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Abstract. Despite low plant diversity and structural simplicity, mangroves offer various ecosystem services to local human communities, including sheltering coastal social-ecological systems from high-energy storm damage. The expected increasing intensity of hurricanes due to climate change raises questions concerning the capacity of mangroves to resist and recover from such disturbances. Herein, this study contributes to a better understanding of (1) the relation between storm intensity and damage to mangrove vegetation, (2) the contributions of species-specific as well as stand-specific components of mangrove vegetation to ecosystem resistance, and (3) the recovery of pre-hurricane forest structure through time. The first two issues have been addressed using a stand-level approach implemented at two east Caribbean mangrove sites in response to three storm events. The third was addressed through a 23-yr survey of forest recovery following the passage of a high-energy storm across one of the two study sites. Generally, hurricane damage was primarily controlled by wind velocity, followed by the hydro-geomorphic context of mangrove forests and species-specific composition, respectively. The relationship between damage to trees and wind velocity evidenced a sigmoidal trend, with a maximum slope at a wind velocity averaging 130 and 180 km/h for higher vs. lower canopy stands, respectively. The red mangrove, *Rhizophora mangle*, was significantly less resistant to hurricane damage than was the black mangrove, *Avicennia germinans*. Unlike the fringe and scrub stands, inner, tall-canopy stands fully recovered by the end of the study (23 yr). These stands were more resilient because of their growth performances. Finally, the time for east Caribbean mangroves to recover from high-energy storms seems to fall within the range of the average return time of such disturbances. This may prevent such ecosystems from ever reaching a steady state.

Key words: Caribbean; forest recovery; high-energy storms; mangrove; resilience; resistance; Special Feature: High-Energy Storms.

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Introduction

Mangrove forests are commonly found along tropical shores and estuaries. They offer various goods and services to local human communities including food supply, wood products, and shoreline protection (e.g., Ewel et al. 1998, Quoc Tuan Vo et al. 2012). Mangrove forests are particularly effective in attenuating storm damages to human and ecological coastal systems (Zhang et al. 2012, Das and Crépin 2013, Liu et al. 2013). Because of an expected increase in the frequency of the most intense hurricanes (Knutson et al. 2010), especially in the Atlantic Ocean basin

(Elsner et al. 2008), mangrove conservation is of high concern to coastal managers (McLeold and Salm 2006, Alongi 2008, Gilman et al. 2008).

Mangroves characteristically have low plant diversity and structural simplicity at the stand level (Janzen 1985, Tomlinson 1986, Snedaker and Lahmann 1988). This results from highly selective conditions that are required for mangrove persistence: salted groundwater, periodic flooding, and hypoxic low-nutrient substrates (e.g., Chapman 1976, Feller et al. 2010). However, landward-to-seaward ecological gradients coupled to geomorphological discontinuities and site history produce a high level of spatial heterogeneity across mangrove areas (Smith 1992, Duke et al. 1998). The particularly contrasted physiognomy of Caribbean mangroves has led to the characterization of five major community types, the so-called fringe, riverine, overwash, basin, and dwarf forests (Lugo and Snedaker 1974). Moreover, hurricanes that periodically cross the Caribbean enhance structural heterogeneity within mangrove ecosystems through various kinds of impact on soils and vegetation, such as windthrow, storm surge, salt spray, and sediment transport (Smith et al. 2009).

During the last thirty years, over 55 studies have been published that explicitly deal with hurricanes and mangroves. Most focus on the impacts on and the early response of mangrove stands following hurricanes. This has led to voluminous data that sometimes appear confusing (e.g., discordant species-specific sensitivity, Piou et al. 2006) and leave a number of unanswered questions (Greening et al. 2006, Alongi 2008, Smith et al. 2009). Among such questions are the predictability of hurricane impacts and the possible long-term effects of (single or multiple) hurricanes, as well as the return time for forest structure to recover from the disturbance. Furthermore, because of their recurring, large-scale impact, hurricanes may shape the structure of tropical forests located within the hurricane belt (De Gouvenain and Silander 2003) and may prevent them from ever reaching a stable forest state (Webb 1958, Lugo and Snedaker 1974).

Mangrove forests are much less resistant to hurricanes than are the more diverse rain forests and semi-deciduous dry forests (Imbert et al. 1998). Early recovery of vegetation is mostly due to initial floristic composition (Egler 1954) in mangroves as well as in other tropical forests (Bellingham et al. 1994, Vandermeer et al. 1995, Imbert et al. 1996). However, due to the lack of long-term studies in mangrove forests, no comprehensive information on the whole resilience processes after hurricanes is available.

This study provides a better understanding of mangrove resistance and resilience with respect to hurricane disturbances in the Caribbean. More specifically, it addresses three questions: (1) What are the respective contributions of mangrove species-specific and stand-specific characteristics to resistance and resilience? (2) Is damage to mangrove vegetation a linear function of storm intensity, or do response thresholds exist? (3) To what extent do structural aspects of mangrove forests recover or reach a steady state in hurricane-prone areas? The first two questions were addressed using a stand-level approach implemented at two east Caribbean mangrove sites subject to three storms. The third question was addressed through a 23-yr monitoring survey of forest recovery following the passage of Hurricane Hugo (1989) across one of the two study sites.

