

Visible and invisible effects of hurricanes on forest ecosystems: an international review

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Abstract Hurricanes have visible and invisible effects on forests. The visible effects are dramatic, noticeable over the short-term and relatively well documented in the literature. Invisible effects are less understood as they require well-focused research both in the short- and long-term time scales. This review of the literature on hurricane effects focuses on the Neotropics and the temperate zone of North America. The material is organized according to a heuristic model that distinguishes between immediate effects (0 to 3 years), immediate responses (0 to 20 years), trajectories of responses (0 to 100 years) and long-term legacies (>100 years). It is suggested that the ecological role of hurricanes involves six principal effects: 1. they change the ecological space available to organisms; 2. they set organisms in motion; 3. they increase the heterogeneity of the landscape and the variability in ecosystem processes; 4. they rejuvenate the landscape and its ecosystems and redirect succession; 5. they shape forest structure, influence their species composition and diversity and regulate their function; and 6. they induce evolutionary change through natural selection and ecological creativity through self-organization. A new approach to hurricane research will study hurricanes at the same scale at which they operate (i.e., across latitudes and longitudes and over disturbed and undisturbed landscapes). This research will require networks of observation platforms located along expected hurricane paths to facilitate forest structure and functioning observations across gradients of hurricane frequency and intensity. This research will also require use of remote sensing and automated wireless technology, hardened to survive hurricane-strength winds and floods to assure real time measurements of the characteristics of hurricanes and ecosystem responses. No progress will be forthcoming in the understanding of hurricane effects if we do not learn to quantify objectively the energy dissipation of hurricanes on the full grid of affected forests as the hurricane passes over a landscape.

Key words: hurricane effects, typhoon effects, cyclone effects, Luquillo Experimental Forest.

Present observations in north Queensland suggest that cyclones are a potent ecological factor which regularly upsets forest equilibrium, with far-reaching consequences for the regeneration, suppression, and reproduction of species.

L.J. Webb (1958, 227)

INTRODUCTION

The visible effects of the event impress any ecologist who has experienced the passage of a hurricane¹. Massive defoliation, snapped and wind-thrown trees, large debris accumulations, landslides, debris flows, brown landscapes, altered stream channels and transformed beaches exemplifies visible effects of hurricanes. A large body of information is accumulating on these effects because they are normally

documented and quantified by scientists. However, as hurricane research expands into long-term observations, invisible effects on forests also become apparent. These invisible effects are a challenge to ecologists because they can be uncovered only through research specifically designed for this purpose. Advances in our understanding of hurricane effects will increasingly depend on our ability to understand their invisible effects, and in so doing we will come to the realization that hurricanes affect all aspects of the functioning of ecosystems along their path.

I review literature that describes how hurricanes influence short- and long-term aspects of forest ecology. The review is illustrative of the breadth of effects that hurricanes have on both tropical and temperate forests with particular attention to the Neotropics and the USA. My objective is to identify generalizations involving both visible and invisible effects of hurricanes that apply to all events. However, I emphasize invisible effects because Everham and Brokaw (1996) published a comprehensive review of the visible effects of over 100 storms on forests worldwide.

¹I use hurricane as synonymous with tropical cyclone and typhoon. In the review I also include information from blow-down and strong windstorm events.

The review begins with an overview of hurricanes to develop some of the basis for a heuristic model of hurricane effects and consequences on forests. The model is described later in this review with examples. I will use this model to organize the literature review material, which I present as four consecutive sections dealing with immediate effects, immediate responses, trajectories of response and long-term legacies. Each of these sections is in turn subdivided by ecosystem sector to include forest structure, physical environment, animals, tree species and processes or ecosystem functioning. I then present a section summarizing generalizations about the ecological role of hurricanes. The review ends with a discussion of research needs in the context of the confounding problems we face when trying to relate hurricane effects to anthropogenic activity and climate change.

Throughout the review I avoid several terms abundant in hurricane (tropical cyclone) literature: ‘impact’, ‘destroyed’, ‘catastrophic’ and ‘damage’. Instead I use ‘affects’, ‘modified’, ‘changed’ and ‘effects’. I strive to present information with minimal bias and not assume that because trees snap or are blown over, the effect has negative repercussions to forests. I recognize that this terminology may be adequate for hurricane effects on the economic infrastructure, but it does not necessarily apply to natural ecosystems, particularly on the long term. Research has shown that forests are not ‘damaged’ or ‘destroyed’ by hurricanes and that there are adaptive responses that follow such hurricane effects. For example, studies in Puerto Rico and New England, USA, show that changes in key ecosystem processes were often slight following even major hurricanes (Foster & Boose 1995). Specifically, nutrient losses were minimal, soil moisture changed little, minor changes in trace gas fluxes returned rapidly to pre-hurricane rates and biotic control over biogeochemical cycles was asserted (Cooper-Ellis *et al.* 1999). Also, Foster and Orwig (2006) evaluated the ecosystem-level consequences of intensive windstorms and invasive pests and found that in spite of the large physical changes in forest structure induced by these disturbances, little disruption of biogeochemical processes or other ecosystem functions, such as water quality services, typically follows these disturbances. Foster *et al.* (1997) concluded that: ‘Comparison of results from the different experiments led to the surprising conclusion that structural integrity is not a good indicator of forest ecosystem integrity’ (p 439). Consistent with this view, they found that in a soil warming experiment the structure of the forest was visually intact, but measurements of ecosystem functioning suggested important imbalances with future implications to structure, function and exchanges with the global environment. Thus, while the negative implications of current terminology might reflect the perceptions of human observers of

the phenomenon, such perception might not be the reality of how these effects fit into the adaptive *milieu* and persistence of forests.

I also avoid the concept of ‘recovery’ of communities and use instead ‘trajectories of response.’ This is to recognize that succession after a hurricane does not always follow a direct path to the pre-disturbance condition. Instead, as I will discuss below, a hurricane opens opportunities for community change both in the short- and long-term basis, and thus the trajectory of the response, like most successions, can follow many alternative pathways to maturity (Ewel 1980).

CHARACTERISTICS OF HURRICANES

Hurricanes are tropical phenomena of immense proportions. Their radius can attain 1000 km with a weight of 3×10^{13} Mg and water yield of $16 \text{ km}^3 \text{ day}^{-1}$, or equal to the annual run-off of the Colorado River in the USA (Riehl 1979). However, the actual length of the radius of maximum winds (about 50 km) is a subject of debate (Kerr 2000a). Hurricanes can dissipate 36×10^{10} kWh day^{-1} or 36 times the electrical output of the USA in the 1970s (Riehl 1979). This gives hurricanes a global role in the heat balance of the Earth by transporting excess tropical heat to higher latitudes. Over the last 100 years there have been some 800 hurricane and tropical storm passages through the Caribbean. Salvia (1972) documents 101 events between 1492 and 1970. When viewed together, hurricane and storm passages over this region exhibit predictable spatial and temporal patterns (Neumann *et al.* 1978); fig. 16.7 in Lugo *et al.* (2000a). The frequency of passage of the hurricane eye over a particular location ranges from annual in places like Taiwan, to decadal in Puerto Rico, to centennial in New England, and millennial in Minnesota, USA. The frequency of events drives different levels of forest response, as suggested by Walsh (1996) and discussed in this review.

Hurricanes are classified by their intensity into five wind speed categories according to the Saffir/Simpson Hurricane Scale (Neumann *et al.* 1978) and their size can be assessed by satellite images. This scale differs slightly from the Australian Tropical Cyclone Scale (see Turton 2008). From the velocity of movement and direction, it is also possible to estimate the duration of the event over specific geographic areas (cf. Lugo *et al.* 1983; Scatena & Larsen 1991; Boose *et al.* 1994). Therefore, it is possible to use the following equation to estimate the long-term kinetic energy (J/century) of hurricanes over any location:

$$\text{Kinetic Energy} = (\text{Intensity}) \times (\text{Frequency}) \times (\text{Duration}) \times (\text{Size}) \times (\text{year}/8760 \text{ h})$$

where intensity is measured in $\text{J ha}^{-1} \text{ year}^{-1}$, frequency in events per century, duration in hours per event, and size or spatial scale in hectare.

The relevance of these calculations to ecological understanding is that they contribute to the expression of ecological processes (disturbances, primary productivity, carbon fluxes, etc.) in common energy units. A common energy unit is also useful for comparing different types of disturbances and their effects on different ecosystems. For example, Lugo *et al.* (2000b) compared the kinetic energy of hurricane winds and waves to show the disparity of the physical environment between coral reefs and rain forests (Table 1). The kinetic energy of hurricane winds is in the order of 3500 and 15 000 times higher than the kinetic energy in the average global wind, but the kinetic energy of maximum waves that strike coral reefs is between 3000 and 13 800 times higher than the kinetic energy of hurricane winds. One could hypothesize that the effect of a disturbance on an ecosystem is a function of the magnitude of its kinetic energy dissipation in synergy with the state of the affected ecosystem at the time of the event (Lugo 1978).

Hurricanes are external factors to forests. Forests have little influence on their passage, which is controlled by sea surface temperature, atmospheric pressure and high-altitude wind conditions (Emanuel 1987, 2005; Gray *et al.* 1997). However, the location of landmasses and local topography play a role in

determining the direction and speed of passage of the storm as well as the effects on vegetation (Boose *et al.* 1994; Foster and Boose 1995; Turton 2008; Turton & Stork 2008) suggested that landscape patterns of wind exposure depended on the interaction between topography and peak wind velocity. When these storms achieve landfall, their strength diminishes because they require warm water to maintain their strength. Also, their speed of forward movement is faster at high latitudes than at lower latitudes, which means that they have a longer period of interaction with tropical forests than they do when they strike temperate forests (Foster & Boose 1995).

Hurricanes are an example of large and infrequent disturbances (LIDs, *sensu* Turner & Dale 1998). A disturbance is a disruption of any state variable or flux of an ecosystem by any force external to the system of interest (wind, water, radiation, gravity, organisms). Disturbances have five components that are relevant to assessing their potential ecosystem effects. These components are: (i) severity or intensity, (ii) frequency of occurrence, (iii) duration, (iv) spatial scale, and (v) point(s) of interaction with the ecosystem (cf. Lugo 1978; White 1979; Sousa 1984; Pickett & White 1985a,b). Describing the five components of natural disturbances quantitatively requires interdisciplinary collaboration.

A distinction is made between external (allogenic) forces that converge on ecosystems and the internal (endogenic) processes of the system (Pickett & White 1985b). Such distinction facilitates analysis and understanding of ecological phenomena because it forces the investigator to be cognizant of the boundaries of the ecosystem under study, the fluxes across those boundaries, the effects of these fluxes on biotic processes (and vice versa) and issues of spatial and time scales associated with each type of disturbance and ecosystem type.

A hurricane consists of two environmental factors that have strong and independent interactions with forests. These are rain and wind. Rain and wind interact but must also be evaluated separately as they have different effects, interact with different sectors of the ecosystem, can have different intensities and return frequencies during particular hurricane events and often occur in the absence of hurricanes (Scatena & Larsen 1991; Nelson *et al.* 1994). This means that a strong category 5 hurricane is the terminus of a gradient of meteorological events that begins with a rain shower or a light breeze. Thus, at a given location sectors of the hurricane (eye, outer bands, quadrants) can be characterized by the predominance of wind or of rain, or have high intensities of both factors or exhibit low intensities for both wind and rain. These alternatives depend on the trajectory and the developmental stage of the hurricane at the time it interacts with the forest.

Table 1. Kinetic energy of wind and waves

Disturbance force	Kinetic energy ($\text{J m}^{-2} \text{ s}^{-1}$)
Winds	
Global yearly average	0.014
Winter storm wind, Long Island Sound, USA	2
Hurricane Hugo over Puerto Rico	210
Hurricane Daisy	
0–37 km radius core	1.6
37–74 km radius ring	72
74–111 km radius ring	38
111–148 km radius ring	27
Area-weighted mean	47
Waves	
Yearly average waves on Grand Cayman Island coral reef, Caribbean Sea	20–25
Zones of maximum wave energy from Trade Winds, Bikini Atoll reef, Pacific Ocean	200–300
Waves on exposed rocky coast, Northeast Pacific	3000
Maximum waves from Hurricane Allen on Jamaican coral reefs	550 000–750 000

These data and the sources for their calculation are from Lugo *et al.* (2000b) and (Scatena *et al.* 2002).

Hurricanes are associated with other disturbance events, exacerbating the effects of winds and rain. For example, many times hurricanes are followed by drought events, with drought causing its own effects on surviving organisms (Covich *et al.* 2006) and ecosystem processes (Beard *et al.* 2005). Also, fires can follow hurricanes and consume much of the accumulated debris while also stressing surviving organisms. For example, Hurricane Gilbert, one of the strongest hurricanes to pass over the Yucatan Peninsula in recorded history, had lower effects on bird populations than the fire that followed the hurricane (Lynch 1991). A year later, while hurricane-affected avifauna was well into establishing its pre-hurricane numbers, the state of avifauna affected by the hurricane and fire was well behind. The hurricane-fire combination of effects is believed to be important in the development and maintenance of particular plant communities in Australia (Webb 1958), the long leaf pine (*Pinus palustris*)/savanna vegetation of southern USA (Myers & van Lear 1998), and the *Svietenia macrophylla* forest stands of Central America (Snook 2003). Hurricanes are also accompanied by high seas, storm waves and storm tides that modify coastal areas and affect coastal forests including mangroves, freshwater swamps and forests that seldom flood.

In summary, a hurricane is a complex event involving rain, wind, stream discharge, low atmospheric pressure and direction and speed of movement. Such an event is best described by applying the five components of a disturbance to each of the hurricane's components (Table 2). The matrix in Table 2 is illustrative of the complexity of a hurricane, which translates to an even more complex suite of effects on the biota and the landscape. Moreover, such a 'hurricane' interacts with vegetation, geologic substrate and topography to trigger several additional types of forest disturbances such as tree-fall gaps and landslides in montane forests, and storm waves, swash and floods in lowland coastal forests. Therefore, the evaluation of hurricane events involves the evaluation of a complex array of forces that generate a variety of ecosystem disturbances that normally can occur independently of each other, but which can dissipate

very high quantities of kinetic energy when conditions maximize the effects of all its components. Given this complexity at the level of the triggering of a disturbance event such as a hurricane, coupled with the complexity of landscapes, soils and states of affected ecosystems, it should not be surprising then, that studies that describe hurricane effects show so much variation, at times contradictions, and in general few consistent generalizations.

Because of a lull in hurricane activity in the western tropical Atlantic-Caribbean region between 1968 and 1991 compared with the interval between 1944 and 1967 (Gray *et al.* 1997), ecologists had few opportunities to observe and study the effects of hurricanes in Caribbean, Central and North American forests. However, hurricanes have struck land numerous times since the 1990s, allowing significant literature to emerge on the effects of hurricanes on tropical and temperate forests. To organize this literature, I use a simple heuristic model that illustrates the interaction between hurricanes and forests.

