamic systems whose structure, species composition, species density, and processes are finely coupled to frequency and intensity of hurricanes. Because Palm forest dynamics are closely tied to hurricanes, it is possible to anticipate that any future change in the frequency or intensity of hurricanes is likely to influence these forest attributes, including species ranking by importance value.

Introduction

Large and infrequent disturbances (LIDs sensu Dale et al. 1998) influence the structure, functioning, and species composition of ecosystems. Hurricanes are the predominant natural LID in the Caribbean, and many characteristics of Caribbean forests reflect persistent exposure to these events (Lugo 2000, 2008). Hurricanes cause elevated rates of tree mortality (Lugo and Scatena 1996), alter the 3-dimensional structure of a forest, and set in motion ecological changes that last decades (Crow 1980, Lugo 2008). Thus, the conservation of Caribbean forests requires understanding of both their short- and long-term responses to hurricanes.

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Researchers have been collecting data about the short-term effects (<20 y) of hurricanes on Caribbean forests since the 1980s, following the passage through the region of several severe hurricanes (Lugo et al. 1983; Walker 1995; Walker et al. 1991, 1996). However, less information is available on the long-term response (>20 y) of forests after the passage of a hurricane (reviews in Brokaw et al. 2012, Lugo 2008). We had the opportunity to study the long-term response of *Prestoea montana* (Graham) G. Nicholson (Sierra Palm) forests to 3 hurricanes that passed over or near the Luquillo Mountains of Puerto Rico. We determined the level of change in tree-species composition, species density, and importance value (IV), and asked how successive LID events affect the time required for these forests to reach maturity or steady state. We used the structural criteria of Scatena (1995) to assess maturity, which we use as synonymous with steady state. He evaluated the time required for a forest compartment to reach pre-disturbance values as a measure of recovery, and also estimated turnover times of forest compartments by dividing their mass by the rate of loss or production of mass in the compartment. A mature or steady state system is expected to recover structure and function in the time available between disturbance events as hypothesized by Crow (1980:84, fig. 7). Scatena did not address the response of species in the path to maturity or steady state of a system, but Crow (1980) did, and we expand his analysis by using each species' IV as a relative index of dominance in the plant community (Whittaker 1970).

The frequency of hurricane passage through a 10-km distance from the El Yunque peak of the Luquillo Experimental Forest (LEF) is about 1 per 60 y (Scatena and Larsen 1991). Scatena (1995) showed that the turnover time of biomass in forest compartments in the LEF could achieve steady state within a time interval equivalent to the 60-y return time of hurricanes. In developing this turnover rate, Scatena (1995) assumed continuous growth after the disturbance event, i.e., no additional perturbation in developing forest compartments or stands. Also, he found that the time from disturbance to steady state varied with the size of the compartment: small forest-components such as leaf or litter biomass recovered much quicker than larger ones such as woody material. Scatena (1995) described the Luquillo Mountains landscape (vegetation, soils, landforms) as dynamic, with a wide range of subsystems in different stages of response to a diverse number and types of disturbances. Sectors of this landscape are constantly in transition because of the high frequency of natural disturbances and the broad range of time intervals required for its different components to reach steady state.

What remains unknown is if stand structure and species density and composition achieve mature states after successive hurricane events. To address this question, we used permanent-plot information for 2 Palm forest stands (known as Palm brakes sensu Beard 1944) measured between 1946 and 2010, and a Palm floodplain forest measured between 1980 and 2000. Palm brakes occur on steep, wet Caribbean slopes while Palm floodplains develop on flat terrain on streamsides. Both forest types are wetlands with saturated soils and distinct hydroperiods within their montane location (Lugo et al. 1990:67, figure 4.8). Our study included forest responses to hurricanes that passed over the region in 1932, 1989, and 1998 (hurricanes San Ciprián, Hugo, and Georges, respectively). Other events involving high rainfall, drought, and high winds affected the study stands during the measurement interval (Peters et al. 2013:2, figure 9.8), but none had the visible effects that the 3 hurricanes had.

Methods

Study sites

The 3 study sites consisted of 2 Palm brakes and a Palm floodplain forest located within 10 km of each other but in different Holdridge life zones and with different wind exposures and geology (Table 1). Location and plot maps of the study sites are available in Lugo et al. (1995) and Frangi and Lugo (1985) for Palm brakes and Palm floodplain forest, respectively. Palm brake 1 (PS-1) was on a windward exposure and Palm brake 2 (PS-2) and the Palm floodplain forest were on leeward exposures. Lugo et al. (1995) described the species composition, vegetation structure, soils, and other structural and functional characteristics of the Palm brakes for the period between 1946 and 1989, and Frangi and Lugo (1985, 1991, 1998) provided similar description for the Palm floodplain forest for the period between 1980 and 1995. We updated all vegetation structure and composition measurements in 2000 for the Palm floodplain forest and in 2010 for the Palm brakes. We used the plant nomenclature of Little and Woodbury (1976), Molina and Alemañy (1997), and Liogier and Martorell (2000).

Measurements

In 1946, two 40 m x 100 m Palm brake plots were established by F.H. Wadsworth of the USDA Forest Service (research files available at the Internaltional Institute of Tropical Forestry), and all trees with diameter at breast height (dbh) ≥ 4 cm at 1.3 m were measured in both plots, identified by species, and tagged for future re-measurement. Trees were painted at dbh to assure that subsequent measurements were done at the same spot. The Palm height was also measured in 1946, 1949, and

Table 1. Characteristics of Palm-forest study areas in the Luquillo Experimental Forest. Data are from Lugo et al. (1995) and Frangi and Lugo (1985).

	Study area		
Charactersitic	Juan Diego (PS1)	El Verde (PS 2)	Espíritu Santo floodplain
Elevation (m)	700–750	700–750	750
Mean annual rainfall (mm)	4000–5000	3500–4500	3725
Life zone (subtropical)	Lower montane rain to rain forest	Lower montane wet to wet forest	Lower montane wet to wet forest
Aspect	E–NE	N–NW	N–NW
Geology	Volcanoclastic sandstones of Tabonuco Formation	Volcanoclastic sandstones of Hato Puerco Formation	Volcanoclastic sandstones of Hato Puerco Formation
Surrounding forest type	Cloud and *Dacryodes-Sloanea*	*Dacryodes*-*Sloanea*	Colorado (*Cyrilla racemiflora*)

1951 directly by climbing the palms. Subsequently, we used a ranging optimeter. PS-1 vegetation was measured in 1946, 1949, 1951.8, 1982.8, 1989, 1990, 1995, 2001, 2006, and 2010 (decimals indicate, where available, the month of measurement needed for more accurate rate estimates). PS-2 vegetation was measured in 1946, 1949.9, 1951.8, 1976.3, 1982, 1989, 1996, 2001, 2006, and 2010. Dead trees were noted at each measuring date as were trees entering the minimum dbh class (ingrowth). Ingrowth trees were tagged and identified to species.