Materials and Methods

Study sites

The two study sites are located within the two largest coastal wetlands of the Lesser Antilles (Fig. 1) that spread along the bays of Fort-de-France (Martinique, site 1) and of the Grand Cul-de-sac Marin (Guadeloupe, site 2). As in the other Caribbean islands, mangroves are subject to a microtidal regime with strong climatic seasonality. Local variation in microtopography and freshwater availability cause high spatiotemporal variation in water level and ground salinity (Lambs et al. 2015). The resulting heterogeneity, coupled with the high morphological plasticity of the dominant mangrove species (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*), leads to a wide range of vegetation types (Lescure 1980, Imbert and Portecop 1986, Imbert and Ménard 1997).

Three major vegetation types are present at each of the two sites. Representative stands of each type were studied to assess resistance to hurricanes at both sites. According to the classification of Lugo and Snedaker (1974) and taking into account variation of dominant species (Fig. 2), the eight selected stands should be

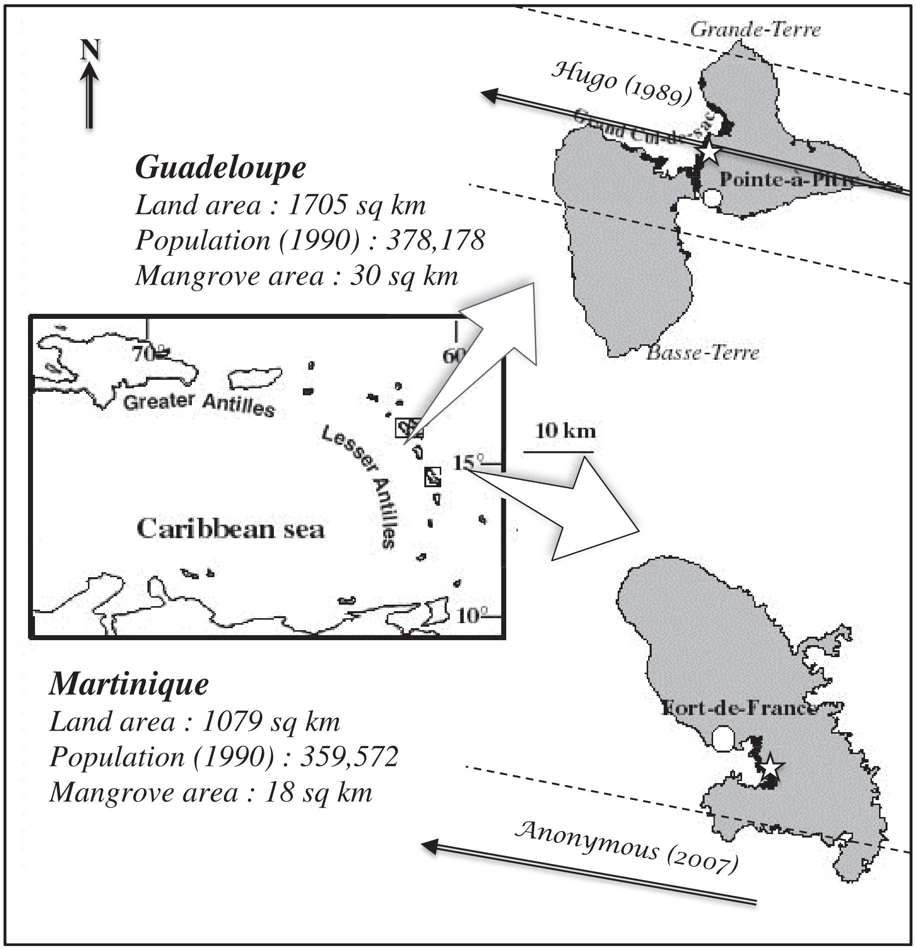

Fig. 1. Location of main mangrove areas (black) and study sites (stars) in Martinique and Guadeloupe islands. Arrows and dashed lines represent the eye paths of the two hurricanes that crossed these islands in the course of the study.

referred to as fringe mangrove (FR1, FR2), basin mangrove (*R. mangle*-dominated stands BR1 and BR2, *A. germinans*-dominated stands BA1 and BA2), or scrub mangrove (*A. germinans* stand SA1 and mixed *A. germinans*/*R. mangle* stand SM2). Stand characteristics prior to hurricane disturbances are given in Table 1. These data were collected in 1990 (Imbert and Ménard 1997) and in 1983 (Imbert and Portecop 1986; D. Imbert and B. Rollet, *unpublished data*), 27 and 17 yr after the last hurricane impact on site 1 and site 2, respectively.

Assessment of structural changes

Six inventory plots were established within each stand along a transect perpendicular to the seashore or canal. Plots were 10 × 10 m, except in the fringe mangrove, where they were 5 × 5 m due to high stem density and stand narrowness. At each plot, all stems with girth at breast height (GBH) ≥ 10 cm were identified to species and tagged. Horizontal stand structure was assessed from stem density, mean GBH, and basal area. Average canopy height represented the vertical component of forest structure. It was calculated for each stand from the five highest trees *via* a telescopic rod or a clinometer (PM-5/1520, Suunto Instrument, Finland). Monitoring began in 1990 on site 1 (Imbert and Ménard 1997) and in 1991 on site 2 (Imbert et al. 1996). Saplings reaching 10 cm GBH in the interval between two censuses were referred to as recruits.