DISTURBANCE EFFECTS, CONSEQUENCES, AND TRAJECTORY OF RESPONSE

The interaction between any individual disturbance and an ecosystem can be summarized with a simple feedback system composed of five elements (fig. 5 in Lugo *et al.* 1999). The first element is the disturbance, usually triggered by an external force that may or not be modified by physical and biotic components of the affected ecosystem. The second element is the point of interaction between the disturbance force and some ecosystem component, identified here as the interface (Lugo 1978; Lugo & Scatena 1995; Silver *et al.* 1996). Interfaces are usually biotic, such as the canopy, although they can be physical, such as the soil. The third element is the result of the interaction between the disturbance force and the components of the interface. This interaction is measurable by ecological effects such as mortality, alteration of ecosystem structure, or change in rates of processes. The consequences

Table 2. The many ways of evaluating the characteristics of a hurricane disturbance using as an example Hurricane Hugo as it passed over Puerto Rico in 1989 as a category 3 hurricane with a recurrence interval of 60 years (Scatena & Larsen 1991)

Component	Intensity	Frequency (year)	Duration (h)	Spatial scale (km ²)	Point(s) of interaction
Rain (mm [†])	339 [‡]	5	<4	Hundreds	Canopy/soil
Wind (km h ⁻¹)	148	100	4	Hundreds	Canopy
Peak Stream discharge (m ³ s ⁻¹)	70–666	10–31	12–24	Tens	Stream channel
Barometric pressure (mbs)	946.2		<4	Hundreds	Leaves

Similar patterns characterize typhoons (Lin *et al.* 2003). Empty spaces mean there is no information. [†]Units in parenthesis correspond to values in the Intensity column. [‡]Generated 285 landslides, considered a low number for the Luquillo Mountains.

of the effects are the fourth element of the model. These consequences apply to the environmental conditions of the ecosystem, that is, microclimate, substrate, distribution of resources, and to the processes of the ecosystem, that is, nutrient cycling, regeneration, succession, etc. Another consequence of the disturbance is the possibility of species invasions, species turnover and local species extinctions. The fifth and final element in the disturbance model is the trajectory of the response by the ecosystem, shown as a feedback loop with many alternative pathways. The trajectory of ecosystem response in terms of ecosystem structure and function involve opportunities for changes in species composition, stand structure and differential reproduction of organisms. The alternative trajectories recognize the possibility for pathways to different ecosystem states, including the potential of a flip in stability domains (*sensu* Carpenter *et al.* 2001; Gunderson & Pritchard 2002).

This simple feedback system is elaborated in Fig. 1 to describe the interaction of Hurricane Hugo and the Luquillo Experimental Forest (LEF) of Puerto Rico (Fig. 2 shows the locations of all Puerto Rican sites mentioned in this review). The hurricane is shown as two external forces (wind and rain), each with a different point of interaction within the LEF and thus interacting with a different interface (canopy for the wind and soil for the rain). Aspect and topography are

the physical modifiers of the forces associated with wind and rain (Bellingham 1991; Boose *et al.* 1994). Each interface also acts as a modifier of the other. For example, canopy interception and channelling of water modifies the effects of rainfall on soil saturation, while the soil-root interaction modifies the effects of wind on the canopy. If soils and roots hold the tree upright, the canopy will bear a greater burden of wind effects and more tree snaps and branch fall will occur. If the soil slides, then whole tree biomass will be either transferred to the forest floor, or exported to other locations by debris flows.

The effects of the wind–canopy interaction and rainfall–soil interaction are quite different. Wind causes tree falls and tree snaps *in situ* with the corresponding mass and nutrient transfer to the forest floor (Frangi & Lugo 1991; Lodge *et al.* 1991) and indirect mortality effects (Lugo & Scatena 1996). Rainfall–soil interaction can result in either tip up mound topography (Schaetzl *et al.* 1989; Peterson & Pickett 1990; Peterson *et al.* 1990; Clinton & Baker 2000; Lenart 2003) or in landslides, which transport materials away from the stand (Larsen & Torres Sánchez 1992; Larsen & Simon 1993). The consequences of these two types of effects are also quite different. Mass transfer *in situ* maintains forest stand conditions, which can quickly restore a closed canopy forest through succession. More importantly, tree uprooting affects soil morphol-

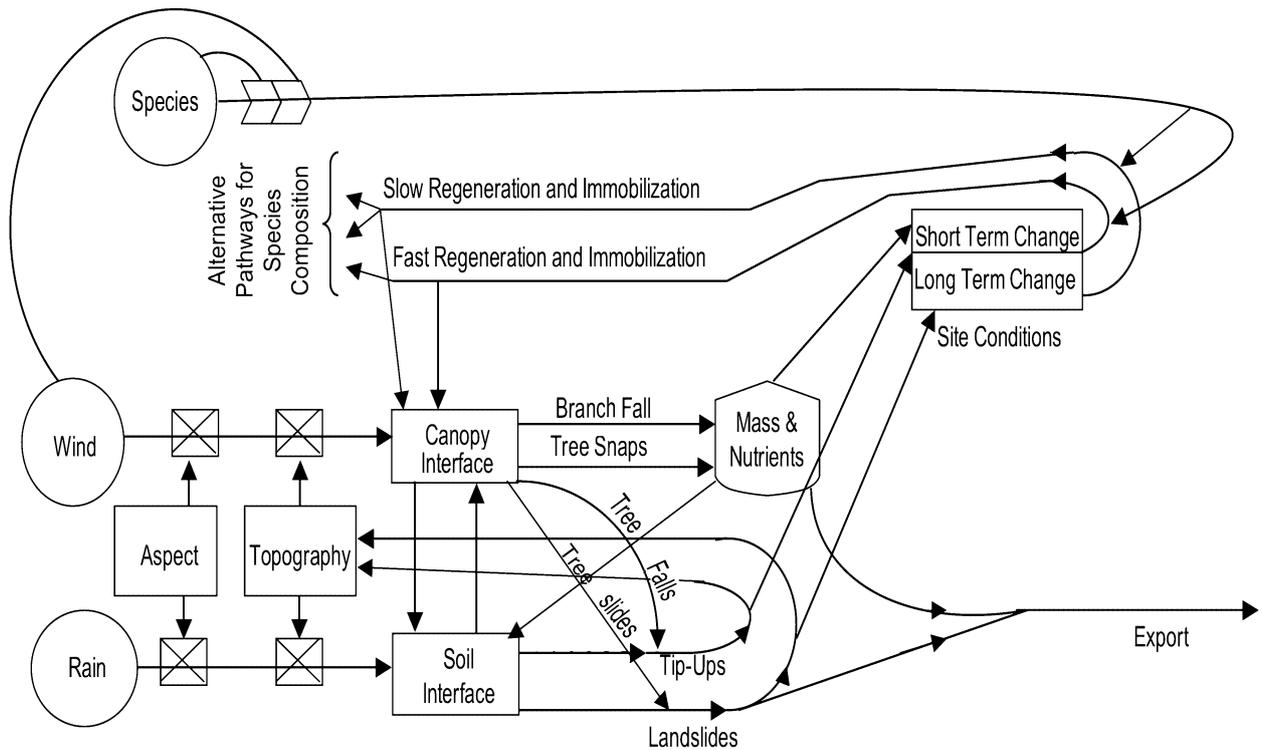


Fig. 1. Diagram of the interaction of the two main forces of a hurricane and two forest interfaces, including the ecological consequences and trajectories of change. The species component of the diagram emphasizes the successional aspects of their role.

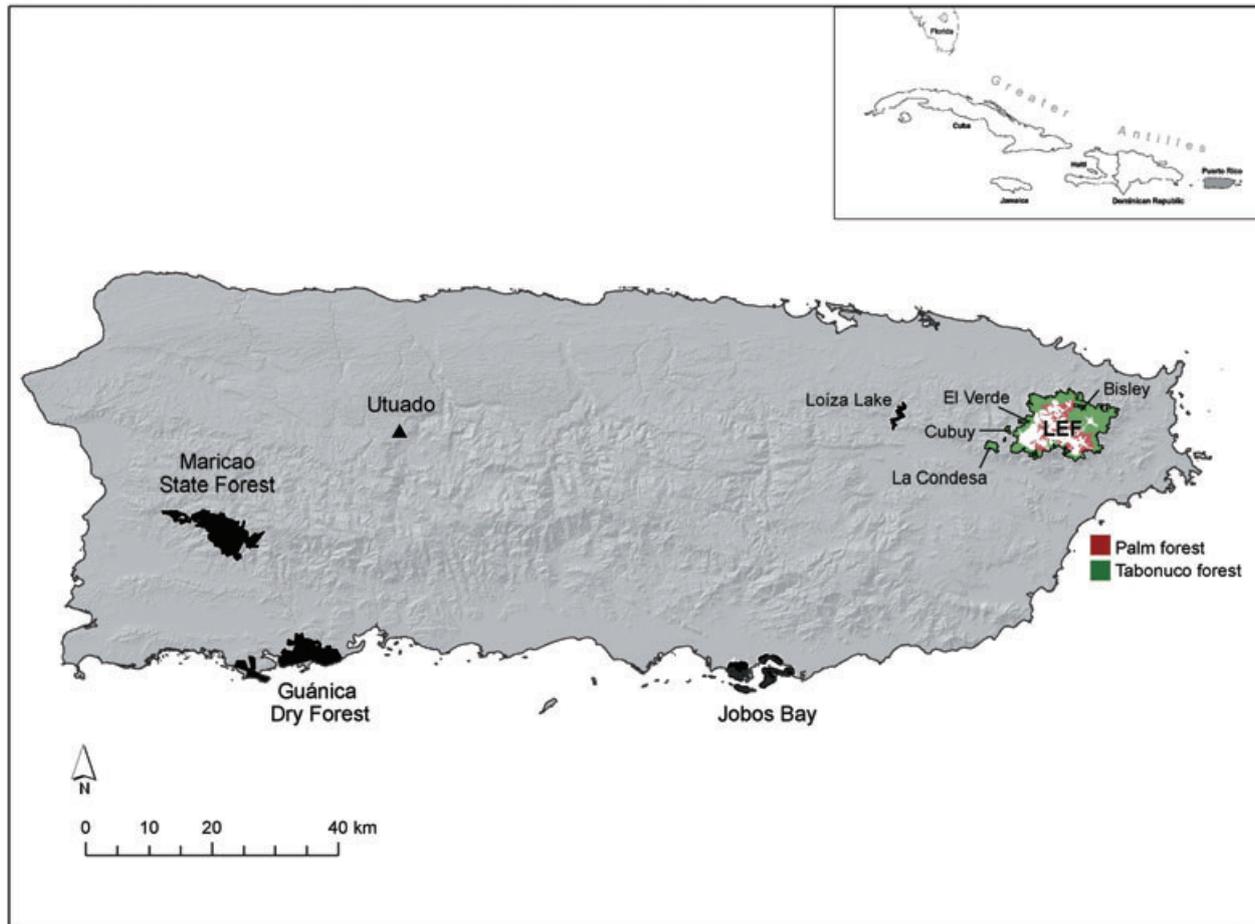


Fig. 2. Location of Puerto Rico, the Luquillo Experimental Forest, and other places in the island mentioned in the text.

ogy, surface characteristics, nutrient availability, regeneration trends and forest age structure (Schaetzl *et al.* 1989). Landslides on the other hand, dramatically change local stand conditions and require more time to restore forest conditions (Walker *et al.* 1996a). The outcome of these effects of, and responses to, hurricanes are trajectories of short- and long-term change in affected stands. These involve both slow and fast changes that culminate in mature stands that can either be similar or dissimilar to the stands that were initially affected by the hurricane.

For the purpose of this review, I use a modified time sequence of hurricane effects and responses in table 16.5 in Lugo *et al.* (2000). They identified five time periods and their durations to depict the effects of, and responses to hurricanes in the tabonuco (*Dacryodes excelsa*) forest at the LEF. These periods are the immediate effects of the event, which I extend to 3 years in the next section of this review. A period of rapid change that lasts up to 20 years after the event, which they subdivide into a 10-year reorganization phase and a 10-year aggrading phase, both included here in the section of immediate responses. A period of

transition that lasts from 20 to 45 years after the storm follows, and finally a period of maturity from 45 to 60 years after the event. Length of these periods is based on data from long-term plots at the LEF, but in general depends on the frequency of passage of major storms over the site of interest. Trajectories of response that begin at time zero after the storm, but mostly apply to the periods of transition and maturity (0–100 years) are discussed later, together with long-term legacies, which transcend the time scale to maturity and extend to centennial and evolutionary time.

IMMEDIATE EFFECTS (0–3 YEARS)

The immediate effects of hurricanes are caused by the intensity of the components of the disturbance (Table 2) impinging on the various interfaces receiving the brunt of the kinetic energy dissipated on the interface. Because of the magnitude of the kinetic energies involved (Table 1), these immediate effects are among the most common and consistent effects reported by most studies. As we will see below, most of

these effects are visible and dramatic and can also have long-term economic effects, as was the case with Hurricane Hugo, which affected about 37% of the commercial forestlands of South Carolina, USA. This affected wood volumes to a level of 1 billion US dollars, and the short- and long-term economy of the state, also creating land use conditions that might benefit the overall state economy, but at the expense of future forestry activities (Marsinko & Straka 1997).

Forest structure

The most common effect of hurricanes on forests is defoliation (Bates 1930; Wadsworth & Englerth 1959), which is the direct result of wind energy dissipation on the canopy interface. Foliage-height profiles before and after a hurricane clearly show the higher defoliation of the canopy compared with the understory in stands affected by hurricane winds, as well as the faster refoiliation at lower canopy strata following the hurricane (Wunderle *et al.* 1992; Brokaw *et al.* 2004). Defoliation, measured by instantaneous leaf fall is a function of maximum daily wind speed (Beard *et al.* 2005). After Hurricane Iniki passed over Hawaii, Herbert *et al.* (1999) studied the effects on a *Metrosideros polymorpha* montane rain forest. They measured an instantaneous litter fall pulse equivalent to 1.4 times the annual litter fall rate and a reduction in Leaf Area Index (LAI) of between 3% and 59% depending on the initial LAI. In Fushan Experimental Forest in northern Taiwan, typhoon strength explained 82% of the litter fall variation over a 9-year record (Kerr 2000; Lin *et al.* 2003) reported the defoliation of vegetation in the island of Guam as a result of the passage of a salt-spray-laden 'dry' (rainless) Typhoon Gay. This island-wide phenomenon caused no stand-level mortality, but in about a year, all vegetation refoiliated.