In March 1980, we established a permanent 5 m x 5 m grid, encompassing the whole area of a small (0.2525 ha) Palm floodplain forest at 750 m elevation in the LEF (Frangi and Lugo 1985). We determined the structure and species composition of this forest through complete inventories in 1980, 1990, 1995, and 2000. Frangi and Lugo (1991) reconstructed the structure of vegetation just prior to the passage of Hurricane Hugo in 1989 and estimated tree mortality and ingrowth rate as in PS 1 and PS 2.

The inventory of Palm floodplain vegetation involved 4 measurements: (1) the number and diameter of all plants with a dbh ≥ 4 cm, (2) the height and stem diameter (at breast height if ≥ 1.3 m tall or at the mid-point of the stem if <1.3 m tall) of all dicotyledonous trees over 1.0 m tall with dbh < 4 cm, (3) the number of tree ferns and diameter of all that were ≥ 0.7 m tall (at breast height if ≥ 1.3 m tall or at the mid-point of the stem if <1.3 m tall), (4) the number of Palms and diameter of all that were ≥ 0.7 m tall (at breast height if ≥ 2.5 m tall or at the mid-point of the stem if <2.5 m tall).

Analysis

We calculated from field measurements tree density and basal area of all trees with dbh ≥ 4 cm in the PS 1 and PS 2 plots. We calculated the IV of each species as the sum of its relative basal area and relative stem density, expressing the sum in percent. At the Palm floodplain forest, we made the same estimates for trees with dbh ≥ 1.0 cm, Palms ≥ 0.7 m tall, and tree ferns ≥2.5 m tall.

Trees had been tagged previously, thus, we estimated tree mortality for dicotyledonous species (≥4 cm dbh), ferns (≥1.3 m tall), and Palms (≥0.7 m tall) from the baseline inventory. We calculated mortality rates, expressed as trees ha^{-1} y^{-1}, as the number of dead trees per hectare divided by the time interval since the last measurement. We also expressed mortality rate as the percent of the living trees at the beginning of the interval, i.e., total number of trees that died divided by the number of trees alive at the beginning of the interval divided by the time interval in years. We estimated tree-ingrowth rate from the density and basal area of untagged trees reaching or exceeding the diameter of the minimum dbh class (4.0 cm and 1.0 cm for Palm brakes and Palm floodplain forest, respectively) during the time interval of measurement divided by the elapsed time since the last measurements. We estimated aboveground biomass in Palm brake and Palm floodplain forest plots from height and dbh (Palms) and dbh (non-Palms) using the allometric equations in Frangi and Lugo (1998).

Results

Stand structure

Before Hurricane Hugo affected the vegetation of PS 1 and PS 2, stands were either losing (PS 1) or had lost stems and reached steady stem-density values (PS 2; Fig. 1A). Hurricane Hugo reduced the tree density of both plots, with a greater reduction in PS 1, followed by a dramatic increase in tree density just before Hurricane Georges. Tree density decreased after Hurricane Georges in both plots to values similar to those recorded before Hurricane Hugo. In the 1940s, the basal area of PS 2 was higher than that of PS 1, but before Hurricane Hugo their basal areas were similar (Fig. 1B). Hurricane Hugo reduced the basal area of both stands with a larger reduction in PS 2 than in PS 1. After Hurricane Hugo, and regardless of the passage of Hurricane Georges, the basal area of both stands steadily increased, but with a higher rate in PS 2. By 2010, the stands had again diverged in basal area, with PS 1 approaching pre-Hurricane Hugo values and PS 2 exhibiting the highest basal-area values measured in the study.

The Palm floodplain forest had a reduction in tree density after Hurricane Hugo followed by an increase (Fig. 1C). Hurricane Georges did not appear to affect tree