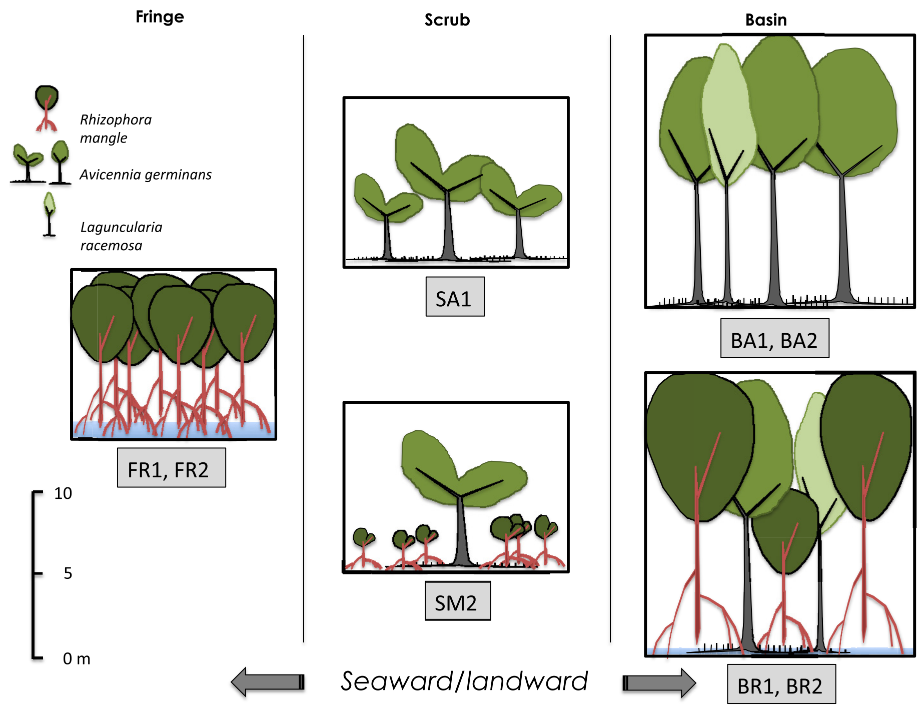

Fig. 2. Diagrammatic representation of the forest structure at the eight study stands. Stand names were derived from the first letter of their forest type (fringe, basin, scrub) and of their dominant genus (*Rhizophora*, *Avicennia*, mixed), respectively, and from their location in Martinique (1) or Guadeloupe (2).

Table 1. Pre-hurricane characteristics of mangrove stands at Martinique and Guadeloupe study sites.

	Coastal fringe		Scrub mangrove		Basin mangrove			
Stand characteristics	FR1	FR2	SA1	SM2	BR1	BR2	BA1	BA2
Stem density (/ha)	2933 (1848)	5133 (689)	1475 (310)	2740 (430)	1433 (176)	1970 (700)	1725 (202)	2817 (913)
Basal area (m^2/ha)	26.1 (18.6)	18.8 (7.3)	12.0 (4.4)	13.7 (5.6)	20.7 (0.6)	25.7 (7.8)	26.3 (5.2)	28.2 (11.1)
Canopy height (m)	8.5 (1.7)	8.4 (0.6)	9.0 (0.4)	7.4 (1.8)	16.3 (0.5)	15.6 (2.2)	12.0 (0.4)	13.7 (1.1)
Groundwater salinity (g/L)	28–42	33–46	56–76	30–57	5–18	19–51	40–63	42–85

Notes: Trees were considered if GBH ≥ 10 cm. Groundwater salinity (min–max values) was measured 20 cm below ground surface. Standard deviation of the mean is given within parentheses.

Because no recent pre-hurricane inventory was available for either site, initial stem density, average GBH, and basal area were assessed from each first post-hurricane census by pooling together surviving stems and stems killed by the hurricane. Particular attention was paid to dead wood remains during each first, post-hurricane census. Damage was attributed to hurricane disturbance only when macroscopic examination of bark and sapwood indicated a quite recent alteration. Damage to trees was classified from most to least severe as follows: toppling (To); lower (Lt) or upper trunk break (Ut) with respect to breast height; and breaks in large (Lb) or small branches (Sb). When the inventory took place at site 1, a few months after Hurricane Dean, plot boundaries of BR1 were not retrievable due to the amount of large fallen dead wood that was entangled with the vines *Cydista æquinoctalis* and *Machærium lunatum*. Therefore, only one rough assessment of the few, still standing stems was made over the whole stand (no replication), while initial stem density and basal area were assessed from the 1990 inventory on that stand.