Other common visible effects of hurricanes on trees include loosening and shredding of the bark due to the whipping action of the winds, as well as abrasion of stem surfaces due to sandblasting. Stem breakage (from small limbs to stem boles, which can snap at the base or at any height) is another visible effect of hurricane winds as is uprooting, which can range from various levels of leaning to complete blowdown of the tree and exposure of its complete root system to the atmosphere (Putz *et al.* 1983; Everham & Brokaw 1996) analysed 310 stems in Barro Colorado Island, Panama, and found that uprooted trees tended to be larger, shorter for a given diameter and to have denser, stiffer and stronger wood than snapped trees. Faster growing trees had lower density wood and experienced more mortality than those with higher density wood. Snapped trees tended to sprout and smaller trees tended to sprout more than larger trees. While these mortalities were not caused by hurricanes and it is not

clear if the observed patterns hold in other locations, the study provides empirical information about the allometry of trees that snap or uproot.

Coincident with the notion of wind energy dissipation on the canopy interface is the consistent finding that large canopy trees and particular canopy architectures experience more wind effects than small understory trees. Such understanding is common knowledge among fisherman who depend on mangroves (Kovacs *et al.* 2004). Mangrove trees with larger diameter at breast height (d.b.h.) were subject to a greater mortality and more snapping than those of smaller d.b.h. in southeast Florida, USA, following the passage of Hurricane Andrew (Baldwin *et al.* 1995). In the Amazon, rare storm events selectively killed or toppled the largest trees in the forest (≥ 63 cm d.b.h.). Such events contribute to high turnover of stems in otherwise mature forests and contribute to canopy roughness and structural heterogeneity (Foster & Terborgh 1998). Tornados have the same effect on temperate forests (Glitzenstein & Harcombe 1988; Nelson *et al.* 1994; Nelson 2005). In the Santee Experimental Forest in South Carolina, the largest trees in terms of d.b.h. and height experienced the greatest hurricane effects (Hook *et al.* 1991). The same pattern was shown after Hurricane Georges in the Guánica Dry Forest, Puerto Rico (Van Bloem *et al.* 2005).

In Hawaii after the passage of Hurricane Iniki, Herbert *et al.* (1999) found that larger trees were visibly affected with double the frequency of smaller trees, and that the severity of the effect increased with the addition of phosphorus fertilizer. Larger trees experienced more effects than smaller trees in a mature secondary forest at Cubuy in the LEF, but topographic position also influenced hurricane effects. For example, trees on ridges and valleys were more affected than trees on slopes, and faster growing trees were more affected than slower growing trees (Ostertag *et al.* 2005). However, in another sector of the LEF (Bisley), ridges exhibited less wind effects than slopes (Scatena & Lugo 1995). The apparent inconsistency is explained by exposure relative to the storm path (windward (Bisley) *vs.* leeward (Cubuy)), strength of winds, soil types and vegetation structure. These differences explain variations in the fraction of trees affected by wind (see below).

About 25% of all trees had some visible wind effects at the El Verde sector of the LEF which was more distance to the eye of Hurricane Hugo and less exposed than Bisley (Zimmerman *et al.* 1994) while over 60% were visibly affected in the windward sector of Bisley (Basnet *et al.* 1992). Larger trees exhibited greater loss of branches than smaller ones, but tree d.b.h. was not correlated with wind effects at El Verde (Zimmerman *et al.* 1994). In Hawaii, 34% of the trees had visible structural effects after Hurricane Iniki (Glitzenstein and Harcombe 1988; Herbert *et al.*

1999) reported after a tornado that 65% and 63% of the trees were affected at two sites in the Big Thicket of Texas, USA. In the Santee Experimental Forest, 80% of the trees experienced extreme wind effects after the passage of Hurricane Hugo and the timber volume decreased from 178 to 24 m³ ha⁻¹ (Hook *et al.* 1991). At scales of 0.25–7 ha, extreme wind gusts of up to 66 m s⁻¹ broke or uprooted all trees. These smaller areas with total uprooting of trees extended up to 150 km inland. In Nicaragua, Hurricane Joan snapped or uprooted 80% of the trees and defoliated all trees over an area of 500 000 ha (Yih *et al.* 1991).

In the mangroves of south Florida after Hurricane Andrew, almost 100% of the trees had some visible structural effect (Baldwin *et al.* 1995). Mangrove forests experienced greater mortality and structural change than terrestrial systems adjacent to them because they were exposed to higher wind energies than inland forests (Baldwin *et al.* 1995). In Guadeloupe, French West Indies, tall mixed mangroves experienced a 78% decrease in average tree density and 71% reduction in average basal area after the passage of Hurricane Hugo (Imbert *et al.* 1996). The respective effect on fringe mangroves was 59% and 68%, followed by mixed dwarf mangroves (26% and 23%) and black mangrove, *Avicennia germinans* (3% and 3%). When Hurricane Gilbert passed over Jamaica, the greatest visible effect was on mangroves and montane pine plantations, which had the largest trees and were located on the most exposed sites (Wunderle *et al.* 1992). Topography, tree stature and species differences were the main factors contributing to the variability of hurricane effects in ten vegetation types that they studied.

Physical environment

In addition to the visible effects on forest structure, hurricanes cause changes in environmental conditions at both small and large spatial scales; from changes in the microenvironment of a leaf or a snail, to changes in the environment of whole regions such as the changes to coastal marine environments. The nature and magnitude of these effects, which basically shift the ecological space available to organisms (*sensu* Hall *et al.* 1992), determines the speed and direction of response by individuals, populations and whole communities. By changing environmental conditions, hurricanes set in motion a plethora of biotic responses that range temporally from seconds to centuries. The variability of biotic response to hurricanes is due in part to the variability of environmental conditions that develop after the passage of the hurricane. I illustrate this range of effects with examples from each spatial scale, starting with the effects on the whole island of Puerto Rico.

Hurricane Georges passed over Puerto Rico as a small category 3 hurricane but it poured 2.6 billion m³ of water over the island of which 1 billion m³ was converted to run-off, and as much as 5–10 million Mg of sediment discharged on the coastal shelf (15–48% of the average annual sediment discharge for the island) with significant effects on coastal ecosystems including coral reefs (Larsen and Webb 2008). Most of the sediment discharge (62–99%) occurred in a single day. The run-off was 13% of the annual total and aquifers responded quickly by storing a portion of the difference between rainfall and run-off. The nitrogen and phosphorus run-off of this event was estimated as 1000 Mg of N and 500 Mg of P. These N and P discharges exceed natural annual export rates of undisturbed forest watersheds by 1300- and 2900-fold, respectively. Larsen and Webb described the effects of these environmental fluxes on coastal marine ecosystems that I do not address, but these events also trigger significant responses in coastal forests. An example is the landscape-level reversal of drought-induced massive mangrove tree mortality on the south coast of Puerto Rico and the explosive post-hurricane re-growth of mangrove stands that I observed in Jobs Bay (see also Cintrón *et al.* 1978).

After hurricane passage, the forest microenvironment changes dramatically owing to the loss of canopy. Changes include increased light intensity and temperature inside the forest and lowering of the relative humidity. The changes in these parameters are complex owing to spatial and temporal variability. After the passage of Hurricane Hugo, Fernández and Fetcher (1991) measured light (photosynthetic photon flux density, PPF) at El Verde. They found dramatic changes in the light environment over a period of 1 year following the hurricane. The PPF showed a highly skewed distribution with most values below 200 µmol m⁻² s⁻¹. Before vegetation re-growth overtopped the sensors (located at 1 m above-ground), spatial heterogeneity peaked at 10 months after the hurricane. Mean daily total values for 10 months after the hurricane (range of 7.7–10.8 µmol m⁻² s⁻¹) were similar to those reported for large tree fall gaps. Vegetation growth reduced the separation of patches of high and low light from 10 to 12 m 6 months after the hurricane to less than a meter 10 months after the hurricane. Bellingham *et al.* (1996) measured photosynthetic active radiation (PAR) during the first 33 months after the passage of Hurricane Gilbert over Jamaica and found significant increases over a large landscape area. Over the period of measurement, the reduction in PAR inside the forest decreased exponentially as the canopy closed. The PAR levels were higher in defoliated areas than in sites where not all the trees were defoliated. After 18 months of measurements, PAR levels were still comparable to those in non-hurricane forest gaps.

Animals

The passage of a hurricane can kill birds owing to exposure to wind and rain, particularly those vulnerable to wind and rain prior to the storm (Wiley & Wunderle 1993). Bird survivors can be weakened and subject to additional mortality or predation following the hurricane. Bird counts 8 months after Hurricane Hugo in the US Virgin Islands showed significant reduction in birds in each stop across road transects with pre-hurricane data (Wauer & Wunderle 1992). The number of species each time (before and after the hurricane) did not change. A higher proportion of nectarivores and fruit/seed eaters declined than did insectivores or raptors. Askins and Ewert (1991) obtained similar results in the US Virgin Islands National Park in St. John.

After Hurricane Gilbert passed over Jamaica, Wunderle *et al.* (1992) found no overall change in the number of species nor the total number of individual birds detected, however, at the smaller scale of individual habitats, they found dramatic changes in the avifauna, depending on the structural effects on the forest canopy and the resilience of vegetation following the hurricane. Montane habitats experienced greater changes than lowland habitats. Diet appeared to be the greatest contributor to bird declines in the montane forests, with particular effects on nectarivores and seed/fruit eaters. Thus, the greatest effect of the hurricane on birds occurred after the passage of the hurricane, not during the period of high winds and rain.

With the opening of the forest canopy and the transfer of large amounts of biomass to the forest floor, conditions for animals change dramatically. By altering the structure of the canopy, basically compressing the forage space available to organisms, hurricanes alter the stratification of foraging normally associated with different canopy layers (Wunderle 1995). Canopy birds are forced to feed on the forest floor or understory, which increases interactions among species that normally do not interact owing to their vertical segregation (Wunderle *et al.* 1992). In several studies, the capture of birds with mist nets located at ground level increased. For example, after the passage of Hurricane Georges over the Maricao State Forest in Puerto Rico, counts increased from 26.8 to 57.9 individuals per net hour (Tossas 2006). Similar to plants, bird responses to the hurricane are species- and/or guild-dependent, with some species or guilds showing no net effects, other disappearing from plots even though they might have been dominant before the hurricane, and still others showing various patterns of decline (Tossas 2006). The high elevation avifauna studied by Tossas recovered at a slower pace than the avifauna at El Verde in the LEF (lower elevation), suggesting that the avifauna reflects the slower re-growth of forests at those elevations.

Bird migration and foraging patterns are affected by hurricanes and those species capable of moving across different habitats are prone to increase their movements both vertically in the forest and horizontally across habitats (Wauer & Wunderle 1992; Wunderle *et al.* 1992; Wiley & Wunderle 1993). In the Dominican Republic, the Hispaniolan parrot *Amazona ventralis* increased its home range from 864 ha before Hurricane Georges to 1690 ha afterwards; they increased their total area traversed by over 300% (White *et al.* 2005).

Inside the forest, bird assemblages that before the hurricane reflected both vertical (understory/canopy) and horizontal (gap no-gap) stratification lost this distinctiveness owing to the opening of the canopy and lack of clear distinctions between gaps and no-gaps (Wunderle 1995). After some time (198 days in this case), fruit production peaked in some locations but not in others, and birds flocked to those areas where fruit was available. As vegetation profiles began to define gaps from no-gap areas, bird assemblages initially do not develop because fruit production might not be sufficient, creating a lag between the re-establishment of feeding guilds and the development of vegetation structure that normally supports those guilds (Wunderle 1995). However, the return of avian populations to pre-hurricane numbers within 6–10 months, suggested that, rather than mortality, the reductions in populations were mostly due to bird movements in search for food (Waide 1991). Examination of stomach contents demonstrated changes in diets (insectivorous birds feeding on different kinds of arthropods) and reductions in consumption, suggesting that hurricanes induce feeding plasticity in Caribbean birds (Waide 1991).

Strong fliers such as the Jamaican Fruit Bat (*Artibeus jamaicensis*) left the LEF after Hurricane Hugo, and did not return for 2 years after the re-establishment of fruit production in the forest (Gannon *et al.* 2005). The Red Fig Eating Bat (*Stenoderma rufum*), an endemic bat, had a large reduction in numbers following Hurricane Hugo in the LEF (captures decreased by 80%) and it took 5 years for the population to restore its numbers to pre-hurricane levels (Gannon *et al.* 2005). However, the passage of Hurricane Georges 9 years after Hurricane Hugo again decreased the number of bats in this population and 4 years after the second hurricane there was no sign of recovery in numbers. The hurricane also affected the reproduction of the species, and the representation of young bats decreased from 30–40% of the population before Hurricane Hugo to 10–20% after the hurricane. Unlike other frugivorous bats and birds, this bat remained in the LEF and survived by expanding its home range within the forest. It appears that *S. rufum* might be important in the dispersal of seeds of

successional plant species. In contrast to the above two species and *Erophylla sezekorni* (the Brown Flower Bat), which also experienced declines in populations after hurricanes, the population of *Monophyllus redmani* (the Greater Antillean Long-tongued Bat) increased dramatically after Hurricane Hugo. This last species took advantage of the rapid flowering by plants in the open forest understory. Many plant species flower profusely after hurricanes. For example, Richards (1964) reported that in Mauritius, *Homalium paniculatum* exhibited gregarious flowering after severe cyclones.

The loss of the canopy also creates cover problems for predators such as the Puerto Rican Boa *Epicrates inornatus*, which become more visible to observers in the LEF (Wunderle *et al.* 2004). Before Hurricane Georges observers could see 15.5% of radio-tagged boas whose fix was known while after the hurricane the visibility of these boas rose to 19.6%. After the hurricane, the boas moved more frequently and over larger distances than they did before the hurricane.

Other animals were affected by the loss of the canopy at the LEF. For example, *Anolis stratulus*, a canopy lizard, had to forage on the forest floor after Hurricane Hugo and as the canopy redeveloped 1 year later, it reinvaded the upper strata of the forest (Reagan 1991). In contrast, *Anolis gundlachi*, a forest interior species, responded to the changes in the microenvironment (light and humidity) by moving to available suitable habitats at different heights than before the hurricane. As with birds, the effect of the hurricane on lizards was through its effect on the habitat rather than by direct mortality. Arboreal spiders also adjusted to the effects of the hurricane by establishing their webs closer to the ground. Those that did increase in numbers while others that could not attach their webs to the resulting forest structure decreased in numbers (Pfeiffer 1996).

Similar to other animal groups in the LEF, frogs survived the hurricane winds, but in contrast to lizards, young frogs of the genus *Eleutherodactylus* were affected by the reduction in relative humidity owing to the drought that followed Hurricane Hugo (Woolbright 1991). However, once the developing canopy restored the relative humidity, frog populations (adults and juveniles) increased rapidly and reached numbers higher than pre-hurricane counts. These increases were attributed to abundance of retreat sites and the reduction in invertebrate predators. Pre- and post-hurricane surveys of six invertebrate species in the LEF revealed dramatic decreases in all species. In fact, *Nemia tridens* and *Gaetis nigrolineata* (snails) and *Agamemnon iphimeida* (walking stick) were reduced to the point that no specimens were detected in post-hurricane surveys (Willig & Camilo 1991). It is believed that these species could not react to, or overcome, the large-scale changes in microenvironment

induced by the hurricane. Subsequent studies in these populations uncovered complex interactions between shifts in ecological space, land use legacies and cross-scale responses of biodiversity (Willig *et al.* 2007).