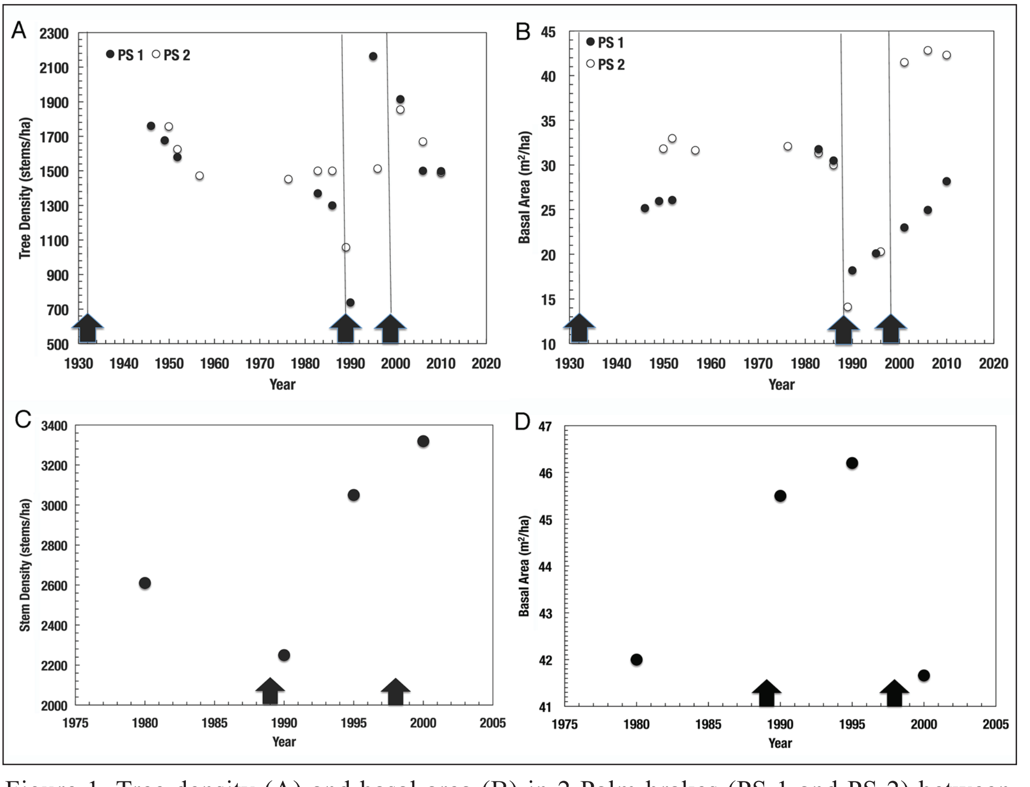

Figure 1. Tree density (A) and basal area (B) in 2 Palm brakes (PS 1 and PS 2) between 1946 and 2010, and tree density (C) and basal area (D) of a Palm floodplain forest between 1980 and 2000 in the Luquillo Mountains. These plots were affected by hurricanes (black arrows) San Ciprián (1932), Hugo (1989), and Georges (1998). Data are for trees with a dbh ≥ 4 cm in the Palm brakes and ≥ 1 cm in the Palm floodplain forest.

density in this forest, where tree density continued to increase through the year 2000. However, the basal area in this forest increased between 1980 and 1990 in spite of Hurricane Hugo, but had a reduction to slightly below pre-Hurricane Hugo basal area after Hurricane Georges (Fig. 1D).

Tree-mortality rates in both PS 1 and PS 2 were low before Hurricane Hugo and spiked afterwards as a result of both hurricanes Hugo and Georges (Fig. 2A). The tree-mortality rate after the hurricanes was lower in PS 2 than PS1, and the rate at PS 2 oscillated more than the rate at PS 1. The peak tree mortality rate at PS 2 was followed by a reduction, but at PS 1 the tree mortality rate remained high between hurricanes Hugo and Georges, and then decreased after Hurricane Georges. In terms of annual percent tree mortality, pre-Hurricane Hugo values were 1.1 and 1.7 for PS 1 and PS 2, respectively. These annual percent mortality rates spiked after Hurricane Hugo to 18 and 7 for PS 1 (1990 and 1995) and 11 and 4 for PS 2 for 1989 and 1996. The annual percent tree mortality rates post Hurricane Georges were 9 and 8 for PS 1, and 8 and 4 for PS 2 for 2001 and 2006, respectively.

Tree mortality in the Palm floodplain forest was 269 stems ha^{-1} y^{-1} between 1995 and 2000 or 8.8% per year. Of dead trees tallied, 45% were Palm trees, and 29 tree species experienced some mortality. Considering only stems with a dbh ≥4 cm, the rate of ingrowth in the floodplain was 164 stems/ha/y or 5.4% per year. This group of plants comprised 26 species, including *Cecropia schreberiana* Miq. (Yagrumo), which had the highest IV (17%). When we considered all ingrowth plants with a height >0.7 m regardless of their dbh, the ingrowth rate reached 557 stems ha^{-1} y^{-1} or 18.2% per year, with Palm accounting for 204 stems ha^{-1} y^{-1}.The standing density and basal area of ingrowth plants in 2000 was 820 stems/ha and 1.46 m^2 ha^{-1}, respectively.

Tree ingrowth rates at PS 1 and PS 2 changed dramatically after hurricanes Hugo and Georges (Fig. 2B). Rates prior to Hurricane Hugo were well below 50

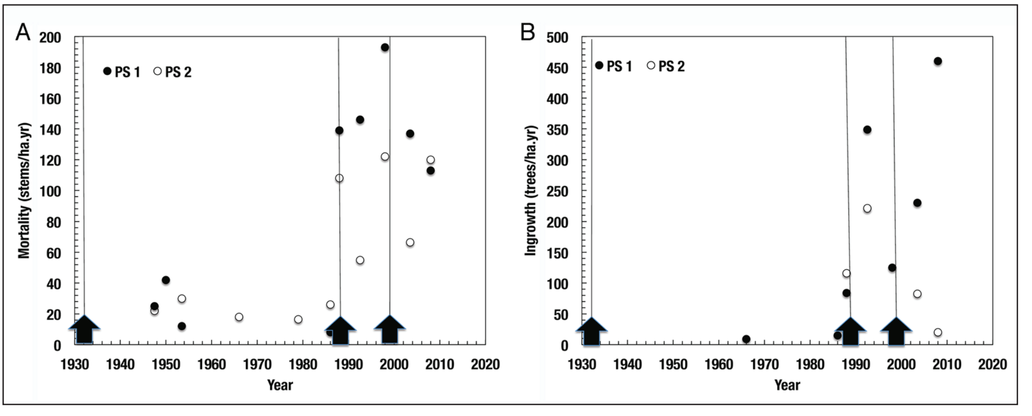

Figure 2. Tree-mortality rates (A) and tree-ingrowth rates (B) in 2 Palm brakes (PS 1 and PS 2) in the Luquillo Mountains between 1946 and 2010. These plots were affected by hurricanes (black arrows) San Ciprián (1932), Hugo (1989), and Georges (1998). Data are for trees with a dbh ≥ 4 cm in the Palm brakes and ≥ 1 cm in the Palm floodplain forest. The rates are plotted at the mid-point of the time interval.

trees ha^{-1} y^{-1}, but the ingrowth rate at PS 1 more than doubled immediately after Hurricane Hugo, and by the 1990–1995 interval peaked at about 350 trees ha^{-1} y^{-1}. Just before Hurricane Georges, the ingrowth rate at PS 1 decreased to about 100 trees ha^{-1} y^{-1}, still higher than just after Hurricane Hugo, and peaked by the 2006–2010 interval at about 450 trees ha^{-1} y^{-1}. Ingrowth at PS 2 also responded to both hurricanes, but peak values were much lower than at PS 1. In fact, by the 2006–2010 interval, ingrowth rates at PS 2 had returned to pre-Hurricane Hugo values. The differences in ingrowth rates between PS 1 and PS 2 are reflected in the rate of basal-area increase, with increasing rates in the 2001–2006 and 2006–2010 intervals for PS 1 (from 2.5 to 4.8 m^2 ha^{-1} y^{-1}) and corresponding decreasing rates for PS 2 (from 0.6 to 0.2 m^2 ha^{-1} y^{-1}). The contribution of ingrowth to the basal area of the stand was much higher at PS 1 than at PS 2.