A long-term, post-hurricane monitoring of vegetation response was implemented at site 2 from 1991 to 2012 in order to quantify the variation in four descriptors of stand structure (i.e., stem density, average GBH, basal area, and canopy height). Inventories were initially yearly (1991–1993), then biennial (1995–1997), and finally at multi-year intervals (2002–2012). Pre-hurricane canopy height was assessed from a 1983 inventory (D. Imbert and B. Rollet, *unpublished data*), whereas the other pre-hurricane structural characteristics were assessed from the first post-hurricane census, as explained hereinabove. These data served as reference points to evaluate the degree of forest recovery at stand level by the end of the study.

Hurricanes

When Hurricane Hugo passed over Guadeloupe archipelago during the night of 16–17 September 1989, it was classified as Category 4 storm on the Saffir-Simpson wind scale (SSWS). It was moving on a straight W/NW trajectory at 26 km/h, with an eye width of 37 km (SMIAG 1990). Maximum sustained winds of 230 km/h with gusts up to 260 km/h were measured from a US National Hurricane Center (NHC) reconnaissance aircraft, whereas gusts up to 296 km/h were recorded from a boat in Pointe-à-Pitre harbor (Table 2). The strongest winds blew 2.5 h before and after the passage of the eye wall. Site 2 was exactly on the axis of the eye path. Rainfall associated with the storm totaled about 225 mm close to the study site (Le Raizet meteorological center), with a maximum of 50 mm/h. Barometric pressure at sea level reached a minimum of 941.4 hPa, causing a storm surge estimated to be about 3 m in height.

Hurricane Dean upgraded to Category 2 storm as it passed about 25 km south of site 1 on 17 August 2007. The eye was about 22-km wide, moving W/NW at 35 km/h. According to the available data (Anonymous 2007, Franklin 2008), site 1 probably experienced a minimum barometric pressure of 971 hP at sea level, whereas maximum sustained winds reached about 160 km/h, with gusts up to 209 km/h and rainfall totaling about 260 mm. A 3.6-m storm surge occurred at the entrance of the Bay of Fort-de-France.

In September 1995, two hurricanes successively crossed the Lesser Antilles with some impact on the archipelago of Guadeloupe. During the night of September 4–5, Hurricane Luis (Category 4 storm) passed about 100 km to the northeast of site 2. Ten days later, Hurricane Marilyn (Category 1 storm) passed about 50 km to the southwest of the same site. Atmospheric disturbances recorded at Le Raizet Meteorological Center were similar for both hurricanes: Maximum sustained winds reached 75–80 km/h, winds gusted up to 110 km/h, and rainfall averaged 115 mm (AGUAMET 1995).

The return time of hurricanes within a distance of 30 km (average eye width) from our study sites is 39 yr for site 1, and 30.5 yr for site 2 (computed from SMIAG 1990). In the French West Indies, 87% of hurricanes have occurred during August and September. However, a hurricane was recorded in January (1908) and another in March (1955; SMIAG 1990).

Data analysis

Resistance of mangrove vegetation to hurricane disturbance was assessed through the percent change in basal area, which is a widely used, synthetic characterization of horizontal stand structure. We considered structural resilience (i.e., time of complete recovery) to be reached when each attribute of horizontal and vertical structure returned to pre-hurricane values. Initial and final values were compared using a paired (or unpaired, for canopy-height values only) *t*-test. A χ^2 contingency test was used to evaluate species-specific differences regarding the distribution of stems among types of damage, and for stand differences regarding the proportion of *Avicennia* sprouts.

Due to the scarcity of the other mangrove species *Laguncularia racemosa*, species-specific responses to hurricane damage were investigated only on *Rhizophora mangle* and *Avicennia germinans* by testing the influence of stand structure and wind velocity on loss of basal area. The adjustment to a linear model was tested by means of the coefficient of determination (R^2) at the confidence level of 95%. Bravais-Pearson r statistics were run to specify linear correlation. Regarding the influence of wind velocity, as the datasets evidenced non-linear relationships, we tentatively tested a simple logistic model:

Table 2. High-energy storms occurrence during the study period.

Storm characteristics	Hugo 1989 (September 17)	Luis 1995 (September 5)	Marilyn 1995 (September 15)	Anonymous 2007 (August 17)
Study site impacted	Site 2	Site 2	Site 2	Site 1
SSWS Scale	4	4	1	2
Distance from study site (km)	5	100	50	25
Max sustained winds (km/h)	230	78	75	160
Wind gusts (km/h)	296	106	111	209
Rainfall (mm)	225	117	110	260
Barometric pressure (hPa)	941	994	ND	971

Note: Related meteorological characteristics are on-site assessments based on computed data or close-to-site records.

$$y = \frac{c}{1 + b \cdot e^{-ax}}$$

where y is the loss of basal area, x is wind speed, and a, b, and c are fitted constants.

All statistics were run on Xlstat 17.05 software (Addinsoft, New York, New York, USA, 1995–2017).

Results

Immediate effects

*Resistance at stand level.—*No difference among the three vegetation types occurred based on the analysis of hurricane damage. However, when considering only the most impacted stand of each vegetation type for each hurricane, the basin stands appeared to be the most severely damaged, followed by the fringe and, finally, the scrub stands (Fig. 3). During Hurricane Hugo, maximal basal-area loss ranged from 71% (BR2) to 19% (BA2). When hurricanes Luis and Marilyn passed near site 2, mangrove stands had not fully recovered from Hurricane Hugo, with FR2, SM2, BR2, and BA2, respectively, at 65%, 62%, 48%, and 96% of basal areas reported for 1989. Because Hurricanes Luis and Marilyn occurred within a short period, it was not possible to assess the impact of each separately. However, based on the testimony of people from the neighborhood, most of the damage should be attributed to Hurricane Luis.