Hurricanes have significant effects on insects as has been documented in Puerto Rico (Torres 1988, 1992). First, hurricanes transport and disperse insect species to great distances and account for numerous introductions into the Caribbean (Torres 1988). Through effects on either food sources and/or predators, hurricanes also affect insect population numbers, causing local extinctions or dramatic outbreaks of populations (Torres 1992). After the passage of Hurricane Hugo over the LEF, Torres observed population outbreaks of 15 species of Lepidoptera, including larvae of *Spodoptera eridania* (Noctuidae). *Spodoptera eridania* was observed feeding on 56 plant species belonging to 31 families. All plants were early successional and many were new hosts plants for the Lepidoptera. The outbreak of these insects ended with the decline of the host plants and had measurable influence on insect-insect interactions such as predation and parasitism involving other insect groups.

Tree species

For practical as well as theoretical reasons ecologists and foresters have an interest in assessing the resistance of tree species and groups of tree species to hurricane winds. Wind resistance is an attribute related to the life history strategies of species and understanding of how this attribute plays out under natural conditions sheds light on evolutionary and ecological processes. But such knowledge is also of practical relevance to the selection of species for plantations, reforestation or urban tree planting. As we will see with the examples below, wind resistance of tree species is difficult to establish given the many factors that affect it, such as position in the canopy, soil conditions, stage of growth, physiognomy, etc. Moreover, there is a wind velocity beyond which all species are affected by the sheer magnitude of the wind's kinetic energy (Francis & Gillespie 1993). I group the examples below into individual tree species and groups of species reports.

Wadsworth and Englerth (1959) classified 32 tree species into three groups according to their response to hurricane winds after Hurricane Betsy crossed Puerto Rico. Their categories were susceptible to windthrow (eight species), susceptible to breakage (12 species), and wind resistant (12 species). Some species fit the two first categories, because their response was site dependent. For example, forests on slopes were subject to the hazards of wind effects regardless of aspect. Similarly, the effectiveness of anchoring, depth of soil and other site conditions influenced the effects of wind on trees. After Hurricane San Felipe passed

over Puerto Rico in 1928, Bates (1929) reported the visible effects and response to the hurricane of over 100 tree species. Duryea *et al.* (2007) developed a similar list for trees in urban forests in Puerto Rico and Florida with species classified into four categories (highest wind resistance (34 species), medium-high wind resistance (17 species), medium-low wind resistance (22 species) and lowest wind resistance (21 species).

In the lower montane forest of Guadeloupe after Hurricane Hugo, *D. excelsa* and *Tapura latifolia* were more wind resistant than *Richeria grandis* and *Simaruba amara* (Imbert *et al.* 1996). In forest stands dominated by *Amanoa caribaea* and *T. latifolia*, larger trees experienced greater structural change than smaller ones, but in stands dominated by *D. excelsa* the opposite occurred, perhaps because smaller trees were affected by large branch fall. In semi-evergreen forests, *Canella winterana* (30%) and *Chionanthus compacta* (80%) had high instantaneous mortality while *Sideroxylon obovatum* (4%) and *Lonchocarpus benthami-anus* (9%) had low instantaneous mortality. Uprooting was particularly high in *C. compacta*. For most species, over 50% of the dead stems had minor visible wind effects.

In Puerto Rico, *Pinus oocarpa* was more susceptible to mechanical injury from hurricane winds (Hurricane David) and rainfall associated with tropical storm Frederic than *Pinus caribaea* (Liegel 1984). This study raised the possibility that these species were susceptible to hurricane effects and that caution was needed before planting them for timber production in the Caribbean. Hurricane Allen caused significant structural change in *P. caribaea*, *Eucalyptus* sp. and *Hibiscus elatus* plantations when it passed near Jamaica (Thompson 1983). Of the three plantation species, the *Hibiscus* exhibited the least visible effect (mostly branch losses). The other species had significant blow downs and snapped trees. Between 64% and 73% of the wood volume was blown down in some locations. In contrast, native forests mostly lost their leaves and had minimal loss of small branches. Populations of pine bark beetles, pinhole borers and *Heterobasidion annosum* (as *Fomes annosa*, a pathogenic fungus that kills trees and increases susceptibility to windthrow) increased in pine plantations after the hurricane. As a result of these and other experiences, pine plantations have been effectively eliminated as potential commercial timber plantations in the region.

The location of trees relative to the wind quadrants of hurricanes determines the effect of wind on species. For example, within the eye wall of Hurricane Hugo, with winds of 43–66 m s⁻¹, there was little difference between the wind resistance of loblolly pine (*P. taeda*), longleaf pine (*P. palustris*) and a variety of *Quercus* species in the bottomlands hardwoods of South Carolina (91%, 89% and 86% of trees broken or uprooted,

respectively; Hook *et al.* 1991). However, about 100 km from the eye wall of the hurricane, the percentage of these species without visible wind effects was 48%, 73% and 80%, respectively (Hook *et al.* 1991). All trees with broken tops, windthrown, or that lost their boles became infected with bark beetles. The per cent of trees affected by hurricane winds increased with age of hardwood stands in New England but not in pine stands (Foster & Boose 1995). Conifers were more susceptible to wind effects and thus had a steeper relation with age than hardwood stands. Wind effects had a positive relation with age and height and a negative one with tree density.

Mangrove species exhibited different rates of mortality, capacity to sprout and regeneration strategy after the passage of Hurricane Andrew over south Florida (Baldwin *et al.* 1995). Mortality rates were highest in *Rhizophora mangle* (85%), followed by *A. germinans* (65%) and *Laguncularia racemosa* (60%). *Avicennia* and *Laguncularia* sprouted vigorously but *Rhizophora* did not and it regenerated quicker by recruiting seedlings. In Guadeloupe, *R. mangle* was more susceptible to wind effects than *A. germinans* (Imbert *et al.* 1996). *Avicennia germinans* was susceptible to windthrow and trees usually died if windthrown. *Rhizophora* did not survive trunk breakage as it could not coppice or resprout. However, its reproductive strategy via seedlings compensated for the effects of winds on adult trees.

The canopy of species-rich forests in the Solomon Islands in the Pacific experienced greater canopy disturbance (over 80%) after Cyclone Annie than species-poor ones (less than 70%; Burslem & Whitmore 1999). However, tree recruitment and turnover increased with increasing species richness. After Hurricane Betsy in Puerto Rico, plantations had more hurricane effects than native forests (Wadsworth & Englerth 1959). In Dominica, West Indies, following Hurricane David, trees in complex vegetation had higher survivorship without visible wind effects than trees in vegetation of low complexity (Lugo *et al.* 1983). However, reduced stature (height and d.b.h.) of dry forest trees appear to give these forests a greater resistance to wind than to trees of greater stature in moist and wet forests (Van Bloem *et al.* 2005). Tanner and Bellingham (2006) also found that less diverse montane forests in Jamaica were more resistant to hurricanes than higher diversity ones.

Pioneer species experienced large wind effects in terms of stem breakage and mortality at El Verde following Hurricane Hugo (Zimmerman *et al.* 1994; Everham 1996). This was correlated with wood density and shade tolerance. Non-pioneers lost many branches and had some mortality but the effects were low to moderate. This was not the case in Cubuy, where neither wood density or biogeographic origin had no influence on hurricane effects (Ostertag *et al.* 2005).

Slow growing trees had lower wind effects, suggesting that they can slowly but steadily become dominant in a high or frequent disturbance regime. Growth rate might represent a hurricane response syndrome among tree populations that includes architecture, elastic modulus, successional status and wood density. When growth was stimulated by fertilization, it was found that pioneer species in lower elevation forests and graminoid species in elfin woodlands benefited from the fertilization after a hurricane, and responded quicker than mature forest species (Walker *et al.* 1996b). They concluded after the experiment that: 'Factors regulating primary productivity are influenced not only by the physical characteristics of the site, but also by the range of potential species-specific responses represented in the flora' (p. 877).

The variability in the results of wind effects on trees is illustrated by the results presented by Duryea *et al.* (2007) for urban trees in Puerto Rico and Florida after the passage of four hurricanes: Georges, Andrew, Jeanne and Charley. Non-native species survived better than native species after Hurricane Georges but not after Hurricanes Jeanne and Charley. Trees growing in groups had greater survival and lower branch loss effects than trees growing individually after Hurricane Jeanne. Wood density had no relation to survival or wind effects in any of the four hurricanes. Modulus of elasticity and modulus of rupture were related to survival and branch loss after Hurricane Jeanne but not after Hurricane Charley. Tree species with dense crowns had greater survival and less branch loss than moderate- or open-crowned species. Species with decurrent growth form survived better than excurrent trees after Hurricane Jeanne but not after Hurricane Charley. Trees with the most rooting space lost the lower number of branches and had the highest survival after Hurricane Georges. After Hurricane Andrew, 73% of the trees pruned before the event survived compared with 47% for unpruned trees. While no tree is completely windproof, the factors that contribute to wind firmness include soil conditions, wind velocity, cultural practices, tree health and age.

Processes

Processes are the least visible of all hurricane effects because they require repetitive measurements to establish their rates. The example from Hawaii with instantaneous litter fall was given in an earlier section to illustrate canopy defoliation, but that flux also includes instantaneous nutrient return to the forest floor. Instantaneous tree mortality (Lugo & Scatena 1996) is another process linked to hurricane effects, but the process of hurricane-induced mortality also applies to

roots and animals. The examples that follow illustrate some of the complexities associated with immediate responses to hurricanes of mortality and nutrient and carbon fluxes.

Tree mortality can follow as a result of almost any of the hurricane effects including defoliation, shaking of trees, wind throws, stem breakage, etc. (Lugo and Scatena 1996) and Burslem and Whitmore (1999) recorded a range of annual tree mortalities of 1.1–2.4% in six forest types of the Solomon Islands during non-hurricane intervals. These rates increased to a range of 2–24% after Cyclone Annie. Trees can also die owing to sun scalding on the limbs (Wadsworth & Englerth 1959) or owing to no apparent cause (Imbert *et al.* 1996). Injuries to the trees plus loss of vigour as a result of loss of limbs and leaves can also lead to trees being prone to insect and fungal attacks. The formation of compression wood as a result of long-term leaning reduces the timber value of the wood (Wadsworth & Englerth 1959). Nevertheless, many trees recover from these effects through root or stem sprouts, epicormic growth, and re-establishment of bark over wounds. Trees in Caribbean dry forests sprout abundantly at their base as a result of hurricane winds, even in the absence of wind-induced structural effects (Van Bloem *et al.* 2003, 2007).

After hurricane passage, the event leaves a signature that can be interpreted depending on how fast organisms consume the evidence. In montane forests, where wood decomposition is slow, it is possible to reconstruct tree mortality patterns owing to hurricanes. Arriaga (2000) was able to estimate the effects of hurricanes on tree mortality by analysing woody debris on the forest floor of a montane cloud forest in Mexico. She found 91 fallen logs per hectare of which 48% were uprooted trees, 38% snapped trees and 11% died standing, representing 20 species. A smaller proportion of trees died of other causes unrelated to hurricanes. By analysing the direction of tree falls, and recording sprouting, she could reconstruct the effects of hurricane winds on forest mortality and identify the species most capable of responding to hurricanes through sprouting and re-growth.

Fine root mortality ranged from 35% to 48% after the passage of Hurricane Iniki over Hawaii (Herbert *et al.* 1999). There was a related decline in stem diameter increment and above-ground net primary productivity (ANPP). In the tabonuco forest of Puerto Rico, fine root biomass decreased to zero at the 0–10 cm depth over a 3-month period after Hurricane Hugo (Parrotta & Lodge 1991). In another study in the same forest, Silver and Vogt (1993) found a 70–77% fine root decline occurring with a 6-month delay. Because root decay was slow, 48–65% of the fine root necromass remained on site, which retained nutrients within the ecosystem. However, high root mortality may result in significant declines of nutrient availability to trees.

Instantaneous nutrient-return via litter fall in Hawaii was equivalent to the annual litter fall input (Herbert *et al.* 1999). Although nutrient concentrations in hurricane-caused leaf fall were higher than pre-hurricane concentrations, the values for Hawaii leaf fall were lower than those in the tabonuco forest at the LEF. This difference may be attributed to differences in soil chemistry. In the LEF, the concentrations of N and P were, respectively, 1.1–1.5 and 1.7–3.3 times higher in hurricane leaf fall than in non-hurricane leaf fall (Lodge *et al.* 1991). In Fushan, Taiwan, however, there was no difference in the concentration of typhoon or non-typhoon leaf fall (Lin *et al.* 2003). Lin *et al.* (2003) point out the adaptive significance of these comparative data as trees in the Caribbean can replace their nutrient pool between hurricane events, while those of Taiwan, do not have the time given the higher frequency of typhoon events. In fact, Scatena *et al.* (1996) showed that it takes 30–40 months for leaf fall to return to pre-hurricane nutrient concentrations in Puerto Rico. In contrast, the nutrient contribution of throughfall water decreases immediately after the hurricane because the nutrient concentrations of throughfall water decrease for several weeks owing to the reduction of leaf surfaces after the hurricane (Heartsill Scalley *et al.* 2007).

In Fushan, even LAI does not recover during periods of frequent typhoons, while it recovers quickly in Puerto Rico. Lin *et al.* (2003) also observed that the prominent leaf flush that usually follows hurricanes in other parts of the world is lacking in these forests. They propose this as an adaptation to annual passage of typhoons over Taiwan. The extreme conditions in Taiwan are underscored by the high proportion of the nutrients stored in above-ground biomass that returns to the forest floor in N, P, and K fluxes associated with typhoon-induced litter fall: 19–41%, 15–40% and 5–12%, respectively (Lin *et al.* 2003).

After hurricane Iniki in Hawaii, several ecosystem processes returned to pre-hurricane conditions within varying time lengths. For example, LAI recovered within 9 months and fine roots and litter fall within 2 years (Herbert *et al.* 1999). Phosphorus fertilization accelerated the response of ANPP and tree diameter growth to Hurricane Iniki. These processes recovered in 2 years, while rates in untreated stands remained low after 2 years (Herbert *et al.* 1999). In Puerto Rico, litter fall rates return to pre-event values in proportion to the intensity of the event (Beard *et al.* 2005). Higher intensity events are associated with longer time periods before rates return to pre-hurricane values (F.N. Scatena, unpubl. data 2007).