Species dynamics

The temporal pattern of tree-species density in PS 1 and PS 2 was dramatically altered by Hurricane Hugo, although the effect was not instantaneous, and the effect of Hurricane Georges on species density is unclear (Fig. 3A). Before Hurricane Hugo, the 2 stands had diverging trends of species density. A pattern of species-density reduction was in progress at PS 1, while PS 2 had a pattern of species-density increase. After Hurricane Hugo, the 2 stands converged around 1995 and 1996 at a species density that was the historic low for PS 2 and represented an increase for PS 1. After 1996, PS 2 returned to the species-density values measured in the 1940s and its species density was again higher than that of PS 1, but PS 1 had species densities higher than in the 1940s with a slight temporal trend of decline.

The species density of the Palm floodplain forest did not change after Hurricane Hugo, but it almost doubled after Hurricane Georges (Fig. 3B). This flux of species into the floodplain did not change the order of tree species when ranked by IV, but it added a long tail of low-importance species to the stand's IV curve. The effect on

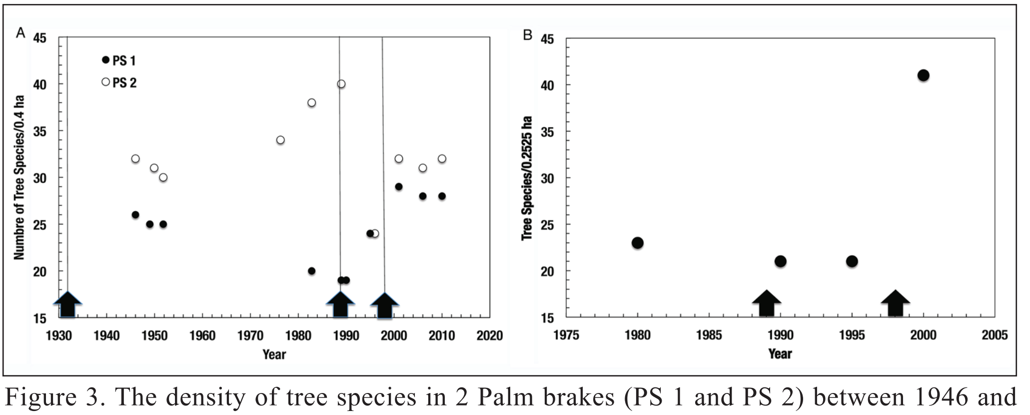

Figure 3. The density of tree species in 2 Palm brakes (PS 1 and PS 2) between 1946 and 2010 (A) and a Palm floodplain forest (B) between 1980 and 2000 in the Luquillo Mountains. These plots were affected by Hurricanes (black arrows) San Ciprián (1932), Hugo (1989), and Georges (1998). Data are for trees with a dbh ≥ 4 cm in the Palm brakes and ≥ 1 cm in the Palm floodplain forest.

stand composition was a reduction in the IV of Palm from a historic high of 53.5% in 1995 (Frangi and Lugo 1998) to 35% in 2000.

The IV of Palm in PS 1 and PS 2 changed greatly between 1946 and 2010 (Fig. 4). Before Hurricane Hugo, Palm had a higher IV at PS 2 than at PS 1, but it was decreasing in both stands. The IV of Palms was dramatically reduced 6 y after Hurricane Hugo, when Palm at PS 2 had a lower IV than at PS 1. However, after Hurricane Georges, Palm's IV increased at both stands until 2010, when the Palm IV was greater at PS 2 than at PS 1.

Hurricane Hugo also caused Yagrumo IVs to increase (Fig. 4). This species almost disappeared from PS 1 and had low and declining IVs in both stands prior to Hurricane Hugo. In 1995 and 1996, Yagrumo had the highest IV of any species in both PS 1 and PS 2 and remained the most important species until 2010. At PS 1, Yagrumo declined sharply after the 1996 peak in IV, but by 2010 it was still ranked second in IV with a value almost as high as that of the Palm. In the Palm floodplain forest, Yagrumo was not present in 1980 or 1990 and was a minor component of the forest 6 y after Hurricane Hugo (IV of 0.1%). In 2000, Yagrumo importance in the Palm floodpplain forest increased to 3.1%—a higher but still low value.

The changes in species' IVs varied over time by species and site (Fig. 5). For example, the IV of *Croton poecilanthus* Urb. (Sabinón; Fig. 5A) before Hurricane Hugo was higher at PS 1 than at PS 2 and was increasing in both stands. It decreased at both stands after Hurricane Hugo, but the decline of this species at PS 1 was steeper. The species disappeared from PS 2 and then returned to pre-hurricane values. By 2010, Sabinón had not recovered to its pre-hurricane IV at PS 1.

Before Hurricane Hugo, *Cyathea arborea* (L.) Sm. (West Indian Tree Fern) was a low-importance species in both PS 1 and PS 2, but had a higher IV at PS 2 than at

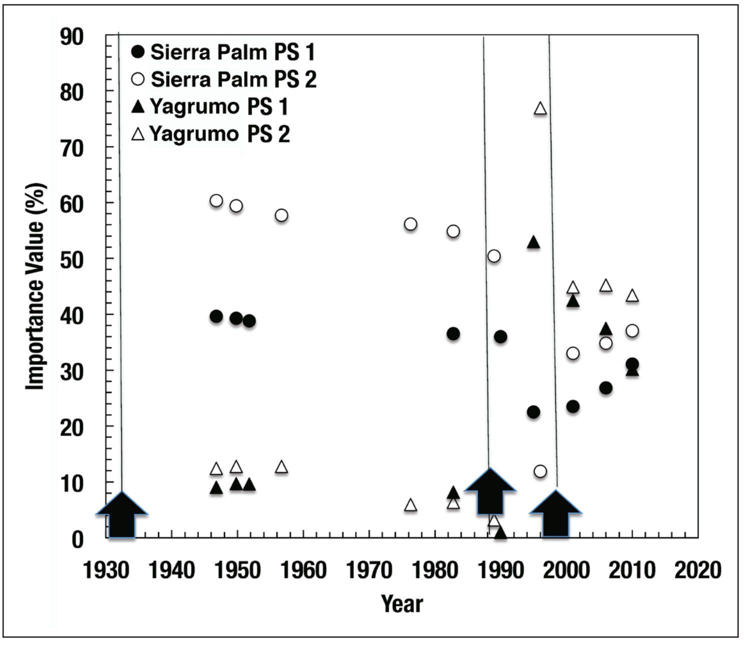

Figure 4. Importance value of Sierra Palm and Yagrumo in 2 Palm brakes (PS 1 and PS 2) in the Luquillo Mountains between 1946 and 2010. These plots were affected by hurricanes (black arrows) San Ciprián, Hugo, and Georges, 1932, 1989, 1998, respectively. The importance value includes the density and basal area, and data are for trees with a dbh ≥ 4 cm in the Palm brakes and ≥ 1 cm in the Palm floodplain forest.