*Species-specific resistance.—*During this study, 609 stems belonging to the dominant species (*R. mangle* and *A. germinans)* were recorded immediately after hurricanes Hugo and Dean (stand BR1 excepted). Among them, 206 were dead as a result of hurricane disturbance. The distribution of dead stems among the five categories of damage (Fig. 4) shows that *R. mangle* is far more susceptible to damage from windstorms than is *A. germinans*. Except for small branch breaks (Sb), any damage to tree structure was associated with over 60% mortality in *Rhizophora*. Conversely, only major damage such as toppling (To) or trunk break below breast height (Lt) caused mortality of *Avicennia* stems to rise over 10%. In fact, when considering both surviving and dead trees, *Rhizophora* was significantly more prone to toppling ($\chi^2 = 17.17$, $P < 0.001$, df = 1) or lower-trunk break ($\chi^2 = 17.57$, $P < 0.001$, df = 1; respectively) as compared to *Avicennia*.

Based on the response of basal area to wind velocity (maximum sustained wind speed), *Rhizophora* (Fig. 5b) was much more sensitive to wind damage than was *Avicennia* (Fig. 5a). For each species, the whole dataset fitted a sigmoidal relationship ($R^2 = 0.78$ and 0.69 for *Rhizophora* and *Avicennia*, respectively) quite better than the linear model ($R^2 = 0.69$ and 0.60 for *Rhizophora* and *Avicennia*, respectively). Except BA2, basin stands were always more sensitive than the others to major hurricane disturbances. Splitting the data in two subsets (basin vs. other stands) and excluding stand BA2 evidenced an increasing rate in damage to a maximum for hurricanes winds averaging Category 1 (i.e., 110–150 km/h); such a threshold appeared for fringe and scrub stands for winds reaching Category 3 (178–209 km/h).

Context-dependent resistance.—Rhizophora was less affected in the low scrub and fringe stands than in the much taller basin stands. Such an

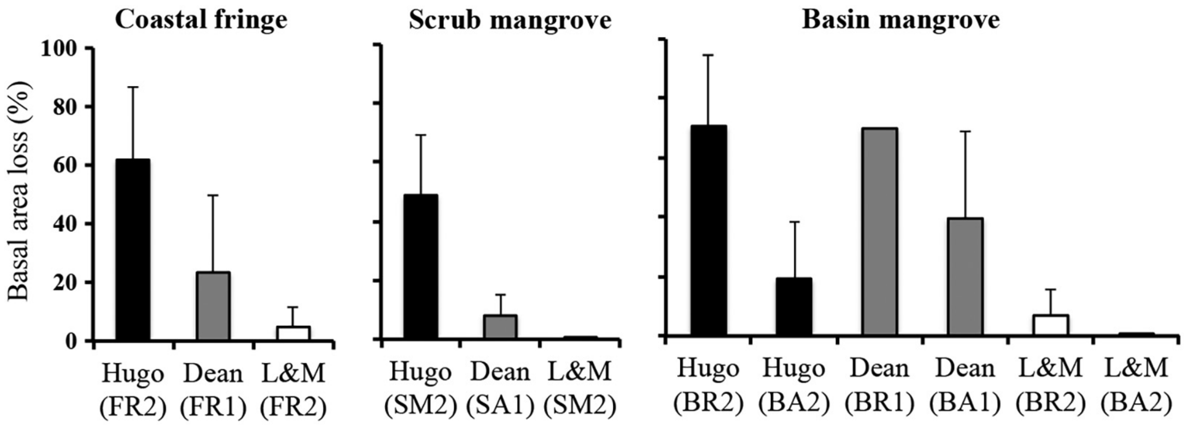

Fig. 3. Hurricane impacts (percentage loss of basal area) for each forest stand in each of three mangrove types at the study sites. Vertical bars figure standard error of the mean. No replication could be made at stand BR1 (see Assessment of structural changes in the Material and Methods section).

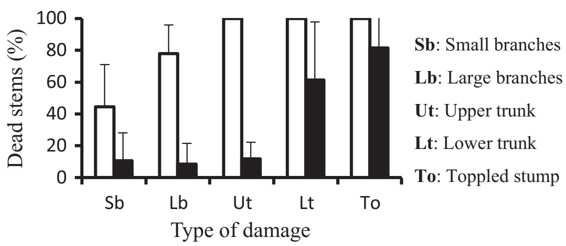

Fig. 4. Distribution of the dead stems (175 *Rhizophora mangle*, white chart; 31 *Avicennia germinans*, black chart), in relation to the type of damage. Vertical bars figure standard error of the mean.