An apparent contradiction with the post-hurricane development of the LAI was uncovered with LiDAR data for the Prospect Hill tract at the Harvard Forest in New England. The data reveal that 65 years after the 1938 hurricane, the canopy had not recovered its

original height and structure (Weishampel *et al.* 2007). They found subtle but statistically significant difference in canopy height and vertical profiles corresponding to the level of 1938 hurricane effects. The more severely affected stands are shorter with less vertical distribution of laser backscatter (reflecting fewer surfaces in the profile), higher levels of autocorrelation for canopy height (reflecting similar types of textures), and lower levels of canopy height diversity and evenness. They raise the point that these differences can affect biomass productivity. The apparent contradiction is the fact that research on canopy processes such as LAI development and litter flux has led us to assume that the canopy returns quickly to pre-hurricane states. However, if the LiDAR is correct and applies to other forest types, it would mean that we have to differentiate canopy morphology from canopy processes when assessing the resilience of forest canopies to hurricane effects. In Bisley, for example, canopy morphology has not returned to pre-hurricane conditions almost 20 years after Hurricane Hugo, but LAI, litter fall and hydrologic fluxes (interception and throughfall) have (F.N. Scatena, unpubl. data 2007; Heartsill Scalley *et al.* (2007); Fig. 3).

Ostertag *et al.* (2003) attributed some of the resilience of tropical forests to hurricanes to the rapid recycling of nutrients through litter decomposition of hurricane debris. They documented the pulse of litter and nutrient transfer from the canopy to the forest floor and followed the decomposition of the litter in six types of forests following the passage of Hurricane



Fig. 3. Canopy structure of a tabonuco (*Dacryodes excelsa*) forest in the Bisley Watersheds of the Luquillo Experimental Forest in Puerto Rico. This photo was taken in March 2007, 18 years after Hurricane Hugo passed over the forest in 1989. Notice the taller canopy of the tabonuco trees on the ridges (above) and the emerging new canopy of the pioneer *Cecropia schreberiana* on the slopes (centre). Photo by the author.

Georges over Puerto Rico. Their results showed that in less than 10 months hurricane-produced litter is decomposed and the nutrients probably incorporated into the soil where plants could recycle them back to standing biomass. Species-specific chemistry regulates decomposition rates (rather than weather) and contributes to faster forest resilience after hurricane passage (Beard *et al.* 2005).

When hurricane litter decomposes slowly after the storm, the accumulation of organic material can have an effect on tree regeneration, as happened in commercial forestlands in southern USA after Hurricane Hugo. Pine regeneration was poor and unsuitable for restocking lands affected by the hurricane in spite of abundant cone production. The majority of cones failed to release their pine seeds, excessive litter prevented released seed from contacting mineral soil, and a drought led to poor survival of pine seedlings on well-drained to upland sites (Hamilton *et al.* 1992).

In some cases the intensity of hurricanes affects the seed bank of successional species. In South Florida, the strong diurnal soil temperature fluctuations associated with the passage of Hurricane Andrew stimulated the germination of a dormant seed bank of *Lysiloma latifolium*, a late secondary canopy tree species (Pascarella 1997).

Angulo Sandoval *et al.* (2004) suggested that the understory benefits from opening of the canopy after a hurricane. They studied understory leaf phenology of secondary forests in Puerto Rico after Hurricane Georges and found a more even or continuous pattern of seasonal leaf production. Leaf production increased two to twelve times, but herbivory decreased 1.2–30 times. It was hypothesized that after a hurricane herbivore satiation, changes in leaf chemistry, changes in herbivore populations and changes in herbivore predator populations all combine to decrease herbivory rates.

Hurricane Opal influenced herbivory rates in North Carolina through an invisible and indirect process. The hurricane affected the variability of light and nutrient availability and foliar astringency of red maple (*Quercus rubra*) and red oak (*Acer rubrum*). Affected trees had greater foliar astringency than sites with no hurricane effects. Later in the growing season, tannin levels were higher in affected trees. However, herbivory rates were higher in affected trees than in control trees of both species. The increase in defensive compounds did not protect trees from greater herbivory (Hunter & Forkner 1999).

Land–water interactions

The passage of Hurricane Hugo over the Bisley watersheds at LEF affected the hydrologic cycle by decreasing evapotranspiration and increasing throughfall

owing to the loss of leaf area (Scatena & Larsen 1991; Scatena *et al.* 1996; Heartsill Scalley *et al.* 2007). These effects lasted for about 30 days and contributed to increased stream discharge with consequences to stream organisms such as changes in species composition (Masteller & Flint 1992). Initially, shrimp were flushed, affecting the level of predation in streams, and light intensity plus litter reaching the stream increased owing to the effects of the hurricane on vegetation. As a result, caddisflies (mostly grazers) and algal abundance changed. The net effect was a change in species composition and abundance, while seasonal emergence remained stable.

Riparian vegetation at Bisley was also effective in absorbing a portion of peak influxes of NO_3^- , NH_4^+ and dissolved organic N as a result of the invisible effects of Hurricane Hugo to vegetation and soils (McDowell *et al.* 1996). As vegetation re-grew, concentration of these N species and other cations and anions returned to pre-hurricane levels in streams.

Hurricanes can lower the sediment load of rivers by dislodging and displacing vegetation, debris accumulated on hillslopes and small channels, blocking bridges and forming debris dams as shown in Lake Loíza, Puerto Rico, by Gellis (1993). These debris dams caused backwater effects that reduced stream velocities and decreased suspended-sediment loads. Mechanisms that retain forest structure inside stands or in stream channels are also responsible for the high retention of nutrients and food resources with consequences to population- and ecosystem-level processes. For example, Silver (1992) found that the survival of root structures of stands resulted in high nutrient retention by vegetation. At the population level, shrimp populations increased after the hurricane owing to the availability of food and reduced washout of invertebrate consumers (Covich *et al.* 1991).

Management and land use

Strategic approaches to the management of hurricane-prone landscapes have been suggested and evaluated in the coastal plain of northern Gulf of Mexico after hurricanes Rita and Katrina (Stanturf *et al.* 2007). Today ecosystem management is recommended in the context of LID's (Dale *et al.* 1998), but attention to forests management in the context of hurricanes began decades ago. Webb (1958) was among the first to understand the silvicultural problems associated with frequent hurricanes. Distortion of growth form, random effects on desirable girth classes and saplings, smothering of regeneration by vines and weed trees, fire risk, subsequent parasite attack of affected trees and extraction difficulties were among the complications he foresaw to foresters. In the short term, stand thinning and tree pruning are management tools

available to mitigate wind effects. Evaluating these and other management practices after hurricanes yield mixed results. For example, the location, extent and timing of thinning and clear cutting influence the vulnerability of residual stands to wind effects (Zen *et al.* 2006). In Puerto Rico, Wadsworth and Englerth (1959) found that thinning made stands more susceptible to wind effects, as did Thompson (1983) in Jamaica. However, regularly pruned trees will withstand strong winds better than those with dense canopies and dead, weakened branches (Chaney 1997).

Cooper-Ellis *et al.* (1999) experimentally simulated a hurricane blowdown in New England, and analysed forest response to the event. They found lower mortality than in disturbance events when trees were removed from the affected site. Downed wood had ecological functions in the recovery of stands; functions that are lost when salvage operations removed downed wood. They recommend treating stands to withstand wind events rather than removing downed wood after an intense event.

Rotenberry *et al.* (1993) recommended managing large patches of lands, including establishing corridors, for the purpose of facilitating the offering of food resources to birds after the passage of hurricanes. They recognized as a research need the establishment of the proper scale at which this management was to take place, but their focus was to address the effects of food reduction to nectar, seed and fruit feeders after hurricanes.

Hurricane effects are also affected by the changes in land cover and land use near forests affected by the hurricane. This interaction is best illustrated by the response of birds to hurricanes. Birds experience the greatest effects after the hurricane itself, because they must deal with the changes in food availability as well as the modification of forage and reproductive habitats (Wiley & Wunderle 1993). Nectarivores and seed/fruit eaters are particularly affected by changes in food supply and must migrate in search of food. When land cover or land-uses surrounding their original habitats are fragmented or modified to exclude food resources, these organisms are then doubly affected by the passage of the hurricane. Changes in land cover and land-use in the vicinity of natural forest stands also facilitate the invasion of non-native species and diseases into the affected stands (Wiley & Wunderle 1993). The combination of these deleterious conditions may lead to local species extinctions.

Zimmerman *et al.* (1995a) found that management practices had no effect on tree and shrub species richness, on species diversity, species evenness, stem density, or basal area. However, species composition was significantly affected by management practices and land-use. Pastures and coffee plantations had different complements of dominant species, which in turn were different from those in native forests

re-growing after the hurricane. A key finding of this study and others in the LEF (Thompson *et al.* 2002, 2007) was that regardless of their intensity or frequency, hurricane passages do not erase the signature of land-use history on species composition of affected sites (Zimmerman *et al.* 1995a). However, in the Guánica Dry Forest, the effects of Hurricane Georges were similar although variable among fragments for a large reference and 19 small forest fragments previously affected by human activity (Van Bloem *et al.* 2005). Nevertheless, past land use activity and disturbances influenced the responses and rates of recovery of wet forests after the hurricane. For example, if the legacy made the site more productive, it also made it more resistant to hurricanes and droughts and coarse wood inputs than less productive sites (Beard *et al.* 2005).

IMMEDIATE RESPONSES (0–20 YEARS)

Regeneration

Studies of forest regeneration following hurricanes have expanded the debate over what controls the diversity of tropical forests (Vandermeer *et al.* 2000). Before the dramatic increase in hurricane literature following the passage of Hurricane Hugo in 1989, disturbance-based models of tropical forest response were focused on tree fall gaps resulting from the fall of old trees (Denslow 1987). In contrast, a hurricane not only creates many canopy gaps, but they do so independently of the age of trees and stands, and over large geographic areas. Vandermeer *et al.* (2000) found that a hurricane increases the species richness of affected stands over that of control stands not affected by the hurricane and that this was a visible effect a decade after the passage of the storm. They attributed the species enrichment to the paucity of pioneer species in their study site after Hurricane Joan. This absence allowed many species from more advanced stages of succession to occupy sites affected by the hurricane.

After Hurricane Joan in Nicaragua, large-scale effects on canopy structure impeded pioneer species regeneration and instead resulted in regeneration of primary forest species and abundant resprouting by late successional species (Yih *et al.* 1991). This regeneration mode was associated with slower and variable tree growth and lower above-ground biomass accumulation (Mascaro *et al.* 2005). The accumulation of above-ground biomass was one-third as fast as in Bisley. Subsequent work at the same site revealed that up to 66% of the regenerating stems were by sprouts (from roots, trunks or fallen logs; Vandermeer *et al.* 1995). All sprouting was from primary forest species.

The sprouting contributed to the ingrowth, thus supporting the direct regeneration hypothesis.

Vandermeer *et al.* (1998) suggested a two-step regeneration model that included a building phase, followed by a thinning phase and a mature forest as the outcome. The time required for these phases is a function of the degree of hurricane effect. Stands with greater effects required more time to complete succession than stands with low levels of effect. Six years after the hurricane event, they measured decreasing height growth rates as succession advanced (Vandermeer *et al.* 1998). The thinning process is a result of the outcome of intense competition at the canopy level by a high density of trees, including pioneer, heliophytes and primary forest species.

A decade after hurricane Joan passed over the forests of eastern Nicaragua, Vandermeer *et al.* (2001) observed a large but diffuse canopy formed by trees that survived the hurricane, while below and between those trees a second shorter canopy of tightly packed smaller trees competed for light and space as the second canopy grew to pre-hurricane height at the level of the taller survivors. In Bisley, we noticed the same phenomena, but associated with topography. The surviving tall canopy belonged to tabonuco trees on ridges, while a shorter canopy of pioneer *Cecropia schreberiana* trees grew on slopes where large trees had been windthrown by the hurricane winds (Fig. 3). The point is that a decade after a hurricane, the competition for canopy space is intense and the competitors include surviving upper canopy elements, sprouting trees and branches, seed regenerated trees and pre-existing seedlings and saplings that sprint skyward stimulated by the high light conditions. Under these conditions the highest photosynthetic and ANPP rates have been measured in Puerto Rico (Scatena *et al.* 1996; Frangi & Lugo 1998, Harris *et al.* in press).

In bottomland forests of south-eastern USA, the effects of Hurricane Hugo on species richness after 12 years of regeneration were not as clear as those in Nicaragua after Hurricane Joan (Zhao *et al.* 2006). While they found changes in species composition after the hurricane, the level of change was not significant in all stands. Their results suggest that disturbances hasten succession rather than setting it back. It is possible that the low inherent species richness of bottomland forests (in the order of 20 species per hectare) prevent much diversification after a hurricane as happens in moist or wet tropical forests where the species pool is much larger (over a hundred species per hectare).

After Hurricane Georges in Puerto Rico, successional stands experienced less effect than mature stands owing to the presence of smaller trees in young secondary forests compared with mature forests. Because seed production was affected by the loss of canopy, seed rain was low and seed banks were not

sufficient to sustain regeneration from seed, even though conditions for germination were optimal. Thus, pre-established individuals were responsible for most of the observed regeneration (Lomascolo & Aide 2001). The study showed that hurricanes could influence the direction of succession.

Forest structure and composition

A long-term process of forest structure and composition involving visible and invisible changes begins within days after the passage of a hurricane and does not stop until the next event strikes the site again (Fig. 4). Table 16.5 in Lugo *et al.* (2000a) contains a description of these events for the LEF after the passage of several hurricanes and up to about 60 years of change. Some of the most visible responses include the massive seed germination of vines, tree seedlings and herbaceous plants (China 1999; Lugo & Zimmerman 2002), which can be heavily attacked by herbivores; the subsequent growth of herbs, vines and tree seedlings; the re-leaving of defoliated plants; abundant sprouting of new branches and stems; and epicornic tree growth (Zimmerman *et al.* 1994; Baldwin *et al.* 1995).

Typically, tree density and above-ground biomass decrease (Scatena *et al.* 1996; Frangi & Lugo 1998) but basal area may or not decrease after a hurricane; it all depends on the strength of the hurricane and the level of tree mortality. For example, after Hurricane Hugo, Fu *et al.* (1996) reported reductions in basal area and tree density in a mahogany plantation and paired secondary tabonuco forest at El Verde. However, after hurricane Hugo in 1989 and Hurricane Georges in 1998, a mature tabonuco forest near the site studied by Fu *et al.* (1996) did not experience basal area reduction (Fig. 4b). However, that forest had apparently experienced a reduction in basal area after Hurricane San Cipriano in 1932 (Crow 1980), Fig. 4b). In the years following strong hurricanes that reduce the level of structural indices, all three structural parameters (tree density, biomass and basal area) increase rapidly in all forest types (Fig. 4a–c, Fu *et al.* 1996; Scatena *et al.* 1996; Frangi & Lugo 1998). Fifteen years or so after the hurricane, tree density reaches a peak and both basal area and above-ground biomass stabilize (Fig. 4b,c). After 15 years, stands enter a thinning phase that increases tree mortality and reduces tree density. The reduction in tree density makes more room for surviving trees and results in a spurt in basal area and biomass increase.