PS 1 (Fig. 5B). After Hurricane Hugo, the IV of West Indian Tree Fern decreased in PS 2 and recovered only slightly between then and 2010. However, by 2010 at PS 1 after Hurricane Georges, the West Indian Tree Fern became a high importance-value species (10%). *Drypetes glauca* Vahl (Guama) experienced small changes in IV at PS 1, although it disappeared after Hurricane Georges and appeared later at low IVs (Fig. 5C). At PS 2, Guama had higher IVs than at PS 1, and remained at higher values after Hurricane Hugo. However, 6 y later, it almost disappeared from this stand and its importance between 2001 and 2010 was at historic low values. *Inga laurina* (Sw.) Willd (Sacky Sac Bean) had its highest IVs just before Hurricane Hugo at both PS 1 and PS 2, although it was more important at PS 1 (Fig. 5D). This species' IV decreased at both PS 1 and PS 2 after Hurricane Hugo, and almost disappeared from PS 2 after Hurricane Georges. By 2010, Sacky Sac Bean had not recovered to its pre-hurricane IV at either stand.

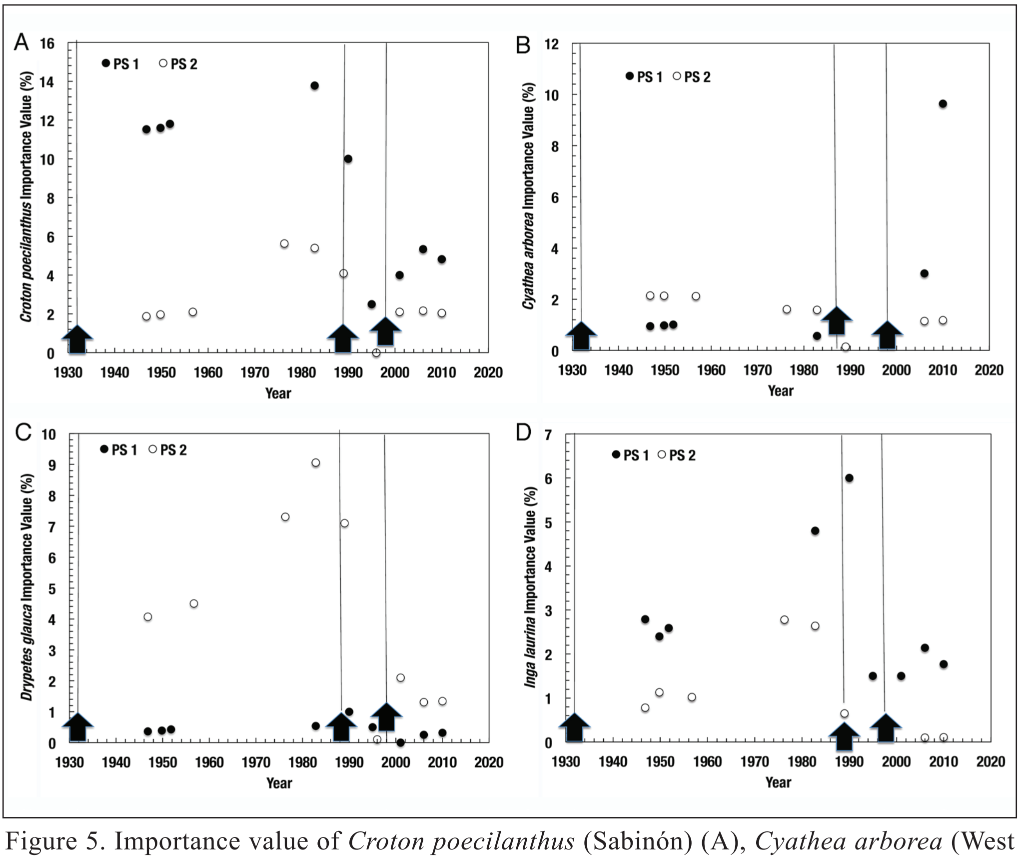

Figure 5. Importance value of *Croton poecilanthus* (Sabinón) (A), *Cyathea arborea* (West Indian Tree Fern) (B), *Drypetes glauca* (Guama) (C), and *Inga laurina* (Sacky Sac Bean) (D) in 2 Palm brakes (PS 1 and PS 2) in the Luquillo Mountains between 1946 and 2010. These plots were affected by hurricanes (black arrows) San Ciprián, Hugo, and Georges in 1932, 1989, 1998, respectively. The importance value includes the density and basal area and data are for trees with a dbh ≥ 4 cm in the Palm brakes and ≥ 1 cm in the Palm floodplain forest. species of trees with a dbh ≥ 4 cm.

Discussion

This study reports the results of re-measurements of 3 Palm-dominated stands in the Luquillo Mountains over a span of 64 years for 2 Palm brakes and 20 years for a Palm floodplain forest. All stands lacked any appearance of human modification and are thus considered primary forests. In 1932, 14 years before this study started, the whole LEF was exposed to Hurricane San Ciprián. The timing of hurricane events and vegetation measurements gave us a window of 78 years of hurricane-response time to assess the successional pathways in these palm forests.

We will organize our discussion around 3 themes. First, we compare Palm forests and include in the comparison *Dacryodes excelsa* Vahl (Tabonuco) forests that are part of the network of Forest Service plots in the LEF. We then discuss the long-term dynamics of Palm and Tabonuco stands in relation to the hurricane disturbance regime at the LEF. In this discussion, we incorporate as a comparison the clear-cut experiment of Borman and Likens (1981) in a temperate forest. After that acute disturbance, the forest transitioned through various successional stages in the path to maturity or steady state. Finally, we discuss the response of species density and individual tree species to hurricanes.