influence of stand structure on species sensitivity to wind damage was evaluated by combining the data for the two powerful hurricanes (Hugo and Dean). Significant correlations characterized basal-area loss in relation to various proxies of stand structure for *Rhizophora.* Canopy height was a good predictor of stand resistance ($r = 0.87$, $P = 0.046$), but the ratio canopy height to mean GBH gave the best fit ($r = 0.90$, $P = 0.038$). Lower mean GBH for this species appeared to increase the susceptibility of high-canopy stands. Conversely, no significant

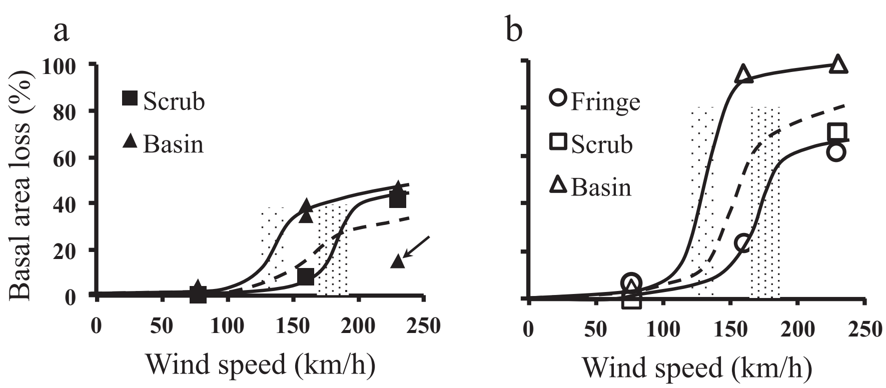

Fig. 5. Loss of basal area with respect to wind speed, mangrove type (fringe, scrub, basin), and mangrove species (*Avicennia*, a; *Rhizophora*, b). Sigmoidal relationships are indicated for the whole datasets (dotted lines) and for subsets (solid lines). Stand BA2 (arrow) was excluded from the basin-type subset (see Context-dependent resistance in the Results section). Wind-speed thresholds are figured in dotted areas.

correlations could be found for *Avicennia*. However, instead of (or in addition to) stand structure per se, structural characteristics of the surrounding vegetation may explain the disproportionally lower impact of Hurricane Hugo on *Avicennia* at BA2 as compared to BR2: Stand BA2 is a small, dense forest patch surrounded by a vast area of taller stands (such as BR2).

Long-term responses

The recovery of vegetation to pre-hurricane structure was monitored at four stands (study site 2) from 1989 to 2012 (Fig. 6). Temporal trajectories differed among stands as well as among structural characteristics (stem density, average GBH, basal area, and canopy height).

Stem density and average GBH.—All stands returned to pre-hurricane stem density by the end of the study, except stand SM2 that remained depleted in 2012 (t = 8.437, df = 5, P = 0.001). In the inner, taller stands (BR2 and, to a lesser extent, BA2) the post-hurricane period of stem depletion was followed by a period of over-recruitment (with regard to stand capacity) that intensified competition and stem mortality (Fig. 6a). In the heavily damaged, mixed *Rhizophora- Avicennia* stand BR2, mean GBH increased shortly after the hurricane due to the disproportionate survival of large *Avicennia* trees (Fig. 6c). In the *Avicennia* stand BA2, post-hurricane mean GBH increased regularly until it exceeded pre-hurricane value (t = −4.978, df = 5, P = 0.004).

Basal area and canopy height.—By the end of the study, basal area of stands FR2, SM2 and BR2 had recovered from hurricane damage (Fig. 6b). The least severely damaged stand (BA2) had higher values than before the hurricane (t = −2.859, df = 5, P = 0.035). However, stand FR2 still showed significantly lower mean canopy height (Fig. 6d) 23 years after the hurricane (t = 2.823, df = 10, P = 0.018).

Species-specific contribution.—The large recruitment of *Rhizophora* saplings from the seedling layer during the period of stand recovery clearly compensates for the inability of this species to resprout. We evaluated the reproductive strategy of *Avicennia* by comparing the number of new saplings vs. sprouts from surviving stumps. Of the 155 *Avicennia* stems recruited after Hurricane Hugo, half were saplings. However, BR2 stand showed a significantly higher proportion of sprouts as compared to the stands SM2 and BA2 (χ^2 = 10.30, P = 0.006, df = 2). Regardless of recruitment pathway, 23 yr after the disturbance, the two dominant mangrove species had recovered their pre-hurricane contribution to both stem density and basal area in each stand.

Discussion

Resistance to hurricane disturbance: from site to species-specific effects

Although a number of studies have focused on the impact of hurricanes on mangrove vegetation, comparison among these studies is often difficult due to the lack of information regarding the context of such disturbances. In fact, several factors may induce variation in damage from hurricanes to mangroves (e.g., wind direction and velocity, local topography, type of vegetation, species-specific susceptibility; Lugo and Snedaker 1974).