The rapid changes in tree density, basal area and above-ground biomass are accompanied by equally dramatic and invisible changes in stand composition and species diversity (Fig. 4d). The hurricane bumps up the species diversity of stands as pioneer and non-

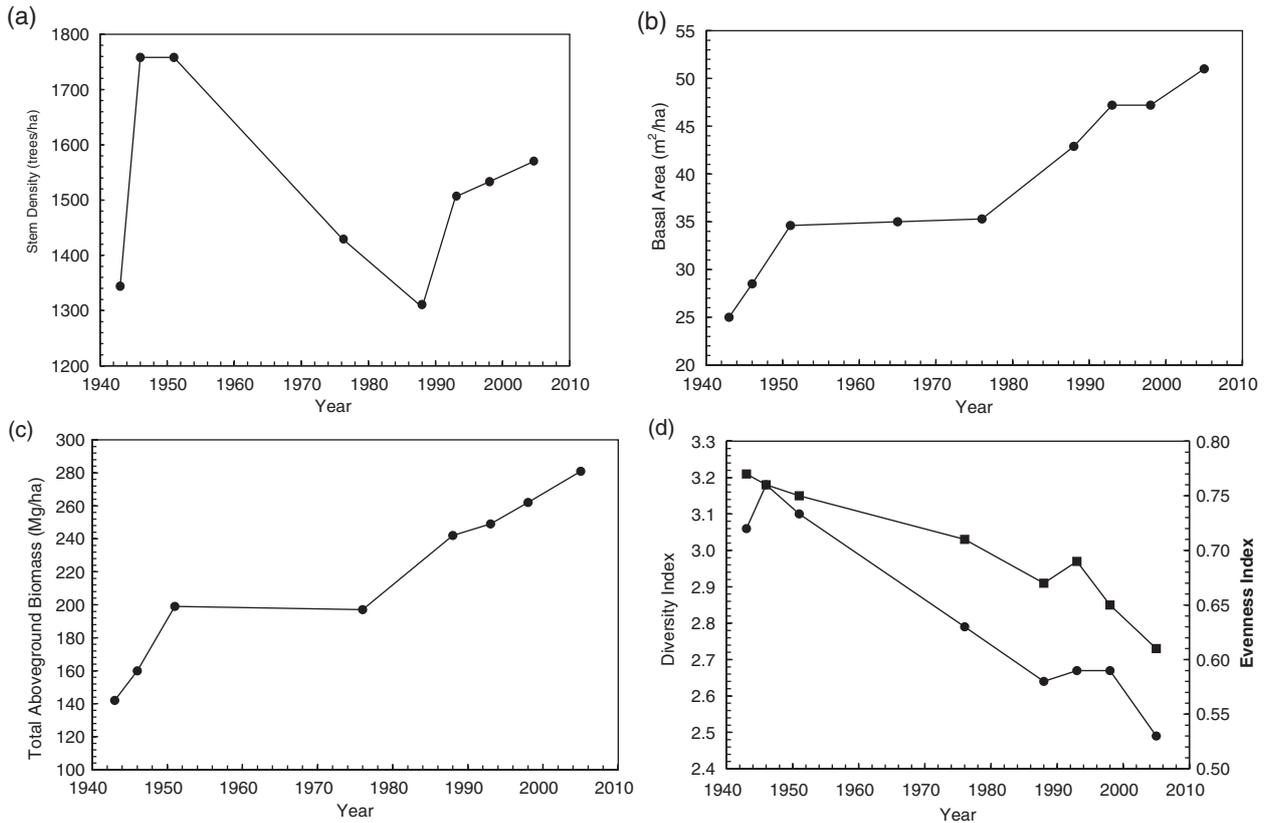


Fig. 4. Long-term trajectories of change (1943–2005) in the structure ((a) is tree density, (b) is basal area, and (c) is above-ground tree biomass) and species diversity and evenness (d) of a tabonuco (*Dacryodes excelsa*) forest plot (EV-3) at El Verde, Luquillo Experimental Forest in Puerto Rico. These data were collected by a variety of people, including F.H. Wadsworth and T. Crow, and were updated and synthesized by Drew *et al.* (unpub.). A major hurricane (San Cipriano) passed over the site in 1932. Hurricanes Betsy (1956), Hugo (1989) and Georges (1998) also influenced stand dynamics. The diversity index is Shannon-Weiner and the evenness index is Pielou's J.

pioneer species grow together and compete for light and space in the developing forest. Four trends are simultaneously in progress regarding the species composition of stands 10 years after a hurricane:

1. Species are entering and exiting forests at a 1-ha scale, but usually change little if at all at watershed scales. This was established at Bisley (Scatena & Lugo 1995); Heartsill Scalley *et al.* in press), El Verde (Fu *et al.* 1996) and at upper elevations of the LEF (Frangi & Lugo 1998). For example, Scatena and Lugo found no gain or loss of species at the watershed scale, but Frangi and Lugo found that at the 1-ha scale 13 species not represented in the canopy entered the forest by regeneration. Similarly, at the scale of 1 ha, Fu *et al.* (1996) found a decrease in the number of species after the hurricane followed by species enrichment in the following years.
2. The Importance Value (IV; sum of relative tree density and basal area in per cent) of species changes as was observed after tornados in Texas where the relative ranking of species in affected

stands also changed (Glitzenstein & Harcombe 1988). These changes in species IV tend to reinforce the dominance of the most important species in stands prior to the hurricane. For example, in secondary tabonuco forest at the LEF, the IV of primary species increased in the years following the hurricane, while those of secondary species decreased (Fu *et al.* 1996). In a mature tabonuco forest, Drew *et al.* (unpub.) found that primary species also increased in IV (Fig. 5a,b), while pioneer species decreased (Fig. 5c,d). In a floodplain palm forest, the IV of the palm *Prestoea montana* increased from 46.4% before the hurricane to 53.5% 5 years after the hurricane (Frangi & Lugo 1998).

3. Species diversity first increases and then decreases steadily and species dominance increases (Fig. 4d). In a mature tabonuco stand, Drew *et al.* (unpub.) found that between 1943 and 2005 the stand lost five tree species, but the dominance of tabonuco increased. This stand had been subjected to the 1932 (San Cipriano), 1956 (Betsy),

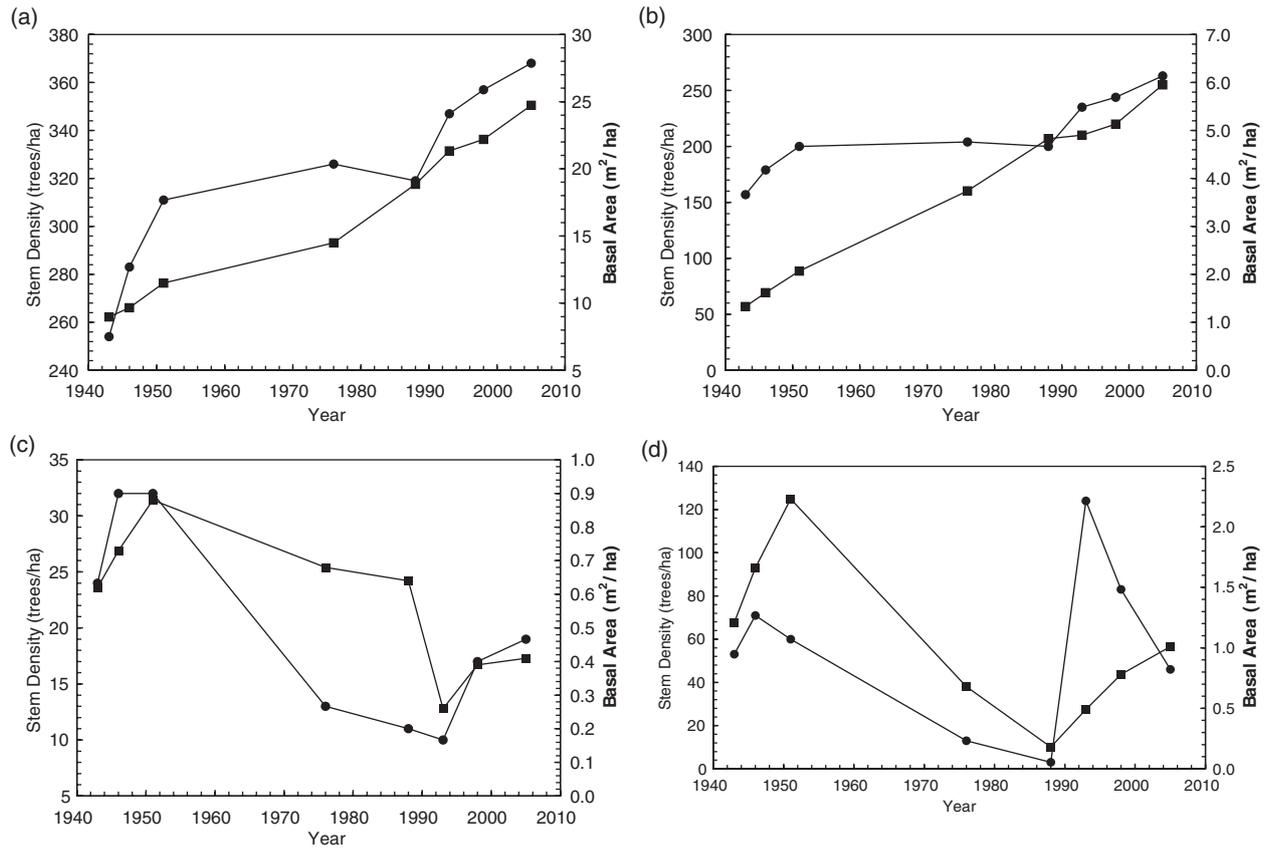


Fig. 5. Long-term trajectories of change (1943–2005) in the basal area (solid squares) and tree density (solid circles) of selected species growing in a tabonuco (*Dacryodes excelsa*) forest plot (EV-3) at El Verde, Luquillo Experimental Forest in Puerto Rico. A major hurricane (San Cipriano) passed over the site in 1932. Hurricanes Betsy (1956), Hugo (1989) and Georges (1998) also influenced stand dynamics. These data were collected by a variety of people, including F.H. Wadsworth and T. Crow, and were updated and synthesized by Drew *et al.* (unpub.). The species in (a) (*Dacryodes excelsa*) and (b) (*Manilkara bidentata*) are primary forest species while those in (c) (*Schefflera morototoni*) and (d) (*Cecropia schreberiana*) are pioneer species.

1989 (Hugo) and 1998 (Georges) hurricanes. The movement of stands towards high dominance by few species might be a characteristic of Caribbean forests subjected to frequent hurricanes (Lugo & Scatena 1995). The significance of this is that the lower species richness of these insular forests may have little to do with insularity and more with a response to frequent disturbances.

4. Tree species are temporarily scattered in ecological space as stand conditions become more heterogeneous after the hurricane and as they return to pre-hurricane conditions tree species tend to re-aggregate. Like animal dispersal in response to habitat changes after a hurricane plants appear to also scatter in ecological space after hurricanes. Heartsill Scalley *et al.* (in press) showed this with species ordinations at the watershed scale. Before the hurricane, species were grouped into four distinct species clusters with particular structural features. After the hurricane, new species combinations developed and the location of plots

expanded into multidimensional space such that species groupings were not detected in ordinations. After 15 years of succession, the original species clustering was not re-established as species continued to migrate in multidimensional space.

Burslem and Whitmore (1999) found that a legacy of hurricanes in the Solomon Islands was the maintenance of different species diversity and composition between forest types. The hurricanes leave behind a mosaic of forest stands with different levels of disturbance and different stages of recovery, reflecting different levels of tree species richness. The presence of elevated numbers of pioneer species is a legacy of the passage of hurricanes over these islands. They concluded that major external disturbances maintain differences in species diversity between forest types, by favouring the maintenance of the status quo. An outlier forest appeared to have been severely disturbed by human activity, which created its own signature on the species composition that hurricanes could not erase. This coincides with the experience in Puerto

Rico where past land-uses influenced the present tree species composition (Thompson *et al.* 2002).

In contrast to the effects of the combination of past land use and hurricane events described above and below, different dynamics occurs when two or more hurricanes succeed each other apparently because the first hurricane removes weak and poorly anchored trees (Everham & Brokaw 1996). Ostertag *et al.* 2005 evaluated the effect of Hurricane Hugo on the response of a tabonuco forest to Hurricane Georges. They found that there was an effect (their fig. 1d) and that a hurricane event is not a discrete event as its effect is influenced by the previous hurricane. Specifically, they found that trees that snapped or uprooted during Hurricane Hugo were significantly more likely to snap again during Hurricane Georges 9 years later. Those with heavy canopy loss after Hurricane Hugo were found to have the same effect after Hurricane Georges.

Invasive species

Horvitz *et al.* (1998) studied the response of hardwood tree island vegetation in south Florida, USA, to the passage of Hurricane Andrew. Twenty-eight per cent of the flora was introduced, including 34% of the vines and 24% of other species. Non-native species generally exceeded native species in either cover or frequency, and non-native species had the species with the highest cover. Both native and non-native species contributed to increases in stem density 2 years post hurricane, and did so by germination and growth. Seed mass was not different between native and non-native species. Native species tended to sprout more than non-native species, which exhibited a wide range of regeneration strategies. However, conditions of each stand in terms of history and level of disturbance and autecology of species present were more influential on regeneration than the native/non-native dichotomy. Hurricanes did not introduce any new non-native species to their sites, but allowed for changes in the relative importance of natives and non-native species, thus accelerating any process of invasion in progress before the hurricane.

In the LEF, Hurricane Hugo was followed by the germination of non-native herbaceous plants in places with an open canopy (China 1999) and non-native trees in a mature tabonuco forest previously affected by anthropogenic activity (Thompson *et al.* 2007). In both cases, the non-native species failed to survive once the canopy closed and native species regained their dominance. The survival of most of the regenerated non-native tree species in the El Verde forest lasted 10–15 years before their populations returned to pre-hurricane low densities (Thompson *et al.* 2007).

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In contrast, Bellingham *et al.* (2005) found that Hurricane Gilbert accelerated the invasion of the alien tree *Pittosporum undulatum* in montane forests of Jamaica. Twenty years after the hurricane, the species was still gaining in density and basal area.

Pascarella *et al.* (2004) studied two successional chronosequences (15–81 years since pasture abandonment) in Puerto Rico both before and after a hurricane. They found that Hurricane Georges did not alter the succession or the species composition along the chronosequence, in spite of the structural and species richness changes that it imposed on the vegetation. Species turnover was greater at the local than at the regional level. Hurricanes have greater effect on succession when they strike old growth or mature forests far removed from a previous event, than they do secondary forests or forests recently subjected to a hurricane.

Lugo and Helmer (2004) described the formation of new forests in Puerto Rico as a result of the invasion of abandoned agricultural lands by non-native species (see also Lugo 2004). One of these species is *Spathodea campanulata*, currently the most common tree species in Puerto Rico (Brandeis *et al.* 2007). *Spathodea* forms impressive forests in karst, alluvial, and volcanic substrates and is a species classified as having the lowest wind resistance (Duryea *et al.* 2007). How does it survive hurricanes, and will it persist in the island given its low wind resistance? The species sprouts profusely and grows so fast, that after hurricane passage and regardless of hurricane effects on its canopy and stems, it maintains dominance over sites and only yields to native species by the inability of its seedlings to grow in the shade of a closed canopy.