The 3 hurricanes that influenced this study were San Ciprián, Hugo, and Georges, in 1932, 1989, and 1998, respectively. San Cirpián passed over the LEF with maximum sustained winds of 194 km/h, Hugo moved by just east of the LEF with maximum sustained winds of 148 km/h, and Georges skirted south of the LEF with maximum sustained winds of ~176 km/h. In their analysis of the passage of' Hurricane Hugo over Puerto Rico, Boose et al. (1994) highlighted the importance of aspect relative to wind direction in the interpretation of hurricane effects, an observation that is important to the interpretation of the effects of these 3 hurricanes on LEF vegetation.

Comparison of forests in the Luquillo Mountains

The range of values of the structural attributes that we observed during the period of study (Table 2) show overlap among the 3 Palm forest stands in spite of the difference in the minimum tree diameter measured and area sampled. The salient tendencies from Table 2 and other studies at these sites (summarized in Frangi and Lugo 1985, 1991, 1998; Lugo et al. 1995) include: (1) the high IV of Palm (Fig. 4, Table 2); (2) the high IVs for just a few species; and (3) a low species-density (Fig. 3) when compared to non-wetland vegetation such as the Tabonuco forests in the Luquillo Mountains (Drew et al. 2009, Heartsill Scalley et al. 2010).

Most Caribbean forests have steep importance-value curves with high dominance by a few species and many low-dominance species (Lugo et al. 2000). We and others have suggested that this community attribute is a result of the hurricane disturbance regime (Lugo 2005, Lugo et al. 2002) and Palms, whose abundance Beard (1945) associated with storms, can exhibit high IVs in both Palm and non-Palm forests (Lugo et al. 1995). Moreover, species-density results in Table 2 and Figure 3 show that Palm brakes and Palm floodplain forests can reach high species-density after hurricanes. The high temporal amplitude of values describing forest structure and species composition in these primary forests suggests that overlaps in the structural indices preclude comparisons of forests using mean values or single-year results of particular forest attributes. Instead, structural and species-density comparisons of Caribbean forests need to be based on the temporal patterns of change of these forest attributes.

The dramatic temporal changes of Caribbean forest structural and species compositional attributes have been previously reported for dry forests (Lugo et al. 2002), *Cyrilla racemiflora* L. (Palo Colorado) forests (Weaver 1986, 1987, 1989, 1995), elfin forests (Weaver 1986, 1989, 1995), and Tabonuco forests (Crow 1980, Drew et al. 2009, Heartsill Scalley et al. 2010, Lugo and Scatena 1995). Our results add to this literature on long-term behavior of Caribbean forests and underscore the dynamic nature of forests in the hurricane belt. Repeated hurricane disturbances cause Caribbean forests to be in a constant state of structural and compostional change and successional transition. However, as our results also show (Figs. 1–6), different stands and stand attributes respond in different ways in terms of direction of change and lags between the passage of a hurricane and measurable responses on the ground. An example is the lag in the establishment of Yagrumo in Palm forests following 2 hurricanes (Fig. 4). These differences in the direction and rate of temporal change help explain the differences and similarities between different types of Palm forests in particular, and Caribbean forests in general. Below we will attribute the diverging species-density response of PS 1 and PS 2 in Fig. 3 to wetland conditions resulting primarily from the interaction of climate and aspect, and the similarities in the response of basal area in Palm floodplain forest (Fig. 1D) and Tabonuco forest at El Verde (Drew et al. 2009:figure1) to low wind exposure due to aspect.

Long-term pattern of stand dynamics

A Tabonuco forest downslope from PS 2 and the Palm floodplain forest exhibited the same successional stages described by Bormann and Likens (1981) for a 500-y succession in a temperate forest following a clearcut (Lugo et al. 2000).

Table 2. Structural parameters of Sierra Palm primary forests in the Luquillo Experimental Forest, PR. The range of values for Palm brakes (PS 1 and PS 2) correspond to the interval between 1946 and 2010, while the range of values for the floodplain forest correspond to the interval between 1980 and 2000. Data are for trees with a dbh ≥ 4 cm in the palm brakes and ≥1 cm in the Palm floodplain forest. Tree-species densities are presented per 0.40 ha for the Palm brakes and per 0.25 ha for the Palm floodplain forest.

Parameter	PS 1	PS 2	Floodplain
Tree density (stems ha^{-1})	738–2163	1058–1855	2250–3319
Basal area (m^2 ha^{-1})	18.2–31.8	14.1–42.8	41.6–46.2
Tree height (m)	6–12	6–12	12–17
Tree-species density	19–29	24–40	21–44
Importance value of the most important species (%)	31–43	35–77	35–54
Ingrowth rate (trees ha^{-1} y^{-1})	9–460	20–221	164–751
Mortality rate (trees ha^{-1} y^{-1})	12–193	16–122	35–269

The response pattern consisted of a 20-y interval with rapid structural change that included a 10-y reorganization phase and another 10 y of agradation. From year 20 to 45 after the hurricane, there was a transition phase followed by a maturity phase 46–60 y after Hurricane San Ciprián. However, the Tabonuco forest (or any forest in the LEF) did not have hundreds of years of uninterrupted growth after San Ciprián because Hurricane Hugo in 1989 interrupted forest-development trajectories in progress at the LEF since San Ciprián. Therefore, Caribbean forests facing frequent LID events have less time to reach maturity than temperate or tropical forests without recurrent disturbances. Moreover, speed of succession has to be faster in the Caribbean if forests are to reach maturity between recurrent disturbances.

If the time interval between hurricanes is shorter than the average passage interval for these events (60 years for the LEF), forests might not have time to reach maturity. For example, Hurricane Georges struck the Palm forests when they were in the first recovery stage of structural change following Hurricane Hugo, thus setting back succession and extending that particular stage of hurricane response in these forests. Therefore, it becomes difficult to anticipate how long it will take these forests to return to a mature steady-state condition. However, when enough time passes between hurricanes such as between San Ciprián and Hugo, stands have more time to develop structure and biomass and reach a mature steady state as did the Tabonuco forest downslope of PS 2. Interruptions of successional trajectories cause stands to oscillate in terms of structural development and species composition, thus delaying attainment of steady-state conditions.