The severity of hurricane impacts to forest structure depends primarily on maximum sustained wind speed close to the study sites. In addition to storm intensity, distance of study sites and orientation with respect to storm track (i.e., backwind vs. forewind) affects the severity of effects (Doyle et al. 1995, 2009, Milbrandt et al. 2006). The present study documents a sigmoidal rather than linear trend in the relationship between lethal damage (as assessed by tree basal area) and maximum sustained winds. A non-linear relationship between canopy opening and wind intensity in mangrove forests was formerly put forward by Doyle et al. (1995). Moreover, Ancelin et al. (2004), using an individual tree-based mechanistic model to predict wind damage within forest stands, described wind damage as a sigmoid function of wind speed. Although such a predictive model needs to gain broader validation, our data suggest a lower critical threshold (Category 1 hurricane winds) for tall, basin stands as compared to lower, scrub and fringe stands (up to Category 3 wind speed).

For a particular wind velocity (especially hurricane-force winds), the amount of damage differs strikingly depending on site and stand characteristics (Doyle et al. 1995, Imbert et al. 1996, Sherman and Fahey 2001). Although taller stands are generally the most damaged, no clear

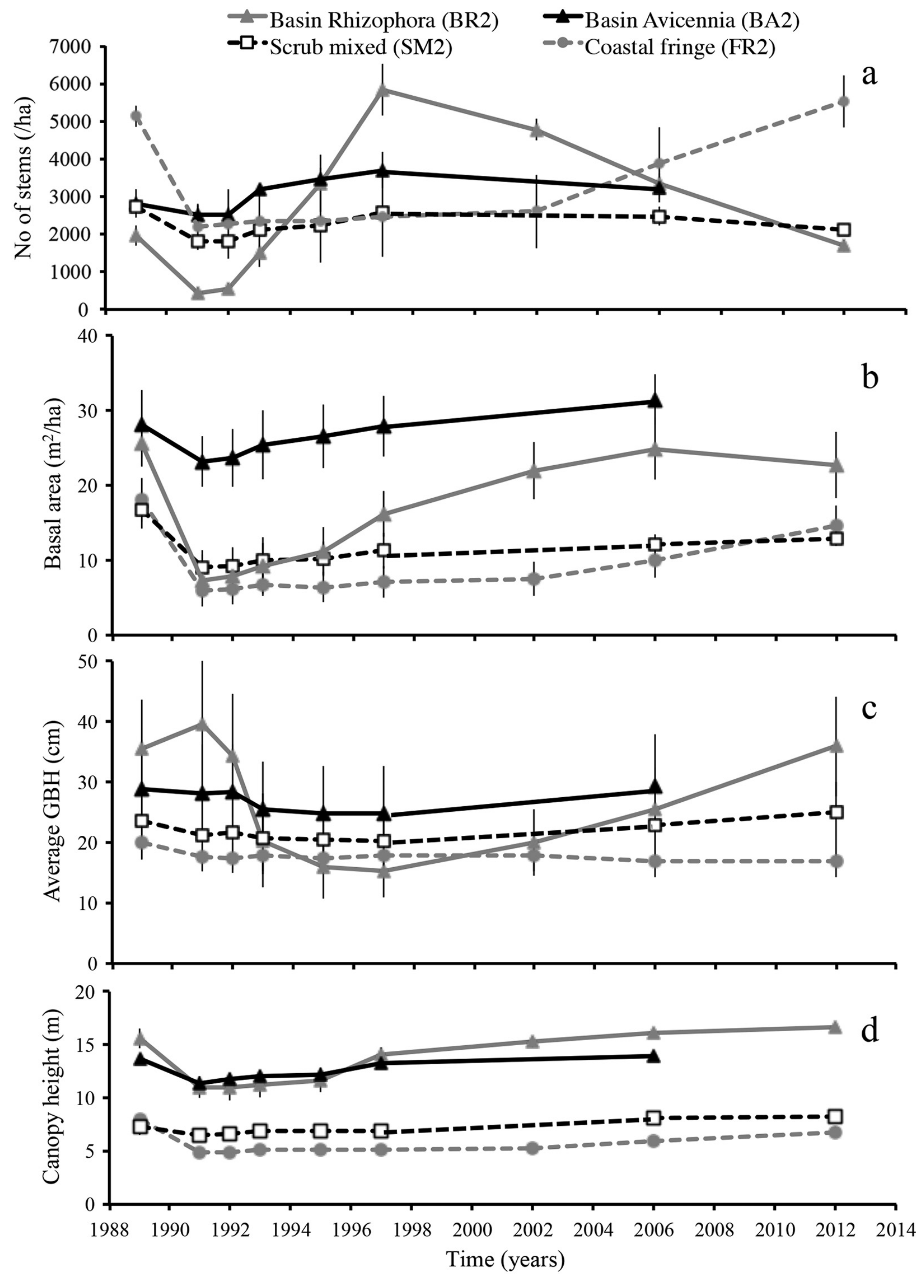

Fig. 6. Changes in structural characteristics of four mangrove stands from 1989 (pre-hurricane values) to 2012 (a, stem density; b, basal area; c, average GBH; and d, canopy height). Each point represents the mean of six measurements ±1 SE (vertical bars). Only stems ≥10 cm GBH were taken into account.

relationship between canopy height and whole stand damage has been demonstrated yet (Sherman and Fahey 2001). As documented herein for *Rhizophora*, the ratio canopy height to mean GBH may be a good proxy of three-dimensional stand structure for predicting hurricane damage in natural forests, like does slenderness at the individual-tree scale (Ancelin et al. 2004). At a broader scale, Smith et al. (2009) found that basin mangroves suffered significantly more damage than did riverine or island mangroves. This is consistent with the results presented here and shows that, for a particular level of disturbance, damage to trees may depend primarily on the hydro-geomorphic context of mangrove forests, which in turn control stand structure (Lugo and Snedaker 1974).