Carbon and nutrient cycling

Massive wood fall of low nutritional quality after a hurricane has the capacity of immobilizing nutrients, particularly N, and thus reducing nutrient availability (Zimmerman *et al.* 1995b). Simulation of results from El Verde after Hurricane Hugo suggested that this invisible effect could reduce ANPP for 13 years and biomass accumulation for 30 years. However, empirical data on both parameters from the windward sector of the LEF do not support the model simulations. After a hurricane, ANPP is high (Scatena *et al.* 1996; Frangi & Lugo 1998; Harris *et al.* in press) and biomass accumulation rate is fast, reaching pre-hurricane values in less than 15 years (Heartsill Scalley *et al.* in press). Nevertheless, at El Verde, microbial biomass and activity, did immobilize nutrients after hurricanes, and reduced soil ammonia, LAI, and the litter fall of control tabonuco forest stands relative to stands that were fertilized or had their woody litter removed (Zimmerman *et al.* 1995b). How this phe-

nomenon relates to rapid ANPP requires investigation. It is possible that nitrogen fixation makes up for the immobilized N. In Bisley, Beard *et al.* (2005) found that adding woody debris to a forest increased, rather than decreased the turnover of organic matter by litter fall and increased fine root biomass. They explained that continuous and rapid wood decomposition mitigated any immobilization that could occur with the addition of wood. Land use legacies, such as presence of N-fixing trees, could have also contributed to overcoming N immobilization by woody debris.

TRAJECTORIES OF RESPONSE (0–100 YEARS)

One-hundred-year trajectories of response to hurricanes are lacking. The longest continuous records available to me are those from the LEF, with about 70 years of data for various forest types (Fig. 4; Weaver 1983; 1986a,b; 1989; Lugo *et al.* 1995). These trajectories are based on the initial analyses of Briscoe and Wadsworth (1970) and Crow (1980). From the trends in these trajectories and the characteristics of resulting mature stands, one can infer the outcomes of succession on these forests. In this section I also include a summary of carbon flux dynamics in the LEF to support the suggestion that hurricanes form carbon sinks.

Forest structure and composition

In earlier sections I have already reviewed the first 20 years of forest response after Hurricane Hugo, which was the next major hurricane to pass over the LEF after Hurricane San Cipriano. Weaver (1986a,b; 1989) analysed the long-term trajectories of change for the forests of the LEF prior to the passage of Hurricane Hugo. His analysis focuses on the characteristics of forests some 50 years after Hurricane San Cipriano in 1932 and they are thus useful for us to infer the mature stages of successional trajectories in the LEF. Weaver's nine-point succinct summary includes:

- Low tree ingrowth rates (1.1%)
- A shift to larger tree diameters and heights
- Three per cent decline in intermediate and dominant crown classes (*sensu* Dawkins 1956) and 6% increase in suppressed crowns
- A 1.9% increase in the weighted mean specific gravity of all stems and 3.9% in dicotyledonous trees alone
- A change in species composition owing to a loss of pioneer species, decreases in secondary species and increase in the dominance of climax species
- A decline in species richness for the whole forest

- A decrease in stem diameter growth rate for all stems
- An increase in standing stemwood and branch volume
- Increase in above-ground woody biomass

These invisible long-term trends in wet forests subject to recurrent hurricanes were modified by topographic and climatic gradients as discussed by Weaver (1983; 1986a,b; 1995) and observed in palm forests (Lugo *et al.* 1995). For example, the trajectory of species richness decreased in windward palm brakes but not in the drier leeward palm brakes, where species richness increased over time. In tabonuco forests, species diversity decreased (Fig. 4d).

Carbon sink

Four hurricanes with landfall over the USA (Fran, Hugo, Camille and the 1938 storm) transferred between 2.9 and 20 Tg of biomass to necromass or approximately 10% of the annual carbon sequestration of all US forests (McNulty 2002). Most of this necromass is left to decompose because only a small fraction is salvaged (15%) or burns. The sink function of these forests depends on the time required for this mass to decompose or be incorporated into soil carbon storage, and the speed of above-ground biomass accumulation while forests return to pre-hurricane conditions. In the short-term, if the woody debris decomposes or burns faster than the above-ground biomass can return to pre-hurricane conditions, a sink would not be possible, unless the above-ground biomass accumulation exceeds pre-hurricane biomass. The arguments in support of a long-term carbon sink include the rapid accumulation of biomass after the event, the continuous growth of large trees, the slow decomposition of coarse woody debris, and the long-term accumulation of carbon in soils (Lugo 2000). However, it is not clear how general this sink is given the variation in post hurricane biomass accumulation in different forests, unknowns about the rates of coarse woody debris decomposition (particularly large boles of primary forest species) and the potential effect of fires in reducing the carbon sink see Mascaro *et al.* (2005) for an example of slow biomass accumulation after a hurricane). Therefore, empirical data on biomass decomposition and accumulation over time are needed to determine whether a sink accompanies hurricanes or not.

Empirical evidence from forests in the LEF support the carbon sink function associated with the passage of a hurricane. After Hurricanes Hugo and Georges passed over the LEF, the measured ANPP in palm forests increased from 3 Mg ha⁻¹ year⁻¹ before the hurricane to 9.2 Mg ha⁻¹ year⁻¹ after the hurricane (all units in this section are dry organic matter), which

resulted in the forest exceeding its pre-hurricane above-ground biomass in just 5 years in spite of a loss of biomass immediately after the hurricane (Frangi & Lugo 1998). In a tabonuco forest, Scatena *et al.* (1996) report ANPP values as high as 40 Mg ha⁻¹ year⁻¹ in tabonuco forest with a 5-year mean of 21.6 Mg ha⁻¹ year⁻¹. This forest exceeded its pre-hurricane above-ground biomass in 15 years (Heartsill Scalley 2008). Harris *et al.* (in press) measured the photosynthesis and respiration of trees and soil respiration from the lowlands to the top of the Luquillo Mountains 15 years after Hurricane Hugo and 6 years after Hurricane Georges. They found that forest NPP ranged 10–52 Mg ha⁻¹ year⁻¹ and estimated a net carbon sink of about 1 g m⁻² over the whole forest. Most of the respiration was due to soil. In summary, the data on the re-growth of above-ground biomass in the LEF reflect the capacity of forests to accumulate biomass after the hurricane at sufficiently high rates as to overcome soil respiration and to reach pre-hurricane above-ground biomass in less than 20 years. Do these rates overcome coarse wood decomposition and other long-term processes?

Odum (1970a) found that the decomposition rate of coarse woody debris in tabonuco forests balances non-hurricane wood fall at about 10% per year. In general, wood decomposition in the LEF is rapid, with most woody debris produced by a hurricane decomposing before the forest reaches pre-hurricane biomass (Frangi & Lugo 1998; Beard *et al.* 2005). However, not all necromass produced by the hurricane decomposes before the above-ground biomass reaches pre-hurricane levels. Coarse wood (>10 cm d.b.h.) of species such as *Manilkara bidentata*, *D. excelsa* and *Cyrilla racemiflora* decompose at rates that require in excess of 20 years to complete the process (Odum 1970a; Torres 1994; Beard *et al.* 2005; Torres & González 2005; Zalamea *et al.* 2007). This is due to wood characteristics and a reduction of decomposition rates, as decomposers encounter the heartwood. For example, Zalamea *et al.* (2007) found that the decomposition rate of *D. excelsa* declines from 3.2% per year the first 6 years after the hurricane to 1.3% per year after 15 years. Torres (1994) and Torres and González (2005) observed that the initial decomposition of coarse wood of *C. racemiflora* is due to the loss of sapwood, and that after 15 years, the heartwood of this species was almost intact. The decomposition process can also be retarded by water saturation of partially decomposed logs, which reduces the supply of oxygen to decomposers (Torres 1994). However, even if we apply constant decomposition rates to *M. bidentata* using the initial average rates of 4% per year (Odum 1970a; Beard *et al.* 2005), it would still require over 20 years to decompose all the material. Moreover, Zalamea *et al.* (2007) found that as the wood decomposes, soil organic matter increases, thus contributing

to a long-term carbon sink. Thus, the data on coarse wood decomposition and production of above-ground biomass support the notion of a carbon sink in post hurricane vegetation. How long does the sink last?

The data on long-term biomass accumulation of forests in the LEF show net above-ground biomass accumulation over the length of the available record. For example, a 62-year record of above-ground biomass in tabonuco forest shows continuous increase in biomass (Fig. 4c). Weaver (1986) and Lugo *et al.* (1995) found the same pattern over 40- to 49-year periods in *P. montana* and *C. racemiflora* forests (respectively), and tabonuco forest (Weaver 1989) in the LEF. Weaver also documented a shift to large trees and a 1.9–3.9% increase in the weighted mean specific gravity of wood. Silver *et al.* (2004) followed a restored forest within the LEF for 61 years, including the passage of Hurricane Hugo 3 years before the last measurement in 1992, and found net carbon accumulation for both above-ground biomass and soil carbon. The soil carbon sink was about 1.8 Mg ha⁻¹ year⁻¹, and was not affected by the hurricane. In summary, long-term data reviewed in this section suggest that the sink function in LEF forests is maintained for decades after the passage of hurricanes. This applies to at least two major hurricanes (Cipriano and Hugo) over the span of about 80 years for which we have data.

LONG-TERM LEGACIES (>100 YEARS)

In this section I address invisible hurricane effects with long-lasting influence on forests. By this I mean effects that influence the species composition, long-term site characteristics, forest physiognomy or the evolution of species. Insight for the identification of these long-term effects might develop from short-term observations or other kinds of research, but they are included here for their long-term implications.

Even the structural legacy of a hurricane can be invisible to an observer not aware of infrequent, but persistent hurricane passages. This is why it is important to understand the nature of hurricane legacies on forest stands within the hurricane belt. Webb (1958) understood and discussed this issue as it pertains to forests in Queensland. He pointed out that where hurricanes were most frequent and severe, particular forest structures converged around the world, that is, cyclone scrubs in Australia, hurricane hardwoods in the West Indies (Murphy 1916), storm forests in Malaya, and so on. These extreme forest types are exposed to the most frequent and stronger winds and all developed similar structural features such as abundance of vines, short and ragged canopies, absence of large trees, reduced floristic variety, high dominance and low biomass. For Caribbean forests, Lugo and Scatena (1995) and Lugo *et al.* (2002) suggested a

similar suite of characteristics believed to be long-term legacies of hurricanes, for example: short trees, smooth and even canopy structure, high species dominance, cohorts of age or size classes, low biomass and similar number of species per unit area for all forests regardless of climate. Finally, Torres (1988) reviews a large bibliography that shows the importance of hurricanes in the dispersal of insects throughout the Caribbean. This invisible function of hurricanes increases connectivity between landmasses and bypasses traditional biogeographic barriers for dispersal of organisms. A plant example is the distribution of Spanish moss (*Tillandsia usneoides*) in the USA, which is maintained by storm passages (Garth 1964).

Ecologists need to identify forest stands with low frequency of hurricane passage, whose structure and functioning is dependent in some measure by large and infrequent hurricane events. These forests develop more robust and complex structure with larger trees, high biomass, abundant epiphytes, and so on, and they require scientific attention to further our understanding of how hurricanes influence ecological processes. I will give one example each from temperate and tropical latitudes beginning with temperate forests. Afterwards, I review other invisible long-term legacies of hurricanes.

In the temperate rain forests of Alaska, USA, Nowacki and Kramer (1998) classified landscapes according to their susceptibility to wind disturbance, and related forest composition and length of succession to recurrent windstorms on those landscapes. Windstorms are sometimes accompanied by downbursts that can cause enormous changes in forest structure. This was the case with the 1977 windstorm in Wisconsin, USA, which turned out to be a natural and recurrent event that has moulded that vegetation for millennia (Loucks 1983). In 1993, a windstorm with 12 downbursts affected a wilderness area in the border between Minnesota and Ontario, Canada, estimated to be a one in a millennium event (Mlot 2003). Such unusual events affect all aspects of the forest's ecology, not only structurally, but also in terms of species composition and functioning. In this particular case, forest succession took dramatic turns, and there were surprises with the appearance of bird species not seen in the region for decades. Bird species responded to insect populations, which in turn responded to abundance of downwood. The appearance of understory shrub communities attracted still other kinds of birds to the region.

Whitmore (1974) conducted detailed analysis of a group of 12 tree species to show that in a rich floristic region of the Solomon Islands, forests could be grouped into types with cyclones becoming critical factors in the separation of types according to their frequency and intensity. But overall, these stands had lower species richness than forests outside the cyclone

belt. The size and abundance of climbers and epiphytes became important indicators of the time since the last cyclonic disturbance. Also, the frequency or grouping of certain species with distinct life history traits was another source of information that allowed Whitmore to distinguish subtle differences among different forest stands. An example is the aggressive response of *Camponosperma brevipetiolatum* in the Solomons, a species that is successful in large canopy openings after hurricanes, but which is also susceptible to the loss of large individuals during cyclones. Long-lived pioneer species or near-pioneers *sensu* Whitmore (1984) tend to dominate in storm forests with low hurricane frequencies. Lugo and Zimmerman (2002) identify the following life history characteristics as associated with tree species adapted to LIDs: sprouting, root grafting, small size, short life spans, rapid change in leaf adaptation to light (from sun to shade and vice versa), rapid establishment of seedling populations, accelerated rates of photosynthesis and nutrient cycling, gap-dependent canopy species, capacity to flower and fruit early in the life cycle or as a result of mechanical injury (i.e., epicormic sprouting or stress flowering).

Forest stature is another invisible legacy of hurricane frequency. Webb (1958) was among the first to hypothesize that short canopies in Queensland were due to frequent hurricane disturbances. In the Caribbean, Odum (1970b) also observed that Caribbean forests were short with smooth canopies in contrast to Central and South American forests not exposed to hurricanes or steady trade winds. This observation was examined and supported by Brokaw *et al.* (2004) with data from Hurricane Hugo. De Gouvenain and Silander (2003) tested Webb's hypothesis on Madagascar forests and found that they had a relatively short canopy and high tree density (their fig. 2) but their basal area showed no relationship to hurricane events. Tropical forests in continental Africa outside the hurricane belt are significantly taller than those in Madagascar. Lin *et al.* (2003) suggested that the short canopy height (9–11 m) in Taiwanese forests is due to the high nutrient loss after the typhoons and their high frequency, which in turn combine to limit tree growth.