Not all forest stands on a landscape affected by hurricanes are exposed to the same temporal constraints because the strength of hurricane winds varies with geographic position relative to the trajectory of the hurricane (Boose et al. 1994). Hurricanes Hugo and Georges had different trajectories such that Hurricane Hugo affected the

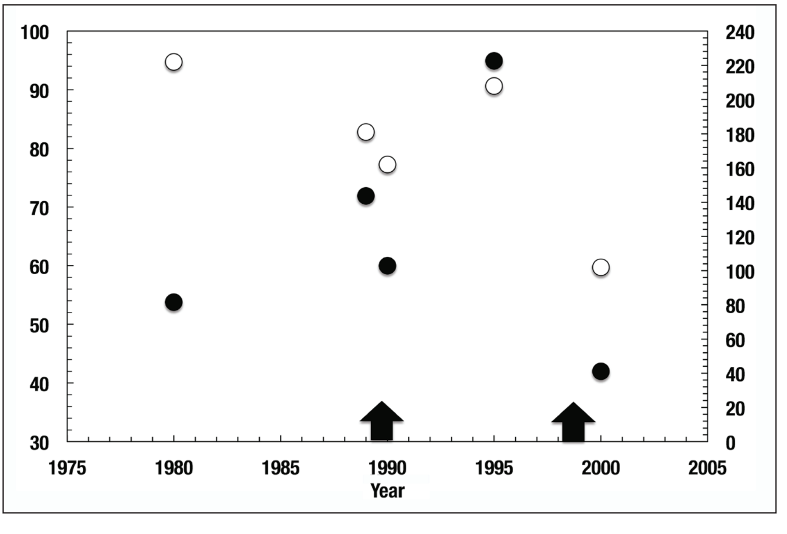

Figure 6. Aboveground biomass (Mg ha^{-1}) for Palm brakes (solid symbol) and Palm floodplain forest (open symbols) in the Luquillo Mountains between 1980 and 2000. Note the different scales of the 2 vertical biomass axes. Larger values on the right axis correspond to stand biomass and lower values on the left axis correspond to Palm-population biomass.This forest was affected by hurricanes San Ciprián, Hugo, and Georges, in 1932, 1989, 1998, respectively. Data are for trees with a dbh ≥ 1 cm. Black arrows indicate the passage of hurricanes.

windward northeastern portion of the LEF while Hurricane Georges, with its southerly direction, affected the windward southern slopes. Both hurricanes exposed to a greater degree the windward slopes where PS 1 and the Bisley Tabonuco stands were located than the leeward slopes where PS 2, the Palm floodplain forest, and El Verde Tabonuco forest were located. However, the floodplain forest was in the lee of Hurricane Hugo but was more exposed to winds of Hurricane Georges.

Given the distance of the eye of the hurricanes relative to the study plots and the trajectory of hurricane passage, Hurricane Hugo was a stronger hurricane than Hurricane Georges. This appraisal is consistent with the historical effects on the LEF of hurricanes with trajectories similar to hurricanes Georges and Hugo (Scatena and Larsen 1991). It is also consistent with the greater reduction of tree density and basal area (Fig. 1A, B), and higher rate of tree mortality (Fig. 2A) in PS 1 compared to PS 2 following the passage of Hurricane Hugo than after the passage of Hurricane Georges. The passage of Hurricane Georges did not interrupt basal area accumulation at PS 2 (Fig. 1B) nor at the El Verde Tabonuco forest (Drew et al. 2009). However, Hurricane Georges caused a larger biomas reduction at the Palm floodplain forest than did Hurricane Hugo (Fig. 6). Moroever, results after hurricanes Hugo and Georges for the leeward El Verde Tabonuco forest (Drew et al. 2009) contrast with those of Heartsill Scalley et al. (2010) for Tabonuco forests at Bisley in the windward slopes of the LEF. For example, the accumulation of basal area and biomass at El Verde Tabonuco forest was not interrupted by the hurricanes, unlike at Bisley, where both basal area and biomass accumulation reversed direction due to the effects of Hurricane Hugo.

The rates of tree mortality increased sharply after each hurricane in both Palm brakes (Fig. 2a), but PS 1 had a continuing acceleration of tree mortality between hurricanes that decreased sharply after Hurricane Georges while PS 2 oscillated at high rates of tree mortality between hurricanes. In contrast, rates of ingrowth increased in both plots after Hurricane Hugo and increased again at PS 1 after Hurricane Georges, while at PS 2 ingrowth rates increased slightly after Hurricane Georges and then quickly decreased (Fig. 2B). These differences could reflect a greater canopy opening at PS 1 (windward) compared to PS 2 (leeward). Stands in windward aspects experience stronger wind intensities that can open the canopy to a greater degree than stands in leeward aspects. The level of canopy opening affects within-stand conditions for regeneration because canopy opening influences light penetration and microclimate conditions inside the stand (Fernández and Fetcher 1991). Thus, forests on leeward aspects experience lower reductions of structural attributes and have more time for recovery than stands on windward slopes.

Although hurricane strength and stand exposure to winds explain many of the structural responses to hurricanes, species composition and density are also affected (Figs. 3–5) and in turn affect other forest processes that contribute to recovery and stand maturation. We believe that hurricane effects on species also help explain the temporal patterns of change at the stand level. In addition, within-stand conditions contribute to stand responses to hurricanes because species survival depends on adaptability to changing stand conditions over successional time.

Species on the move at small spatial scales

At the <1-ha scale of analysis, the gains, losses, and relative importance of species changed dramatically over the study period (Figs. 3–5). During the storm-free interval between hurricanes San Ciprián and Hugo, the Palm brakes exhibited contrasting patterns of species density, which Lugo et al. (1995) intepreted as resulting from the wetter conditions in PS 1 (Table 1). Fewer species are able to cope with saturated soils over the long-term than in the less saturated soils of PS 2. Hurricane Hugo reversed the inter-hurricane direction of change of species density in both plots, causing a decrease in species density at PS 2 and an increase in PS 1 (Fig. 3A). At the Palm floodplain forest, species density increased sharply after Hurricane Georges, but not after Hurricane Hugo (Fig. 3B). However, many species entered and exited the Palm floodplain forest after this hurricane (Frangi and Lugo 1998) indicating a high species-turnover process even if the net species density change was zero. Conditions inside the floodplain limit the establishment success of the many species that reach this site after a disturbance.

Species-density reductions correlate to hurricane strength, regardless of forest type, but the level of species density at maturity is an attribute that appears regulated by stand conditions (higher in forests with aereated soils like the Tabonuco, and lower in wetland forests such as PS 1 and Palm floodplain forest; see Silver et al. 1999). Nevertheless, spikes in species density follow with a lag after hurricanes as a result of ingrowth, and eventually level off or decline as stands mature (Fig. 3; Crow 1980, Drew et al. 2009, Heartsill Scalley et al. 2010).