Species-specific sensitivity of mangroves to storm winds is controversial. For example, Kovacs et al. (2001) found *R. mangle* to be more resistant to hurricanes than was *A. germinans*, but Smith et al. (1994), Imbert et al. (1996), and Ross et al. (2006) came to opposite conclusions, and Sherman and Fahey (2001), Milbrandt et al. (2006), Smith et al. (2009) found no differences among those species. Such apparent contradictions may arise when species-specific comparisons are not based on similar site or stand conditions. This study shows that in mixed stands, *Rhizophora* is always more susceptible to lethal damage as compared to *Avicennia*. More specifically, taller mature stands dominated by *Rhizophora* are more prone to wind damage. Finally, only heavy architectural damage may cause *Avicennia* trees to die from windstorm.

To facilitate informative comparisons of hurricane impacts on mangrove forests, complementary studies should document four characteristics, tentatively ranked in order of importance: on-site wind velocity (or a combination of SSWS category and distance to hurricane track), canopy height (related to mean GBH when available), dominant tree species, and position of the stand (inner vs. border) within the forest.

Mangrove resilience and steady state

The fringe and scrub mangrove stands had not fully recovered to pre-hurricane structure 23 yr after the passage of Hurricane Hugo, unlike basin stand BR2, which was the most severely damaged. As this stand has a higher primary productivity as compared to the two others (Imbert and Portecop 1986, Imbert and Rollet 1989), such results support the hypothesis of a positive relationship between long-term turnover rates and primary productivity (Phillips et al. 1994). So, as biomass resilience of *tierra firme* forests may be primarily controlled by water availability (Poorter et al. 2016), the resilience of mangrove vegetation may be primarily dependent on nutrient availability.

This post-hurricane sequence documents for the first time the entire, complex trajectories of mangrove vegetation recovery from a high-energy storm. The duration of these trajectories is consistent with the time lag of about 20–25 yr. reported for mangrove stand maturity in Florida (Lugo and Snedaker 1974). However, the recovery to pre-hurricane stand structure should not necessarily be viewed as a return to a steady state, which means roughly constant stem density and biomass away from disturbances (e.g., Brock 1967). As exemplified by stand BA2, basal area and mean GBH may continue to increase above pre-hurricane values. This suggests that mangrove vegetation may not have reached equilibrium with stand resources. According to the extent of hurricane-force winds on each side of a hurricane path (Keim and Muller 2007) and based on available Caribbean hurricane records (DOC 1979 in Smith et al. 1994, SMIAG 1990), the expected return time of hurricane-force winds on a same site would be of 20 yr for Martinique and Guadeloupe, and 6.5 yr for South Florida. Moreover, outside of the hurricane belt the life span of the highly sensitive *Rhizophora mangle* exceeds 110 yr (Menezes et al. 2003). It is therefore obvious that, in the Caribbean, hurricanes prevent mangrove ecosystems from ever reaching a structural equilibrium with climatic and soil resources, the so-called steady state (Lugo and Snedaker 1974, Smith et al. 2009).

Canopy closure in mangrove forests involves two main strategies: regrowth from damaged trees or replenishment from new or pre-established seedlings. The latter strategy is commonly observed for all mangrove species. The former is shared by *Avicennia* and *Laguncularia,* but not by *Rhizophora* (Milbrandt et al. 2006). Consequently, the recovery of populations of *Rhizophora* depends on recruitment of pre-established understory seedlings or new colonizing seedlings (Baldwin et al. 2001). As demonstrated in stands BR2 and FR2, this regeneration pathway is efficient for outcompeting more light-demanding species (Ross et al. 2006). However, it may be a limitation in some fringe stands along estuaries and creeks (Imbert et al. 2000, Flower and Imbert 2006, Milbrandt et al. 2006, Smith et al. 2009). In fact, such areas are generally characterized by unconsolidated silty sediments, from which pre-established seedlings may be easily up-rooted by storm surge (Flower and Imbert 2006). Then, forest recovery processes may be delayed for a long period, as propagule delivery and establishment can be impeded by fallen trunks, distance to surviving trees, changes in shore topography, and sediment geochemistry (Smith et al.1994, Imbert et al. 2000, Milbrandt et al. 2006).

Except for local, short-term variations involving herbaceous species or saplings (Baldwin et al. 2001), neither real successional stages (relay floristics, sensu Egler 1954) nor long-lasting shifts in canopy dominance have been reported for mangroves during the course of forest recovery after hurricane disturbance. In fact, in accordance with the early work of Roth (1992), this study exemplify that mangrove forests, like other tropical forests (Vandermeer et al. 1995, Imbert et al. 1998), do conform to the direct regeneration hypothesis: As long as hurricanes do not significantly and persistently modify ground topography (Cahoon 2006), forest recovery is directed by the initial floristic composition (Egler 1954).

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