Differences in wind speeds between temperate and tropical latitudes (higher speeds in the temperate zone) might help explain some of the structural differences between tropical and temperate trees (Ennos 1997). Ennos (1997) suggested that the effects of chronic winds be considered separately from the effects of rare wind such as hurricanes and storms. He argued that hurricane winds 'alter forest ecology by destroying trees rather than altering their distribution or pattern of growth' (p 108). In contrast, he suggests that chronic wind has 'a rather larger effect on forest ecology' by inducing acclimation and exerting selective pressure that may lead to genetic differences within a

species as well as adaptation to wind among different species. While chronic wind can lead to acclimation and adaptation as described by Ennos, for example through the production of 'flexure' wood, one cannot assume that periodic or rare wind events, repeated over millennia might not have equal effects on species and ecosystems.

In contrast, Imbert *et al.* (1996) in Guadeloupe and our own observations in the tabonuco forest of Puerto Rico, reported a cluster effect where groups of trees survived high winds intact. In the tabonuco forest of Puerto Rico, we attribute this clustering to tree unions through root grafting, which steadies trees during the windstorm (Basnet *et al.* 1992). Areas that escape large hurricanes develop larger trees due either to lower exposure or resistance to wind, and reach later stages of maturity between events. These are not only refugia, but paradoxical in the sense that support old trees under a disturbance regime that selects for young rather than old trees.

Caribbean dry forests pose a contrast to taller moist and wet forests in relation to their apparent resistance to hurricane winds (Lugo *et al.* 2002). Van Bloem *et al.* (2005, 2006) confirmed forest resistance to wind after the passage of Hurricane Georges over the Guánica Forest, Puerto Rico. They recorded lower tree mortality and other hurricane effects than expected based on the experience with Hurricane Hugo in the wet forests of the LEF. Van Bloem *et al.* (2003, 2006, 2007) attributed this wind resistance to forest structure, which in turn appeared to be a forest response to hurricane winds. They argued that hurricanes influence Caribbean dry forests by reducing average stem diameter and basal area, and generating significant sprouting responses. Thus, the short, shrubby forest structure common to dry forests in the Caribbean appears to be a legacy of hurricane effects and, unlike the experience in Taiwan, soil nutrients had minor effects on forest response to hurricane winds.

Windthrows lead to pit and mound topography in the southern Appalachian region of western North Carolina, USA (Clinton & Baker 2000). They identified 14 species involved in the formation of pit and mound topography. After Hurricane Opal, older and larger trees with full foliage were more vulnerable to windthrow, particularly in shallow saturated soil. This topography provides soil conditions and microsites for forest regeneration that are different from those caused by senescent tree mortality. In Alaska, windthrow contributes to long-term soil development (Bormann *et al.* 1995). Exposed soil accumulated C, N and P linearly over hundreds of years and help increase stand productivity. After a tornado struck old growth forests in northern Pennsylvania, USA, pits and mounds formed in proportion to the size of fallen trees. Pit-mound microclimate was heterogeneous at the micro-scale, resulting in a facilitation of the maintenance of species

diversity in the plant community (Peterson *et al.* 1990). Vegetation on pits was different from the vegetation on mounds (Peterson & Pickett 1990). By creating pit and mound topography, the hurricane creates conditions that favour some species over others.

Lenart (2003) examined the role of Hurricane Georges in the formation of mounds and pits in Puerto Rico and the turnover period of soil in the forest. She found that 61% and 53% of the variability in mound volume and area, respectively, could be accounted by tree basal area and she also found that the hurricane greatly accelerated soil turnover period. The soil turnover period attributed to the hurricane averaged 2695 years. In contrast, the background rate of soil turnover period due to non-hurricane tree falls was 7700 years and that attributed to landslides was between 5000 and 20 000 years.

Observations along ten different habitats in Jamaica following the passage of Hurricane Gilbert suggested a possible mechanism for the long-term effects of hurricanes on the common characteristics of the Caribbean avifauna (Wunderle *et al.* 1992). They observed that montane forests lagged behind lowland forests in the recovery of canopy conditions, which in turn had greater effects on the bird populations than the actual passage of the hurricane. Walkera *et al.* (1996b) and Weaver (1986a), also observed a slower recovery of forest structure in montane elfin forests in Puerto Rico compared with wet forests at lower elevations. The effects of slow recovery of canopy conditions on avifauna included a greater and more extended stress on montane birds compared with lowland birds. These stresses included alteration of foraging owing to the lag in the recovery of canopy structure and functioning, greater opportunities for local extinctions for those species restricted to montane forests, particularly nectarivores and fruit/seed eaters. These conditions help explain normal patterns of bird distributions commonly observed in the Caribbean, including fewer bird species in montane than in lowland forests, and more endemic species in montane than in lowland forests. Also, the tendency of island birds to use a wider range of habitats than continental species might have a root in the increased survival of those species that are capable of using more than one habitat when conditions become stressful after storms. In short, hurricanes favour reducing the number of bird species in montane habitats, increasing endemism and extinction rates of montane species, and favouring the survival of species capable of using a broad range of habitats. Over longer periods of evolutionary selection in response to frequent hurricanes, this might explain the tendency for Caribbean forest-dwelling species to segregate into two vertical layers, compared with those in Panama, which recognize four (Wunderle *et al.* 1992).

WHAT ROLE DO HURRICANES PLAY?

Earlier, I mentioned the global role of hurricanes in the heat budget of the Earth. Hurricanes play a role in regulating the climatic homeostasis of the planet. In the process of moving heat energy from the tropics to higher latitudes, hurricanes exert enormous effects on the biota and landscape as I have reviewed above. Also, the visible and invisible legacies of hurricanes remain functional for a long time, including the adaptations that organisms display in a dynamic world. In an earlier review, I identified 12 general effects of hurricanes on Caribbean vegetation (Table 3). In this review I have alluded to many of these as they apply to most hurricanes, mostly at the functioning of forest stands. However, with the accumulation of more information, can we look for additional generalizations that we can apply to all hurricanes? By combining the information in the review with an expanded interpretation of Figure 1, I find six general roles that all hurricanes play either individually or cumulative. The strength of the hurricane makes a difference on how visible the role might appear, but regardless of the magnitude, each hurricane contributes in some measure to the following:

1. *Hurricanes change the ecological space available to organisms.* The shift in the ecological space following a hurricane is a fundamental role of hurricanes. By changing environmental conditions in the short and long term, hurricanes influence the ecological behaviour of individuals, populations and communities.
2. *Hurricanes set organisms in motion.* Given the shifts in ecological space, most organisms cannot stay in place after the passage of a hurricane. This is especially true for animals but plant populations are also displaced in ecological. The spread of species, including non-native species and the regeneration of tree species after a hurricane are also examples

Table 3. Known and potential effects of hurricanes on Caribbean vegetation (Lugo 2000)

-
- Sudden and massive tree mortality
 - Delayed patterns of tree mortality
 - Alternative methods of forest regeneration
 - Opportunities for a change in successional direction
 - High species turnover and opportunities for species change in forests
 - Distinct age classes or age cohorts
 - Fast biomass and nutrient turnover
 - Species substitutions are often associated with changes in turnover time of biomass and nutrients
 - Low above-ground biomass in mature vegetation
 - A carbon sink
 - Selective pressure on organisms
 - Convergence of community structure and organization
-

of organisms on the move as a result of the passage of hurricanes.

3. *Hurricanes increase the heterogeneity of the landscape and the variability in ecosystem processes.* Pit topography, debris flows, landslides, modification of river and stream channels, sedimentation and erosion events and movements of organic matter and nutrients from one place to another are all examples of mechanisms by which hurricanes contribute to the heterogeneity of the landscape. After the passage of a hurricane there is so much structural heterogeneity, environmental change and movement of organisms, that measurements of ecological parameters exhibit high coefficients of variation. The changing coefficient of variation of tree growth rates in Figure 6 is a typical example. Selective forces and self-organization act on, and benefit from, this variability (respectively).
4. *Hurricanes rejuvenate the landscape and its ecosystems and redirect succession.* As the kinetic energy of hurricanes is dissipated over forests and landscapes succession is set back; the resources required for ecosystem functioning are redistributed; unfit, wounded, malformed, or poorly located individuals are removed from communities. The shifts in ecological space, the movement of organisms, and the heterogeneity of the landscape contribute to the redirection of succession towards different states. The net result of these

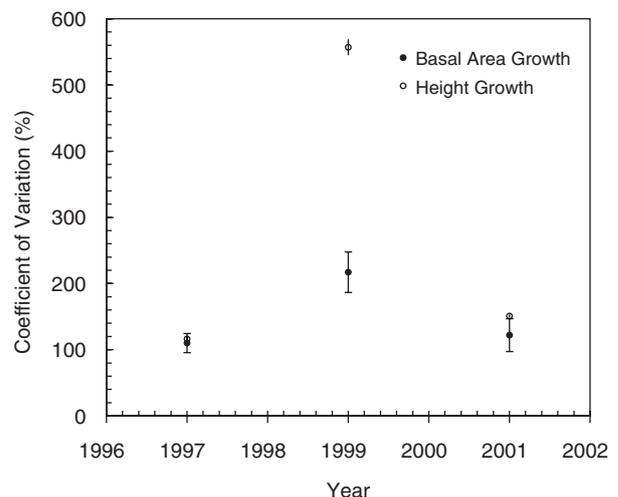


Fig. 6. Temporal change in the Coefficient of Variation for tree-growth data in a secondary forest after the passage of Hurricane Georges over Utuado, Puerto Rico in 1998. The Coefficient of Variation increases immediately after the hurricane and years later returns to pre-hurricane values. Data are plotted in the mid point of the measuring interval. The mean Coefficient of Variation and the standard error are shown ($n = 12-14$). These data are unpublished data collected under an agreement with the Luis Muñoz Rivera Vocational High School in Utuado.

effects is the rejuvenation of populations, communities, and landscapes. Paradoxically, old trees that survive continue to develop into old age classes, but on average the age structure of forests conforms to the frequency of hurricane response (Weaver 1986b; Lugo & Rivera Batlle 1987).

5. *Hurricanes shape forest structure, influence their species composition and diversity and regulate their function.* This outcome of hurricanes follows from the above discussions of effects trajectories and legacies which provide examples from all over the world and the results of more recent long-term observations in the Neotropics and the USA.
6. *Hurricanes induce evolutionary change through natural selection and ecological creativity through self-organization.* All the previous five roles of hurricanes contribute to a remixing of species and populations, often under new environmental conditions. Such mixing of organisms and environmental variability are the prime ingredients for evolutionary change and adaptation through natural selection and self-organization (*sensu* Odum 1988). The environmental pressure exerted by hurricane forces lead to a long list of structural and functional adaptations of organisms in the hurricane belt. There is no reason to believe that evolutionary change in the hurricane belt will stop, on the contrary, it might speed up as climate and anthropogenic change continue to exert their synergy with hurricanes.

RESEARCH PRIORITIES

There will continue to be a need for the documentation of visible and invisible effects of hurricanes in as many forest types and over the longest time possible. However, such a focus will not help us to fully understand the effects of hurricanes nor their ecological roles on the planet. In this section I address climate change, the problem with measuring the strength of hurricanes for ecological purposes and a new focus for hurricane research.

Hurricanes and climate change

The intensification of hurricanes with climate change is still an open question (Bengtsson 2001; Landsea *et al.* 2006). Emanuel (1987) suggested that hurricanes would intensify with climate change. His analysis lead him to conclude that this intensification occurred over the past 30 years owing to longer lasting hurricanes of greater intensity (Emanuel 2005). The intensification is only partially due to increases in sea surface temperatures as other factors such as vertical wind shear also affect hurricane intensity (Goldenberg

et al. 2001; Goldenberg *et al.* (2001; Emanuel 2005) found a doubling of overall hurricane activity and a 2.5-fold increase in major hurricanes in the Atlantic between 1995 and 2000, compared with the period of 1971 and 1994. However, Landsea *et al.* (2006) questions these trends because the data and methods to detect trends in the frequency and strength of intense cyclones are demonstrably unreliable. Donnelly and Woodruff (2007) developed a 5000-year record of hurricanes in the vicinity of Puerto Rico based on the overtopping of dunes by the storm surge of hurricanes and the deposition of sand in adjacent lagoons. They showed that periods of intense hurricanes were associated with the El Niño Southern Oscillation Index, even when sea surface temperatures were lower than today.

While physical scientists resolve the question of intensification of hurricanes with climate change, ecologists have the daunting task of deciphering the synergy between potential changes in hurricane frequency and intensity and the changing states of forests as a result of anthropogenic activity. Climate change can affect the distribution of species, the geography of forests, and the rates of processes. All these changes have an effect on how the resulting forests respond to the forces of hurricanes and we know very little of the consequences. The possibility of shifts in the geography of hurricanes also raise important research questions as posed by Michener *et al.* (1997) who explored the consequences of climate change on hurricanes and sea level change in relation to coastal ecosystems. Their Table 2 contains a review of hurricane effects, both short- and long-term on birds and their implications for trophic structure. They also observed that 35% of endemic birds live in hurricane-prone regions and that this figure could increase with a small change in the geographic distribution of hurricanes.

The problem with hurricane strength categories

The kinetic energy of a hurricane changes dramatically as it moves from warm to cold water or vice versa, or as it moves inland over islands or continents. When a hurricane passes over land, topographic features and aspect also greatly modify its strength. At the beginning of this review I emphasized the importance of kinetic energy in determining the ecological effects of hurricanes. However, the ecological literature lacks objective information to relate observed hurricane effects with hurricane strength; in fact, we lack information about almost all of the various forces that constitute the hurricane (Table 2). This creates a serious problem of data interpretation and comparison as was evident in the apparent contradictions in the data from El Verde, Cubuy and Bisley sectors of the LEF.

Normally, the hurricane literature will include a measure of hurricane strength by citing its classification in the Saffir Simpson scale. Such information is not very useful for supporting generalizations because it is never clear at what distance and time from the observations the hurricane had the attributed strength. Also, the energy of wind varies with the cube of its velocity, such that a small variation of speed, even within a given hurricane category, signifies a large difference in kinetic energy dissipation. For as long as our measures of hurricane strength is so deficient, we will not be able to fully understand the response of the biota to the event. Continuous instantaneous measurements of storm characteristics (wind speed, direction and barometric pressure) over the whole path of hurricanes are now possible and needed to advance the science of hurricane ecology. I consider this the most pressing research priority in the field.

The need for a new approach to hurricane research

A new approach to hurricane research is needed and I believe that such an approach will have the following characteristics (Hopkinson *et al.* in press):

1. The research will study hurricanes at the same scale at which they operate, that is, across latitudes and longitudes and over disturbed and undisturbed landscapes.
2. This research will require networks of observation platforms located along expected hurricane paths from the coast to about 300 km inland to facilitate forest structure and functioning observations across gradients of hurricane frequency and intensity.
3. This research will also require use of remote sensing and automated wireless technology, hardened to survive hurricane-strength winds and floods to assure real time measurements of the characteristics of hurricanes and ecosystem responses.

No progress will be forthcoming if we do not learn to quantify objectively the energy dissipation of hurricanes on the full grid of affected forests as the hurricane passes over a landscape. This will resolve the confusion created by the current accumulation of ecological observations for which we have no idea to what forces the organisms are responding.

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