Changes in species density are accompanied by dramatic changes in Palm IV (Fig. 4). Palm IVs decreased more at PS 2 than at PS 1 because more species were entering that forest, but after Hurricane Hugo, Palm experienced a large reduction in IV at both Palm brakes. However, a different picture emerges if the importance of the Palm is assessed by its aboveground biomass in relation to total-stand biomass (Fig. 6). Since 1980 when Palm biomass was 25% of stand biomass, Palm biomass importance increased steadily to a high of 45.6% in 1985 and was still 41.2% of stand biomass in 2000 in spite of the decline caused by Hurricane Georges. Therefore, a reduction in IV based on basal area and tree density was accompanied by an increase in the proportion of stand biomass in Palm. This result probably reflects a greater resilience of Palm than dicotyledonous trees to hurricanes. The greater Palm ingrowth relative to mortality (Fig. 2) also supports this observation.

Yagrumo was the species that most benefited from Hurricane Hugo because it became the most important species in both Palm brakes. After Hurricane Georges, Palm increased slightly in IV, but it took over 15 years for Palms to overtake Yagrumo as the most important species in these stands, and at PS 1 Yagrumo was still the most important species in 2010 (Fig. 4). It is possible that after Hurricane San Ciprián, Yagrumo also experienced a rapid increase in IV followed by a decline reflected in the low IVs that we observed in 1946. Thus, these dramatic changes in the IV of species such as Yagrumo and Palm support the notion of rapid succession in Palm brakes after the passage of hurricanes. In the Palm floodplain, Yagrumo was not present in the stand for the first 10 to 15 years of study, it entered as a low importance component of the forest after Hurricane Hugo, and its IV increased 30-fold after Hurricane Georges, although it still remained as a low-IV species.We observed many Yagrumo seedlings on the forest floor of the floodplain forest; thus, this species' lack of progress towards larger size classes reflects environmental impediments to its establishment in floodplain forests.

Species like Sacky Sac Bean and Guama increased in importance between hurricanes, but decreased dramatically after each hurricane, while West Indian Tree Fern was relatively more abundant after each hurricane, and Sabinón lost importance at PS 1 but not at PS 2 (Fig. 5). It appears that each species responds independently according to its own natural history requirements, and these changes are reflected in varying IVs. That Palm in Palm forests exhibited a lag in establishment contrasts with its behavior in nearby Tabonuco forests where its populations exploded immediately after hurricane passage. This difference in behavior by the same species may reflect differences in the environmetal conditions for its establishment in the 2 habitat types.

Heartsill Scalley et al. (2010) found that a hurricane such as Hugo sets in motion a process of community change that requires over 20 years before species assemblages return to a composition similar to pre-hurricane conditions. The changes in the relative importance of species as well as the bursts in the rates of tree mortality and ingrowth have direct consequences to the functioning of forest processes, accumulation of biomass, and changes in basal area and tree density beyond those directly attributable to the passage of the hurricanes. As an example, the extraordinary ingrowth, growth, and high IV of Palm in Palm brakes has direct effects on net primary productivity, biomass accumulation, and nutrient retention, which are all high when and where this and other successional species grow after a hurricane (Heartsill Scalley et al. 2010, Scatena et al. 1996). High mortality and ingrowth rates contribute to biomass turnover and reflect changes in light availability to the forest floor, which in turn allows rapid understory growth, and the entry of new species. For example, Frangi and Lugo (1998) found more species in the regeneration class than in the canopy of the Palm floodplain forest after Hurricane Hugo, and we found after Hurricane Georges that 26 of the 44 species in the floodplain were ingrowth species.

Conclusion

Palm forests in the Caribbean are dynamic systems whose structure, species compostion, and processes are finely coupled to frequency and intensity of hurricanes. Observations of Tabonuco forests at the LEF have established that if the period of hurricane-free conditions is long enough, a pattern of reorganization, accretion, and maturity described for temperate northen hardwood forests following a disturbance event can occur in the Caribbean. Our study of Palm forests has shown that they tend to accumulate basal area and biomass as soon as the initial effects of hurricane winds pass and, in some cases on leeward slopes, they accumulate biomass and basal area through periods of hurricane disturbances. Caribbean forests have the capacity to reach steady state faster than forests in temperate zones, as studies of Tabonuco forests demonstrated after Hurricane San Ciprián and before Hurricane Hugo struck the LEF. At LEF, forests require on average about 60 years to reach a steady state condition. However, the passing of 2 hurricanes in less than 10 years altered the temporal response of Palm forests and set them into a new trajectory of change with wide oscillations and temporal lags (i.e., lags in tree mortality, basal area accumulation or loss, species establishment, etc.). This variation in temporal response to hurricanes had already been documented for processes such as tree growth, which exhibited higher coefficients of variation after Hurricane Georges passed over novel forests in central Puerto Rico (Lugo 2008).

The oscillations observed in Palm forests after the passages of Hurricanes Hugo and Georges reflect very high rates of primary productivity, tree mortality, and tree ingrowth as well as dramatic changes in tree-species density and IV. Throughout the study period, the Palm forests seldom reached a steady state but demonstrated a tendency towards positive or negative trajectories of change in which the forests exhibited varying levels of structural development conmensurate with the environmental conditions prevailing on stands. In the 20-year observation of the Palm floodplain forest, the vegetation was always in transition as demonstrated by the oscillations of aboveground biomass (Fig. 6). Our results are consistent with those of Uriarte et al. (2009), who compared the effects of cyclic and random hurricane frequencies in Tabonuco forests and discovered that cyclic frequencies had the most significant effects on structure and species composition because many species took advantage of canopy opening and conditions during the early stages of forest succession after the disturbance. These effects stimulate oscillating patterns of structural and species responses.

The occurence of a long-lasting mature state in which structural and species-composition parameters stabilize for decades does not appear to occur often in Palm forests because hurricane passage repeatedly places the communities in a transition mode. Should hurricane frequency and intensity increase with climate change (Goldenberg et al. 2001), one might expect the structure and species compostion of these forests to become more variable as happened after the passage of Hurricane Hugo with the shift in the top ranking of IV from Palms to Yagrumo and back to Palms some 15 years later.

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